Diversity and species composition of two different moth families (Lepidoptera: Arctiidae vs. Geometridae) along a successional gradient in the Ecuadorian Andes

Dissertation

zur Erlangung des Grades eines Doktors der
Naturwissenschaften
- Dr. rer. nat. -
der Fakultät Biologie / Chemie / Geowissenschaften
der Universität Bayreuth

Vorgelegt von

Nadine Hilt

Bayreuth, Oktober 2005

Die vorliegende Arbeit wurde von März 2002 bis Oktober 2005 am Lehrstuhl Tierökologie I der Universität Bayreuth in der Arbeitsgruppe von Prof. Dr. Konrad Fiedler erstellt und von der Deutschen Forschungsgemeinschaft gefördert (Projekt FOR 402/1-1 TP 15, FOR 402/2-1 TP A3).

Vollständiger Abdruck der von der Fakultät Biologie/Chemie/Geowissenschaften der Universität Bayreuth genehmigten Dissertation zur Erlangung des Grades eines Doktors der Naturwissenschaften (Dr. rer. nat.).

Tag der Einreichung: 17.10.2005
Tag des wissenschaftlichen Kolloquiums: 23.01.2006

1. Gutachter: Prof. Dr. K. Fiedler
2. Gutachter: Prof. Dr. S. Liede-Schumann
Prüfungsausschuss: Prof. Dr. K. H. Hoffmann (Vorsitz)
Prof. Dr. E. Beck
Prof. Dr. K. Fiedler
Prof. Dr. S. Liede-Schumann
Prof. Dr. G. Rambold

Contents

* published

1 General introduction

Tropical rainforests are well known as centres of biodiversity (Mittermeier *et al.*, 1999). Much interest has focused on the ecological processes responsible for generating and maintaining this diversity (e.g. Richards, 1996). The Andean rainforests are acknowledged as global diversity hotspots for vascular plants and vertebrates (Myers *et al.*, 2000; Brooks *et al.*, 2002; Myers, 2003). However, Andean montane forests have already been reduced to less than 10% of their original extent through human activities (Henderson *et al.*, 1991; Hamilton *et al.*, 1995; Armenteras *et al.*, 2003). The annual deforestation rate is estimated at 0.8–2% (Doumenge *et al.*, 1995; Food and Agriculture Association, 1995; Purvis & Hector, 2000), and the remaining remnants are often threatened by fire and logging (Paulsch, 2002), as well as by transformation into pastures or plantations of exotic tree species such as *Eucalyptus* and *Pinus* species (Cuarón, 2000). A particular problem in southern Ecuador is the encroachment of more than 25% of burned areas with bracken (*Pteridium arachnoideum*: Hartig & Beck, 2003). Thus, Andean montane rainforests must be considered as highly endangered ecosystems. Since 1997, the German Research Foundation (DFG) has been funding an interdisciplinary research project in the montane zone of southern Ecuador to examine the edaphic, climatic, zoological and botanical components of the forest ecosystem (see http://www.bergregenwald.de). Altitudinal as well as disturbance gradients were chosen as paradigms to gain a better understanding of patterns of biodiversity (e.g. through inventories of the forest and adjacent habitats), determinants of biodiversity, ecosystem processes, and the conservation needs of this ecosystem (Beck & Müller-Hohenstein, 2001).

Even though preservation of large areas of continuous, pristine habitat is regarded as crucial for the conservation of many species (e.g. Brooks *et al.*, 2002), human-dominated landscapes globally cover major proportions of land area (Ricketts *et al.*, 2001). Fragmented landscapes and secondary habitats thus are becoming increasingly important for consideration with regard to the conservation of biodiversity. A considerable number of studies have dealt with effects of logging on arthropod communities (e.g. Willott, 1999; Schulze 2000; Schulze *et al.*, 2004; Meijaard *et al.*, 2005). Clear-cut logging and subsequent conversion of forest into plantations and agricultural areas generally results in decreased insect diversity (Holloway *et al.*, 1992; Bawa & Seidler, 1998), but effects of moderate disturbance are less clear (Hill, 1999) and frequently less dramatic (e.g. Willott, 1999; Schulze, 2000; Beck *et al.*, 2002; Hamer *et al.*, 2003). So far, little is known about the impact of different land use practices on species-rich neotropical insect assemblages native to the rainforest (Ricketts *et al.*, 1999; Brehm & Fiedler, 2005) and the change of these assemblages along habitat gradients or man-made disturbance gradients, representing different successional stages of forest recovery after logging (e.g. Floren & Linsenmair, 2001 for an example from Borneo). Moreover, effects of forest disturbance on species diversity and composition are heavily scale dependent (Hamer & Hill, 2000; see also Rahbek, 2005).

While relatively many studies were carried out for insects in Southeast Asian forests (e.g. Chey *et al.*, 1997; Holloway, 1998; Willott, 1999; Schulze, 2000; Beck *et al.*, 2002; Fiedler & Schulze, 2004), the neotropical region – even though much richer in species – has received surprisingly little attention (Ricketts *et al.*, 2001; Brehm & Fiedler, 2005). Particularly few studies on insect diversity were performed in the montane regions of the Andes (Janzen *et al.*, 1976; Braun, 2002; Brehm, 2002; Süßenbach, 2003).

Total global species richness is currently estimated to be about 10 million species (summarized in May, 1990; Stork, 1993). A re-evaluation of Erwin’s estimate of tropical arthropod species richness arrived at a total of 4.8 million species (Gaston, 1991; Ødegaard, 2000; Novotny *et al.*, 2002). Insects, including the species-rich Lepidoptera, play a central role in all terrestrial ecosystems. Lepidoptera are important herbivores, pollinators, and serve as food and hosts for multiple other organisms at higher trophic levels (Summerville & Crist, 2004; Summerville *et al.*, 2004). The better-known groups of Lepidoptera (butterflies in particular) have often been advocated as useful indicators of environmental change (Daily & Ehrlich, 1995; Hill *et al.*, 1995; Hill & Hamer, 1998). However, more than 90% of the known lepidopteran species are moths, and the majority of them are nocturnal (Scoble, 1992; Young, 1997). Adult moths are accessible to standardized sampling through light traps, and the Macrolepidoptera (derived large moths; a monophyletic group: Solis & Pogue, 1999) are taxonomically relatively well known (Scoble, 1992, 1999; Holloway, 1993, 1996, 1997; Holloway *et al.*, 2001). Moreover, moths appear to be at least as well suitable as butterflies for assessing environmental impacts (e.g. Holloway, 1985; Kitching *et al.*, 2000; Beck *et al.*, 2002; Fiedler & Schulze, 2004).

Therefore, I chose two different moths families, namely the Arctiidae (Plate 1) and the Geometridae (Plate 2), as model organisms for a biodiversity study in disturbed and succession habitats at the edge of a natural montane rainforest in the Ecuadorian Andes. Species of both families tend to differ in their life histories, their habitat fidelity and habitat preferences (e.g. Holloway, 1984; Schulze, 2000; K. Fiedler, pers. comm.). I thus expected that arctiid and geometrid moths should respond differentially to environmental change.

The **Arctiidae** include about 11,000 species worldwide, with more than 50% occurring in the Neotropics (Watson & Goodger, 1986). In this region, arctiid moths fall into two subfamilies, viz. the Lithosiinae and Arctiinae. The latter can be subdivided into four major tribes (Arctiini, Phaegopterini, Pericopini, and Ctenuchini with the latter including Euchromiini: Jacobson & Weller, 2002).

Five characters support the monophyly of Arctiidae (Jacobson & Weller, 2002). Of the synapomorphies of adult Arctiidae, the most unambiguous is the presence of a pair of dorsal, eversible pheromone glands associated with the anal papillae of females. In addition, there are metathoracic tymbal organs, which occur in both sexes and all subfamilies (Kitching & Rawlins, 1999), although these are reduced or absent in many Ctenuchini. In a number of arctiid species ultrasonic sound production is elicited by tactile stimulation or in response to the hunting calls of bats (review in Waters, 2003). These sounds function as aposematic signals (Dunning *et al.*, 1992; Dunning & Kruger, 1995; Waters, 2003) or confuse bats and jam their echolocation calls allowing the moth to escape (Fullard *et al.*, 1979; Bates & Fenton, 1990). Many arctiids also possess aposematic colouration and are chemically well defended (Häuser & Boppré, 1997; Kitching & Rawlins, 1999).

Arctiid moths are mainly medium to large in size (forewing length often > 20 mm) and are often quite robust (Solis & Pogue, 1999). Arctiid larvae have a dense cover of hairs, feed externally on a wide range of plants, and a substantial fraction of them appears to be rather unspecialized with regard to host-plants (Kitching & Rawlins, 1999; Holloway *et al.*, 2001). Hostplants containing pyrrolizidine alkaloids (PAs) are frequently used in Arctiidae (Arctiini, Ctenuchini and Pericopini) and play a role both in defence and in the synthesis of male sex pheromones (Conner *et al.*, 1981; Boppré, 1995; Kreusel & Häuser, 1998; Weller *et al.*, 1999). Yet very little is known about the host-plant species for Neotropical arctiids (Janzen & Hallwachs, 2005).

Results from lowland habitats in Old World tropical regions suggest that many arctiid species may benefit from anthropogenic habitat disturbance (Holloway, 1998; Kitching *et al.*, 2000; Schulze, 2000). This is facilitated by their good flight capacity and therefore high dispersal ability, as well as the polyphagy of many arctiid larvae (Kitching & Rawlins, 1999; Solis & Pogue, 1999; Süßenbach, 2003).

With more than 21,000 valid described species globally, of which some 6,400 occur in the Neotropical region, **Geometridae** are one of the three most species-rich moth families, apart from Noctuoidea and Pyraloidea (Scoble, 1999). They are characterised as a monophyletic group by the presence of structurally unique tympanal organs at the base of the abdomen (Cook & Scoble, 1992). Their larvae are frequently easy to distinguish from those of other families since the number of prolegs on the abdomen is typically reduced to two pairs (Minet & Scoble, 1999). Geometrid larvae feed on a wide range of plants, although they tend to consume the leaves of trees and shrubs (Scoble, 1992). Adults are usually small to medium-sized with slender bodies (Minet & Scoble, 1999).

Four subfamilies are most prevalent in the Neotropics compared with other faunal regions: Ennominae, Larentiinae, Sterrhinae, and Archiearinae (Brehm, 2002). On the contrary, species richness in the Desmobathrinae, Geometrinae and Oenochrominae is highest in the Indo-Australian region (Gaston *et al.*, 1995; Holloway, 1996). Geometrid moths usually show high habitat fidelity (Holloway, 1984; Chey *et al.*, 1997). Tropical geometrid moth ensembles were previously found to reflect differences between habitats (Intachat *et al.*, 1997, 1999) and to respond sensitively to changes in habitat quality (Kitching *et al.*, 2000; Beck *et al.*, 2002).

In the present thesis I compare these two different moth families along a succession gradient (plate 3) in the Ecuadorian Andes. Collectively, the 21 sites that I selected (15 succession sites and six mature forest understorey sites) depict a succession gradient of forest recovery after a landslide, and also include some of the most relevant types of disturbed habitats which result from human land use practices.

Specifically, in the subsequent five major chapters, I explore diversity and faunal structure, as well as relationships between moths and their abiotic environments, to examine the following questions:

A. Diversity and composition of Arctiidae moth ensembles
    - Does diversity decrease along the succession gradient from early succession stages to the mature forest understorey?
    - Does the composition of arctiid ensembles change with succession and is there a significant difference between the species composition of the succession sites vs. the mature forest?
    - Which environmental factors are correlated with beta-diversity of arctiids?

B. Arctiid moth ensembles along a succession gradient in the Ecuadorian montane rainforest zone: how different are subfamilies and tribes?
   - Do subordinate taxa respond, due to the morphological and ecological differences, differentially in their diversity to changes in vegetation in the course of forest regeneration?
   - Are there discordances in the dynamics of species composition during succession?

C. Morphological traits of arctiid moths along a succession gradient in southern montane Ecuador: clades differ more than habitats
   - Do body size distributions within arctiid moths differ along the succession gradient?
   - Do wing-to-body size ratios vary with the progress of succession?
   - Does the development of a functional proboscis vs. a rudimentary or reduced proboscis change with forest recovery?
   - Does the proportion of aposematic moths change with succession?

D. Diversity and ensemble composition of geometrid moths along a succession gradient
   - Is there an increase of geometrid diversity with forest recovery?
   - Does between-habitat diversity (β-diversity) of geometrid moth ensembles reflect the gradient of disturbance?

E. Temporal dynamics of arctiid and geometrid moth ensembles
   - How variable are the ensembles over time with regard to overall abundance and local diversity?
   - Does the abundances of dominant species vary over time, and does this temporal variability differ between the two different classes of succession habitats?
   - How variable is species composition over time (temporal β-diversity)?

Finally, I will compare the patterns observed in the two moth families, and will relate my findings with the results of other biodiversity studies in tropical forests, as well as with studies from the same Ecuadorian region.

Plate 1: Selected species from the family Arctiidae collected in the study area in South Ecuador (1,800-2,005 m). Bars indicate a length of 10 mm. Letters are different subfamilies and tribes: Arctiinae: (a) Arctiini, (b) Pericopini, (c) Ctenuchini, (d) Phaegopterini; (e) Lithosiinae.

Chlorhoda metamelaena (a) *Hypercompe robusta* (a) *Dysschema semirufa* (b)

Hyalurga urioides (b) *Hypocrita celadon* (b) *Cosmosoma flavithorax* (c)

Cyanopepla alonzo (c) *Eucereon varium* (c) *Mydropastea cephalena* (c)

Amastus aconia (d) *Halysidota underwoodi* (d) *Idalus dorsalis* (d)

Agylla fulvithorax (e) *Gardinia paradoxa* (e) *Macroptila laniata* (e)

Plate 2: Selected species from the family Geometridae collected in the study area in South Ecuador (1,800-2,005 m). Bars indicate a length of 10 mm. Letters are different subfamilies: (a) Ennominae (b) Geometrinae (c) Larentiinae (d) Sterrhinae (e) Oenochrominae. Pictures all © G. Brehm.

Argyrotome prospectata (a) *Eutomopepla rogenhoferi* (a) *Lomographa tributaria* (a)

Pantherodes conglomerata (a) *Pero plenilunata* (a) *Pityeja histrionaria* (a)

Chloropteryx opalaria (b) *Nemoria heterograpta* (b) *Oospila concinna* (b)

Eois paraviolascens (c) *Euphyia consequata* (c) *Eupithecia bullata* (c)

'Cyclophora' globaria (d) *Semaeopus calavera* (d) *Racasta spatiaria*(e)

Plate 3: Selected sites in an altitude between 1,800 to 2,005 m in the study area in South Ecuador. Site A and D1: early succession stages; site G1: later succession stages and site 4a: mature forest understorey in 1,850 m a. s. l. (this picture is from G.Brehm).

Barely vegetated landslide (Site **A**)

Abandoned pasture (Site **D1**)

Shrubs and little trees (Site **G1**)

Mature forest understorey (Site **4a**)

References

Armenteras, D., Gast, F. & Villareal, H. (2003) Andean forest fragmentation and the representativeness of protected natural areas in the eastern Andes, Colombia. *Biological Conservation*, **113**, 245-256.

Bates, D.L. & Fenton, M.B. (1990) Aposematism or startle? Predators learn their responses to the defences of prey. *Canadian Journal of Zoology*, **68**, 49-52.

Bawa, K.S. & Seidler, R. (1998) Natural forest management and conservation of biodiversity in tropical forests. *Conservation Biology*, **12**, 46-55.

Beck, E. & Müller-Hohenstein, K. (2001) Analysis of undisturbed and disturbed tropical mountain forest ecosystems in Southern Ecuador. *Die Erde*, **132**, 1-8.

Beck, J., Schulze, C.H., Linsenmair, K.E. & Fiedler, K. (2002) From forest to farmland: diversity of geometrid moths along two habitat gradients on Borneo. *Journal of Tropical Ecology*, **17**, 33-51.

Boppré, M. (1995) Pharmakophagie: Drogen, Sex und Schmetterlinge. *Biologie in unserer Zeit*, **25**, 8-17.

Braun, H. (2002) *Die Laubheuschrecken (Orthoptera, Tettigoniidae) eines Bergregenwaldes in Süd-Ecuador – faunistische, bioakustische und ökologische Untersuchungen*. Ph.D. thesis, University of Erlangen-Nürnberg.

Brehm, G. (2002) *Diversity of geometrid moths in a montane rainforest in Ecuador*. Ph.D. thesis, University of Bayreuth. URL: http://opus.ub.uni-bayreuth.de/volltexte/2003/20

Brehm, G. & Fiedler, K. (2005) Diversity and community structure of geometrid moths of disturbed habitat in a montane area in the Ecuadorian Andes. *Journal of Research on the Lepidoptera*, **38**, 1-14.

Brooks, T.M., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A.B., Rylands, A.B., Konstant, W.R., Flick, P., Pilgrim, J., Oldfield, S., Magin, G. & Hilton-Taylor, C. (2002) Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology*, **16**, 909-923.

Chey, V.K., Holloway, J.D. & Speight, M.R. (1997) Diversity of moths in forest plantations and natural forests in Sabah. *Bulletin of Entomological Research*, **87**, 371-385.

Conner, W.E., Eisner, T., Vander Meer, R.K., Guerrero, A. & Meinwald, J. (1981) Precopulatory sexual interaction in an Arctiid moth (Utetheisa ornatrix): role of a pheromone derived from dietary alkaloids. *Behavioral Ecology and Sociobiology*, **9**, 227-235.

Cook, M.A. & Scoble, M.J. (1992) Tympanal organs of geometrid moths: a review of their morphology, function and systematic importance. *Systematic Entomology*, **17**, 219-232.

Cuarón, A.D. (2000) A global perspective on habitat disturbance and tropical rainforest mammals. *Conservation Biology*, **14**, 1574-1579.

Daily, G.C. & Ehrlich, P.R. (1995) Preservation of biodiversity in small rain-forest patches: rapid evaluations using butterfly trapping. *Biodiversity and Conservation*, **4**, 35-55.

Doumenge, C., Gilmour, D., Ruiz-Perez, M. & Blockhus, J. (1995) Tropical montane cloud forests: conservation status and management issues. In: *Tropical montane cloud forests. Ecological Studies, vol. 110* (eds. L.S. Hamilton, J.O. Juvik and F.N. Scatena), pp. 24-37. Springer, New York.

Dunning, D.C., Acharya, L., Merriman, C.B. & Dal Ferro, L. (1992) Interactions between bats and arctiid moths. *Canadian Journal of Zoology*, **70**, 2218-2223.

Dunning, D.C. & Kruger, M. (1995) Aposematic sounds in African moths. *Biotropica*, **27**, 227-231.

Fiedler, K. & Schulze, C.H. (2004) Forest modification affects diversity (but not dynamics) of speciose tropical pyraloid moth communities. *Biotropica*, **36**, 615-627.

Floren, A. & Linsenmair, E. (2001) The influence of anthropogenic disturbance on the structure of aboreal arthropod communities. *Plant Ecology*, **153**, 143-167.

Fullard, J.H., Fenton, M.B. & Simmons, J.A. (1979) Jamming bat echolocation: the clicks of arctiid moths. *Canadian Journal of Zoology*, **57**, 647-649.

Gaston, K.J. (1991) The magnitude of global insect species richness. *Conservation Biology*, **5**, 283-296.

Gaston, K.J., Scoble, M.J. & Crook, A. (1995) Patterns in species description: a case study using the Geometridae (Lepidoptera). *Biological Journal of the Linnean Society*, **55**, 225-237.

Hamer, K.C. & Hill, J.K. (2000) Scale-dependent effects of habitat disturbance on species richness in tropical forests. *Conservation Biology*, **14**, 1435-1440.

Hamer, K.C., Hill, J.K., Benedick, S., Mustaffa, N., Sherratt, T.N., Maryati, M. & Chey, V.K. (2003) Ecology of butterflies in natural and selectively logged forests of northern Borneo: the importance of habitat heterogeneity. *Journal of Applied Ecology*, **40**, 150-162.

Hamilton, L.S., Juvik, J.O. & Scatena, F.N. (1995) The Puerto Rico cloud forest symposium: introduction and workshop synthesis. In: *Tropical montane cloud forests. Ecological Studies, vol. 110* (eds. L.S. Hamilton, J.O. Juvik and F.N. Scatena), pp. 1-19. Springer, New York.

Hartig, K. & Beck, E. (2003) The bracken fern (Pteridium arachnoideum (Kaulf.) Maxon) dilemma in the Andes of Southern Ecuador. *Ecotropica*, **9**, 3-13.

Häuser, C.L. & Boppré, M. (1997) Pyrrolizidine alkaloid-related pharmacophagy in neotropical moths (Lepidoptera). In: *Tropical biodiversity and systematic*. Proceedings of the International Symposium on Biodiversity and Systematics in Tropical Ecosystems, Bonn, 1994 (ed. H. Ulrich), pp. 291-296, Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn.

Henderson, A., Churchill, S.P. & Luteyn, J.L. (1991) Neotropical plant diversity. *Nature*, **351**, 21-22.

Hill, J.K. (1999) Butterfly spatial distribution and habitat requirements in a tropical forest: impacts of selective logging. *Journal of Applied Ecology*, **36**, 564-572.

Hill, J.K. & Hamer, K.C. (1998) Using species-abundance models as indicators of habitat disturbance in tropical forests. *Journal of Applied Ecology*, **35**, 458-464.

Hill, J.K., Hamer, K.C., Lace, L.A. & Banham, W.M.T (1995) Effects of selective logging on tropical forest butterflies on Buru, Indonesia. *Journal of Applied Ecology*, **32**, 754-760.

Holloway, J.D. (1984) The larger moths of Gunung Mulu National Park; a preliminary assessment of their distribution, ecology and potential as environmental indicators. *Sarawak Museum Journal*, **30**, 149-190.

Holloway, J.D. (1985) Moths as indicator organisms for categorising rain forest and monitoring changes and regenerating processes. In*: Tropical rain forest: the Leeds symposium* (eds. A.C. Chadwick and S.L. Sutton), pp. 235-242. Philisophical and Literary Society, Leeds, UK.

Holloway, J.D. (1993) The moths of Borneo: family Geometridae, subfamily Ennominae. *Malayan Nature Journal*, **47**, 1-309.

Holloway, J.D. (1996) The moths of Borneo: family Geometridae, subfamilies Oenochrominae, Desmobathrinae and Geometrinae. *Malayan Nature Journal*, **49**, 147-326.

Holloway, J.D. (1997) The moths of Borneo: family Geometridae, subfamilies Sterrhinae and Larentiinae. *Malayan Nature Journal*, **51**, 1-242.

Holloway, J.D. (1998) The impact of traditional and modern cultivation practices, including forestry, on Lepidopteran diversity in Malaysia and Indonesia. In: *Dynamics of tropical ecosystems* (eds. D.M. Newbery, H.H.T Prins and N.D. Brown), pp. 567-597. Blackwell, Oxford.

Holloway, J.D., Kibby, G. & Peggie, D. (2001) *The families of Malesian moths and butterflies*. Fauna Malesiana Handbooks. Brill, Leiden.

Holloway, J.D., Kirk-Spriggs, A.H. & Chey, V.K. (1992) The response of some rain forest insect groups to logging and conversion to plantation. *Philosophical Transactions of the Royal Society of London B*, **335**, 425-436.

Intachat, J., Holloway, J.D. & Speight, M.R. (1997) The effect of different forest management practices on geometroid moth populations and their diversity in Peninsular Malaysia. *Journal of Tropical Forest Science*, **9**, 411-430.

Intachat, J., Holloway, J.D. & Speight, M.R. (1999) The impact of logging on geometroid moth populations and their diversity in lowland forests of Peninsular Malaysia. *Journal of Tropical Forest Science*, **11**, 61-78.

Jacobson, N.L. & Weller, S.J. (2002) *A cladistic study of the Arctiidae (Lepidoptera) by using characters of immatures and adults.* Thomas Say Publications in Entomology: Monographs. Lanham, Maryland: Entomological Society of America, 98 pp.

Janzen, D.H., Ataroff, M., Fariñas, M., Reyes, S., Rincon, N., Soriano, P. & Vera, M. (1976) Changes in arthropod community along an elevational transect in the Venezuelan Andes. *Biotropica*, **8**, 193-203.

Janzen, D.H. and Hallwachs, W. (2005) Dynamic database for an inventory of the macrocaterpillar fauna, and its food plants and parasitoids, of the Area de Conservacion Guanacaste (ACG), northwestern Costa Rica. URL: http://janzen.sas.upenn.edu

Kitching, I.J. & Rawlins, J.E. (1999) The Noctuoidea. In: *Handbook of Zoology. Lepidoptera, Moths and Butterflies, vol. 1* (ed. N.P. Kristensen), pp. 355-401. Berlin, New York, Walter de Gruyter.

Kitching, R.L., Orr, A.G., Thalib, L., Mitchell, H., Hopkins, M.S. & Graham, A.W. (2000) Moth assemblages as indicators of environmental quality in remnants of upland Australian rain forest. *Journal of Applied Ecology*, **37**, 284-297.

Kreusel, B. & Häuser, C.L. (1998) Morphological diversity of the tympanal organ in Wasp Moths (Arctiidae: Ctenuchinae) and its systematic importance. *Memoires de la Societe Royale Belge d'Entomologie*, **38**, 13-23.

May, R.M. (1990) How many species? *Philosophical Transactions of the Royal Society*, **B 330**, 293-304.

Meijaard, E., Sheil, D., Nasi, R., Augeri, D., Rosenbaum, B., Iskandar, D., Setyawati, T., Lammertink, M., Rachmatika, I., Wong, A., Soehartono, T., Stanley, S. & O'Brien, T. (2005) *Life after logging: Reconciling wildlife conservation and production forestry in Indonesian Borneo*. Center for International Forestry Research, Bogor, Indonesia.

Minet, J. & Scoble, M.J. (1999) The drepanoid/geometroid assemblages. In: *Handbook of Zoology. Lepidoptera, Moths and Butterflies, vol. 1* (ed. N.P. Kristensen), pp. 301-320. Berlin, New York, Walter de Gruyter.

Mittermeier, R., Myers, N. & Mittermeier, C. (1999) *Hotspots: Earth's biologically richest and most endangered terrestrial ecosystems*. Cemex, Mexico City, 430 pp.

Myers, N. (2003) Conservation of biodiversity: how are we doing? *Environmentalist*, **23**, 9-15.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853-858.

Novotny, V., Basset, Y., Miller, S.E., Weiblen, G.D., Bremer, B., Cizek, L. & Drozd, P. (2002) Low host specificity of herbivorous insects in a tropical forest. *Nature*, **416**, 841-844.

Ødegaard, F. (2000) How many species of arthropods? Erwin's estimate revised. *Biological Journal of the Linnean Society*, **71**, 583-597.

Paulsch, A. (2002) *Development and application of a classification system for undisturbed and disturbed tropical montane forest based on vegetation structure*. Ph.D. thesis, University of Bayreuth. URL: http://opus.ub.uni-bayreuth.de/volltexte/2002/1/

Purvis, A. & Hector, A. (2000) Getting the measure of biodiversity. *Nature*, **405**, 212-219.

Rahbek, C. (2005) The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters*, **8**, 224-239.

Richards, P.W. (1996) *The tropical rain forest: an ecological study.* Cambridge University Press, Cambridge. 2nd edition, 575 pp.

Ricketts, T.H., Daily, G.C., Ehrlich, P.R. & Fay, J.P. (2001) Countryside biogeography of moths in a fragmented landscape: biodiversity in native and agricultural habitats. *Conservation Biology*, **15**, 378-388.

Schulze, C.H. (2000) Auswirkungen anthropogener Störungen auf die Diversität von Herbivoren – Analysen von Nachtfalterzönosen entlang von Habitatgradienten in Ost-Malaysia. Ph.D. thesis, University of Bayreuth.

Schulze, C.H., Waltert, M., Kessler, P.J.A., Pitopang, R., Shahabuddin, I., Veddeler, D., Mühlenberg, M., Gradstein, S.R., Leuschner, C., Steffan-Dewenter, I. & Tscharntke, T. (2004) Biodiversity indicator groups pf tropical land-use systems: comparing plants, birds, and insects. *Ecological Applications*, **14**, 1321-1333.

Scoble, M.J. (1992) *The Lepidoptera: form, function, and diversity*. Oxford University Press, Oxford.

Scoble, M.J. (ed) (1999) *Geometrid moths of the world – a catalogue (Lepidoptera: Geometridae)*. CSIRO Publishing, Collingwood.

Solis, M.A. & Pogue, M.G. (1999) Lepidopteran biodiversity: Patterns and estimators. *American Entomologist*, **45**, 206-212.

Stork, N.E. (1993) How many species are there? *Biodiversity and Conservation*, **2**, 215-232.

Süßenbach, D. (2003) *Diversität von Nachtfaltergemeinschaften entlang eines Höhengradienten in Südecuador (Lepidoptera: Pyraloidea, Arctiidae)*. Ph.D. thesis, University of Bayreuth. URL: http://opus.ub.uni-bayreuth.de/volltexte/2003/33

Summerville, K.S. & Crist, T.O. (2004) Contrasting effects of habitat quantity and quality on moth communities in fragmented landscapes. *Ecography*, **27**, 3-12.

Summerville, K.S., Ritter, L.M. & Crist, T.O. (2004) Forest moth taxa as indicators of lepidopteran richness and habitat disturbance: a preliminary assessment. *Biological Conservation*, **116**, 9-18.

Waters, D.A. (2003) Bats and moths: what is there left to learn? *Physiological Entomology*, **28**, 237-250.

Watson, A. & Goodger, D.T. (1986) Catalogue of the Neotropical tiger-moths. *Occasional Papers on Systematic Entomology*, **1**, 1-71.

Weller, S.J., Jacobson, N.L. & Conner, W.E. (1999) The evolution of chemical defences and mating systems in tiger moths (Lepidoptera: Arctiidae). *Biological Journal of the Linnean Society*, **68**, 557-578.

Willott, S.J. (1999) The effects of selective logging on the distribution of moths in a Bornean rainforest. *Philosophical Transactions of the Royal Society of London B*, **354**, 1783-1790.

Young, M. (1997) *The natural history of moths*. Poyser, London.

2 Diversity and composition of Arctiidae moth ensembles along a successional gradient in the Ecuadorian Andes

Nadine Hilt[1]*, Konrad Fiedler[2]

[1]Department of Animal Ecology I, Universitätsstrasse 30, University of Bayreuth, D-95440 Bayreuth, Germany

[2]Department of Population Ecology, Faculty Centre of Ecology, University of Vienna, Althanstrasse 14, A-1090 Vienna, Austria

* Correspondence: Nadine Hilt, Department of Animal Ecology I, Universitätsstrasse 30, University of Bayreuth, D-95440 Bayreuth, Germany. Tel: + 49 921 552649; Fax: + 49 921 552784; E-mail: nadine.hilt@uni-bayreuth.de

Published in Diversity and Distributions, (2005), **11**, 387-398

2.1 Abstract

Andean montane rainforests are among the most species-rich terrestrial habitats. Little is known about their insect communities and how these respond to anthropogenic habitat alteration. We investigated exceptionally speciose ensembles of nocturnal tiger moths (Arctiidae) at 15 anthropogenically disturbed sites, which together depict a gradient of forest recovery, and six closed-forest understorey sites in southern Ecuador. At weak light traps we sampled 9,211 arctiids, representing 287 species. Arctiid abundance and diversity were highest at advanced succession sites, where secondary scrub or young forest had re-established, followed by early succession sites, and were lowest, but still high, in mature forest understorey. The proportion of rare species showed the reverse pattern. We ordinated moth samples by non-metric multidimensional scaling using the chord-normalized expected species shared (CNESS) index at various levels of the sample size parameter *m*. A distinct segregation of arctiid ensembles at succession sites from those in mature forest consistently emerged only at high *m* values. Segregation between ensembles of early vs. late succession stages was also clear at high *m* values only, and was rather weak. Rare species were responsible for much of the faunal difference along the succession gradient, whereas many common arctiid species occurred at all sites. Matrix correlation tests as well as exploration of relationships between ordination axes and environmental variables revealed the degree of habitat openness, and to a lesser extent elevation, as best predictors of faunal dissimilarity. Faunal differences were not related to geographic distances between sampling sites. Our results suggest that many of the more common tiger moths of Neotropical montane forests have a substantial recolonisation potential at the small spatial scale of our study and accordingly occur also in landscape mosaics surrounding nature reserves. These species contribute to the unexpectedly high diversity of arctiid ensembles at disturbed sites, whereas the proportion of rare species declines outside mature forest.

Keywords: Arctiidae, Ecuador, habitat disturbance, moths, succession gradient, tropical montane rainforest

2.2 Introduction

Tropical montane rainforests are highly threatened hotspots of global diversity (Mittermeier *et al.*, 1998; Myers *et al.*, 2000; Brummitt & Lughadha, 2003; Myers, 2003). Andean montane forests are particularly rich in species, but forest cover has been reduced by 90% of its original extent (Hamilton *et al.*, 1995) at an annual deforestation rate of 0.8–2% (Doumenge *et al.*, 1995).

Insects play a central role in all terrestrial ecosystems as herbivores, pollinators, for nutrient cycling, and as food and host organisms (Summerville *et al.*, 2004; Summerville & Crist, 2004). They are particularly abundant and species rich in tropical rainforests (Ødegaard, 2000), yet the extent of this diversity, its role for ecosystem function, and the degree of degradation due to anthropogenic habitat alterations are still very incompletely known. Due to their sheer numerical preponderance herbivorous insects comprise a significant fraction of any insect fauna (Ødegaard, 2000; Basset *et al.*, 2001; Novotny *et al.*, 2002). Herbivorous insects are also expected to respond sensitively to deforestation and subsequent forest regeneration, since they have a close functional relationship with the vegetation they live in. Moths are an interesting model group to study such effects. These insects are very rich in species, their larvae are herbivorous, the adults are accessible to standardized sampling, and at least some families (such as the Arctiidae or rather tiger moths, the focal group of the present study) are sufficiently well known to allow for identification of the majority of tropical samples (Holloway, 1985; Kitching *et al.*, 2000). Results from lowland habitats in other tropical regions suggest that Arctiidae may even benefit from anthropogenic habitat disturbance (Holloway, 1998; Kitching *et al.*, 2000; Schulze, 2000). This response has been linked to the high degree of polyphagy shown by the larvae of many arctiid species (Kitching & Rawlins, 1999; Holloway *et al.*, 2001; Süßenbach, 2003).

A number of studies address the diversity of tropical butterflies in response to habitat disturbance (DeVries *et al.*, 1997; Hamer & Hill, 2000; Hill & Hamer, 2004). Nocturnal moths are also suitable indicators for understanding and monitoring effects of habitat changes (Holloway, 1985; Chey *et al.*, 1997; Willott, 1999; Kitching *et al.*, 2000; Schulze, 2000; Beck *et al.*, 2002; Axmacher *et al.*, 2004; Summerville *et al.*, 2004). However, very few assessments (e.g. Ricketts *et al.*, 2001; Brehm & Fiedler, 2005) are thus far available for Neotropical moth faunas, which are far more species rich than in any other tropical realm.

The natural potential vegetation of the Ecuadorian Andes at elevations around 2000 m a.s.l. consists of cloud forests with a high phytodiversity (Homeier *et al.*, 2002; Paulsch, 2002). Landslides are common in this region and play an important role in vegetation dynamics (Kessler, 1999; Ohl & Bussmann, 2004). Accordingly, mosaics of various successional stages during forest regeneration after landslides are an essential natural component of the Andean landscape (Kessler, 1999; Ohl & Bussmann, 2004). One should therefore expect that herbivorous insects are selected for effectively colonising such successional habitats. Due to human land use practices today open grassland (pastures for cattle) and various types of secondary scrub and forest also occur abundantly (Paulsch *et al.*, 2001; Paulsch, 2002; Hartig & Beck, 2003). These secondary habitats nowadays form a landscape matrix in which the few remaining natural montane forests are embedded like islands.

Earlier research on the diversity and composition of moth ensembles (Geometridae, Arctiidae, Pyraloidea) along an elevational transect in southern Ecuador (Brehm, 2002; Brehm *et al.*, 2003a, 2003b; Süßenbach, 2003) revealed that the fauna in the understorey of natural closed-canopy montane forest is extraordinarily species rich. The moth family Arctiidae comprises ca. 11,000 species worldwide and is thus among the four largest families in the Lepidoptera (Scoble, 1992). Arctiidae are better known in terms of taxonomy than most other tropical insect herbivore taxa of similar size. Arctiids also appear to be effective at colonizing habitats after natural or anthropogenic disturbance (Willott, 1999; Kitching *et al.*, 2000; Schulze, 2000; Summerville & Crist, 2004).

The present study aimed at characterizing, at a small spatial scale, the diversity and species composition of arctiid ensembles (terminology: Fauth *et al.*, 1996) along a series of succession sites (i.e. substituting space for time: e.g. Hamer & Hill, 2000; Schulze, 2000; Kessler, 2001) in the montane forest zone of the Ecuadorian Andes, ranging from a barely vegetated landslide to mature closed-canopy forest. Given the dramatic changes in diversity and structural complexity of the vegetation in the course of forest regeneration we expected that

(1) tiger moth diversity is reduced in early successional stages and steadily increases with forest regeneration, in parallel with vegetation diversity;

(2) the proportion of rare species is high in natural forest (i.e. occurrence of many habitat specialists) and in early succession habitats (viz. stray colonists from surrounding forest);

(3) composition of arctiid ensembles changes with succession, with few abundant 'pioneer species' characterising open disturbed habitats, while 'true forest species' are confined to mature forest and tend to be less abundant,

(4) as a result, species composition of arctiid ensembles is significantly different between forest and succession sites and gradually changes with forest regeneration.

2.3 Methods

Study area and sampling sites

The study area in southern Ecuador (Reserva Biológica San Francisco, 3°58' S, 79°5' W) is situated within the Eastern Cordillera of the Andes at the northern border of the Podocarpus National Park (Fig. 1; see Brehm & Fiedler, 2003). There are 10-11 humid months per year (Paulsch, 2002; Richter, 2003). At 1,950 m elevation mean annual air temperature is 15.5 °C, and mean annual precipitation amounts to ca. 2,000 mm with a maximum in June and July and a short dry season in October and November (Bendix & Lauer, 1992; Ohl & Bussmann, 2004).

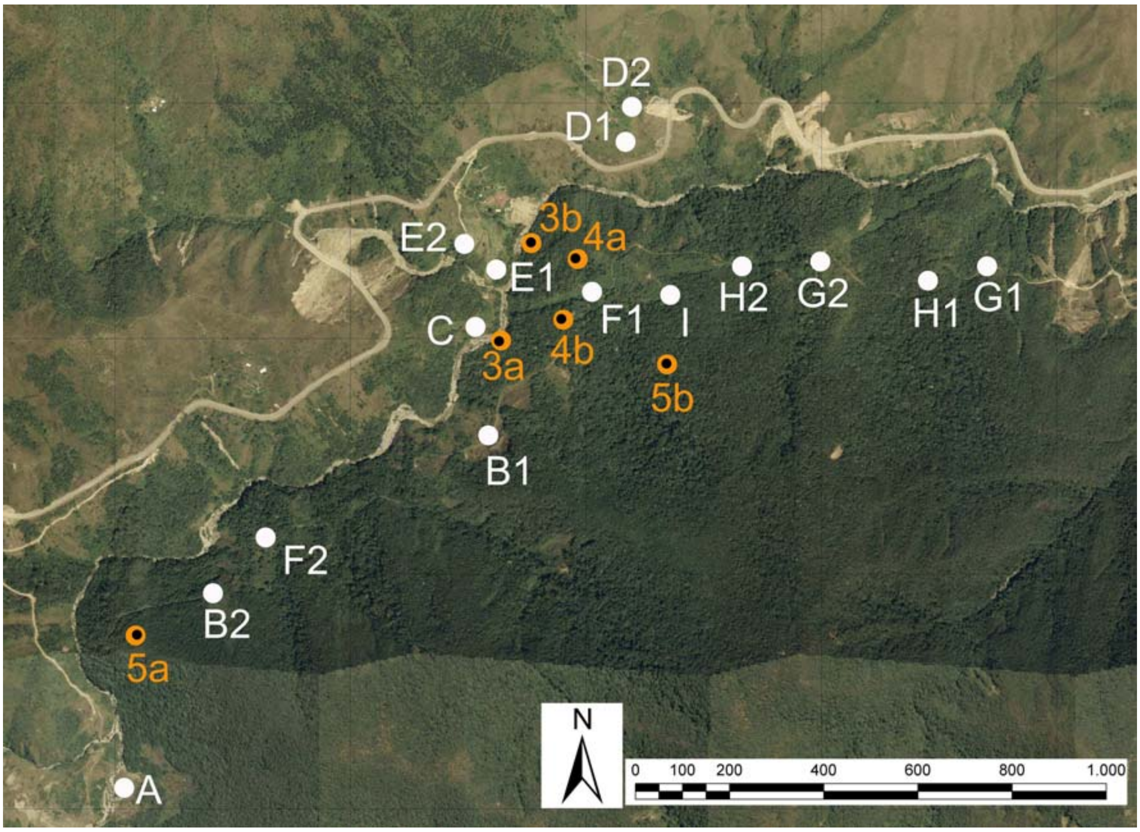


Figure 1: Composite aerial photograph of the study area in southern Ecuador. Sites A to I are the succession sites, 3a to 5b are located in mature forest understorey.

The natural vegetation of the area at altitudes from 1,800-2,800 m is montane cloud forest (Bussmann, 2001; Homeier *et al.*, 2002; Paulsch, 2002). At anthropogenically disturbed sites this is replaced by pastures, thickets of bracken (Hartig & Beck, 2003), shrub encroachment, or regenerating forest (Paulsch, 2002; Ohl & Bussmann, 2004).

We selected 15 sites (labelled A to I) representing seven different stages of vegetation succession and including two abandoned pastures (Table 1). For most of these stages two replicate sites could be found in sufficient proximity, however with a distance between the sites of at least 100 m. In addition, six sites situated in the understorey of natural forest (labelled 3a to 5b) were chosen (two replicate sites at every 100 m elevation). At all sites, vegetation appeared to be homogeneous around the position of the light trap in a radius of at least 50 m. Collectively, these 21 sites depict a succession gradient of forest recovery after a landslide as well as some of the most relevant types of habitats due to human land use practices. Altitude and geographical coordinates of sampling sites were measured with the Global Positioning System (GPS) using a Garmin GPS III instrument (Garmin Instruments Inc., Olathe, KS, USA). Air temperature during moth sampling was measured every 30 min during each catch unit with an electronic thermometer (TFA, Dostmann, Wertheim, Germany) 1.60 m above ground (on top of the light trap). For analyses temperature readings were averaged over all catch nights per site. To measure canopy cover, one hemispherical photograph was taken per site with a Nikon Coolpix 990 with 8 mm lens and an additional hemispheric lens with 180°. From these pictures, the “visible sky” value as an estimate of habitat openness was calculated with the HemiView program (Delta-T & Devices, 1999; Brehm *et al.*, 2003a). Depending on the type of analysis, the progress of succession was either scored on a rank scale (degree of succession) from 1 (young landslide with sparse vegetation) to 7 (mature forest), according to the proportion of woody plants (see Table 1). Alternatively, sampling sites were grouped into three categories according to their successional stage (early [**E**] without woody vegetation: N=10 sites; late [**L**] with shrubs or young secondary forest: N=5; understorey of closed-canopy forest [**F**]: N=6).

Table 1: Sampling sites (sorted by succession stage), with environmental variables and details about moth sampling effort.

Site	Altitude (m)	Vegetation	Latitude (S)	Longitude (W)	Number of nightly samples	Visible sky (%)	Distance from forest (m)	Arctiid species	Arctiid individuals	Mean moths per night	Degree of succession
A	1913	barely vegetated landslide, mosses and lichens	3°58´576	79°05´087	6	79	145	119	646	108	1
B1	1872	mainly orchids, bracken	3°58´335	79°04´442	6	77	200	117	642	107	2
B2	1925	mainly orchids, bracken	3°58´433	79°05´017	6	76	189	109	374	62	2
C	1822	river side, with shrubs and grass	3°58´261	79°04´446	6	60	278	62	204	34	2
D1	1894	abandoned pasture	3°58´177	79°04´251	7	89	389	67	162	23	3
D2	1908	abandoned pasture	3°58´157	79°04´243	7	89	445	71	163	23	3
E1	1830	grass	3°58´223	79°04´435	7	69	111	91	401	57	3
E2	1863	grass	3°58´195	79°04´459	6	85	78	124	561	94	3
F1	1917	bracken thicket with shrubs	3°58´227	79°04´373	6	80	56	90	351	59	4
F2	1921	bracken thicket with shrubs	3°58´407	79°04´598	6	66	78	123	830	138	4
G1	1886	shrubs and little trees	3°58´213	79°04´129	7	74	111	132	882	126	5
G2	1912	shrubs and little trees	3°58´210	79°04´215	6	80	111	124	721	120	5
H1	1900	secondary forest, age 40 yr	3°58´233	79°04´171	6	41	56	92	293	49	6
H2	1920	secondary forest, age 40 yr	3°58´214	79°04´266	6	54	67	121	558	93	6
I	1973	edge of mature forest	3°58´234	79°04´313	6	64	22	156	929	155	6
3a	1800	forest near river, shrubs	3°58´454	79°04´726	7	17	0	59	175	25	7
3b	1800	forest near river, shrubs	3°58´375	79°04´710	7	21	0	59	153	22	7
4a	1850	primary ravine forest	3°58´379	79°04´661	7	8	0	60	192	27	7
4b	1875	primary ravine forest	3°58´431	79°04´661	7	9	0	90	354	51	7
5a	2005	ravine forest under human influence	3°58´710	79°05´063	9	4	0	75	434	48	7
5b	2005	primary ravine forest	3°58´429	79°04´507	9	5	0	49	186	21	7

Sampling and identification

Tiger moths were sampled by attraction to weak light sources (Schulze & Fiedler, 2003; Süßenbach, 2003). Two 15W tubes (Sylvania blacklight-blue, F 15 W/BLB-TB and Philips TLD 15 W 05) in a white gauze cylinder (height 1.6 m, diameter 0.6 m) were operated at ground level. We considered use of these low-power light sources sufficient to minimize cross-attraction of moths between sampled habitats (Schulze & Fiedler, 2003). The 'radius of attraction' of light traps remains partly unsettled in the literature (see discussion in Schulze & Fiedler, 2003), but most studies show that even by much stronger light sources than the ones used in our sampling moths are attracted only from a radius of 10-25 m (Muirhead-Thomson, 1991). We restricted sampling to the peak time of moth activity during the evening hours between 18:30 and 21:30 h local time (closed-canopy forest) or 18:45-21:45 h (succession habitats without closed canopy). Although 'late night species' as well as strictly diurnal arctiids will have been missed by this approach, this is not expected to influence the comparisons between sites. Specimens were collected manually during three field periods in the years 1999 (April-May and October-December) and 2000 (September) (natural forest), and three periods in the years 2002 (March-April and October-November) and 2003 (August-October) (succession sites). At each site six to nine nightly catches were performed until at least 150 arctiid individuals had been assembled (Table 1). Catches were restricted to periods without strong moonlight (McGeachie, 1989; Yela & Holyoak, 1997).

Because we found no evidence of marked seasonal changes in the moth ensembles (Süßenbach, 2003), we collated all catches from a site into one sample to obtain an integrated view of the local moth community. Specimens were sorted to morphospecies and taxonomically identified as far as possible using published literature (Watson & Goodger, 1986; Piñas Rubio & Manzano, 1997; Piñas Rubio *et al.*, 2000; Piñas Rubio & Manzano, 2003) and reference collections (see acknowledgements). Vouchers of all species are deposited in the State Museum of Natural History, Stuttgart, Germany.

Quantitative analyses

Many indices have been developed to measure and compare biodiversity (Magurran, 1988). Andean arctiid ensembles are very rich (see Results) and were not completely covered by our sampling regime. Under such circumstances species numbers are poor descriptors of diversity (Gotelli & Colwell, 2001). We therefore calculated Fisher's alpha of the logseries as a measure of local diversity using a program developed by Henderson and Seaby (1998). Logseries-type species-abundance distributions commonly occur in nature (Engen & Lande, 1996; Hayek & Buzas, 1997; Hubbell, 2001) and measures such as Fisher's alpha are suitable to characterize such data sets. Fisher's alpha has also been extensively used in many other arthropod and especially moth studies, thus facilitating comparisons between studies (e.g. Wolda, 1983, 1987; Thomas & Thomas, 1994; Beck *et al*., 2002; Brehm *et al*., 2003b).

Insect communities in tropical rainforests usually contain large numbers of rare species (singletons). Novotny and Basset (2000) distinguish between 'local singletons', i.e. species found as a single individual in component communities, and 'unique singletons', viz. species found as a single individual in a combined data set. We calculated the proportion of both types of singletons for every sampling site. To compare the proportion of singletons from succession sites vs. mature forest we randomly rarefied the larger cumulative sample (arctiids of all succession habitats, 7,717 individuals) to the level of the less intensively sampled community of natural forest (1,494 individuals). We then compared the proportion of observed singletons in natural forest to the 95% confidence interval for singletons in succession habitats calculated after 10 randomisation runs. Dominance of the commonest species was expressed through the Berger-Parker index (Southwood & Henderson, 2000).

To study species composition of local arctiid ensembles we ordinated moth samples by non-metric multidimensional scaling (NMDS: Clarke, 1993; Brehm & Fiedler, 2004) using the full abundance information for all species. To alleviate sampling effects (which are especially prevalent if sampling is not complete, samples contain many rare species, and are of different size and diversity: Brehm & Fiedler, 2004) we used the chord-normalized expected species shared index (Gallagher's CNESS index: Trueblood *et al.*, 1994) as a measure of dissimilarity between samples. CNESS is a metric improvement of the NESS index originally developed by Grassle and Smith (1976) and varies from 0 (= samples are completely identical) to $\sqrt{2}$ (= samples do not share any species). CNESS can be adjusted by choice of the sample size parameter, m. At its minimum of $m=1$, CNESS emphasises the role of dominant species. At the other extreme, CNESS dissimilarities for maximum m values ($m_{\max}$ = min(N); with min(N) = smallest number of individuals sampled per site) emphasise the contribution of rare species to faunal differences. We also used an intermediate m value ($m = 76$). We calculated CNESS distances using the updated version of the COMPAH program (Boesch, 1977), provided by Gallagher at UMASS/Boston (http://www.es.umb.edu/edgwebp.htm). Ordinations were performed with Statistica Version 6.1 package (StatSoft, 2004). NMDS ordinations based on Bray-Curtis similarities revealed largely similar results and are therefore not shown. The significance of faunal differences between predefined groups of sites was assessed by ANOSIM (Clarke & Warwick, 2001) with 1,000 random permutations. We investigated the association between distance matrices using a rank test based on Spearman coefficients, as implemented in PRIMER v5 (Clarke & Warwick, 2001) with 1,000 random permutations. Where necessary, multiple tests of significance were corrected for a table-wide false discovery rate (FDR) of $P<0.05$ according to the step-up procedure by Benjamini and Hochberg (1995).

2.4 Results

Species richness and local diversity

Altogether 9,211 arctiid individuals, representing 287 species, were collected at the 21 study sites. The minimum and maximum numbers of individuals per site were 153 and 929, respectively (Table 1). Numbers of observed species per site ranged from 49 to 156. Two-hundred-and-four (71%) of these species comprising 7,025 (76%) of all individuals were formally identified at species level. One-hundred-and-nine species (38%) were only found at succession sites, 37 species

(13%) exclusively in mature forest understorey, and 141 species (49%) were shared between both habitat classes.

Mean arctiid abundance per catch unit varied between 21 (site 5b, forest understorey) and 155 moths (site I, forest edge) per night. Arctiid abundance was highest in late succession stages (G-I), and lowest in mature forest understorey (sites 3a to 5b) and on abandoned pastures (D1, D2) (Table 1, Fig. 2). Mean nightly catch was weakly, but significantly correlated with habitat openness (Pearson's r = 0.465, $P<0.05$). There was no significant correlation between mean nightly catch and the distance of the sites from the mature forest (Pearson's r = -0.140, $P>0.05$). Inspection of raw species numbers revealed very similar patterns. Overall, numbers of observed species and individuals recorded per site were highly significantly correlated with each other (Pearson's r = 0.932, $P<0.001$). This underpins that raw species counts are of little use here.

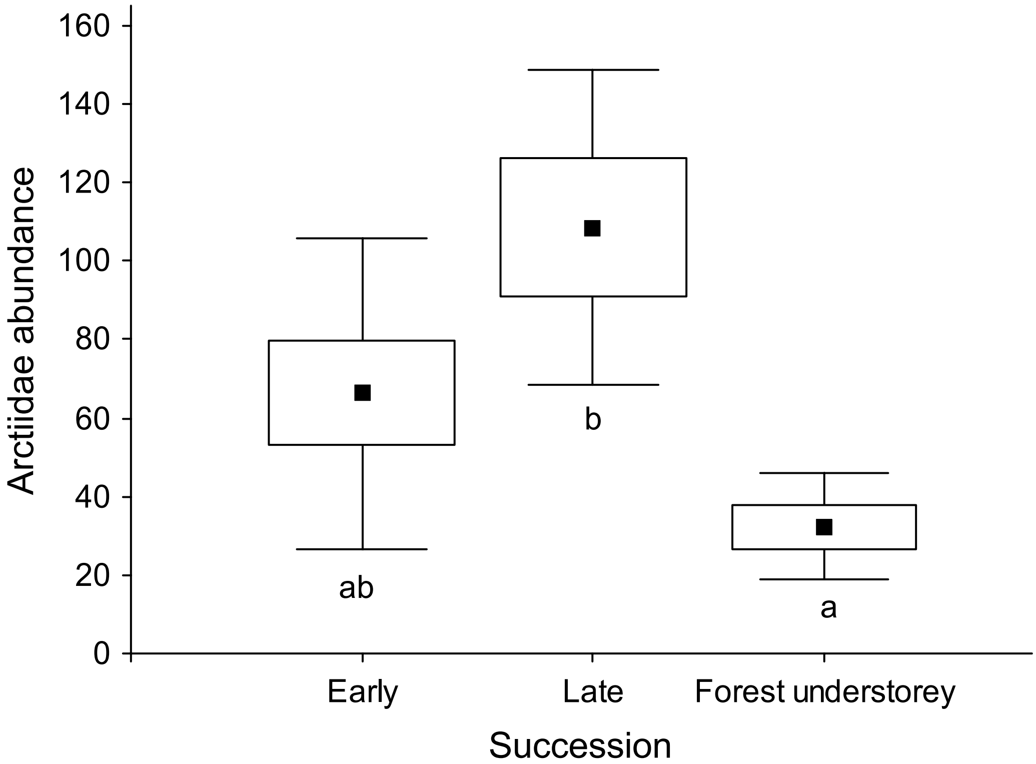


Figure 2: Mean number of specimens attracted per night in the three different succession classes (early with N = 10, late with N = 5, closed-canopy forest understorey with N = 6). Differences between groups are significant (ANOVA: $F_{2,18}$ = 6.73, $P<0.01$). Boxes labelled with different letters differ significantly at $P<0.01$ (Scheffé test). Symbols = means, boxes = ± 1 SE, whiskers = ± 1 SD.

Values of Fisher's alpha (Figure 3) were high at all sites, but varied considerably (range: 21.7-53.6). Highest arctiid diversity was observed in late succession stages, followed by open sites (with the exception of sites C and E1) while it was significantly lower in the forest understorey (Figure 4).

There was no significant correlation between altitude of the sampling site and Fisher's alpha (Pearson's *r* = 0.052, *P* = 0.82), although arctiid diversity decreased slightly but not significantly with distance from closed forest (*r* = 0.386, *P* = 0.08).

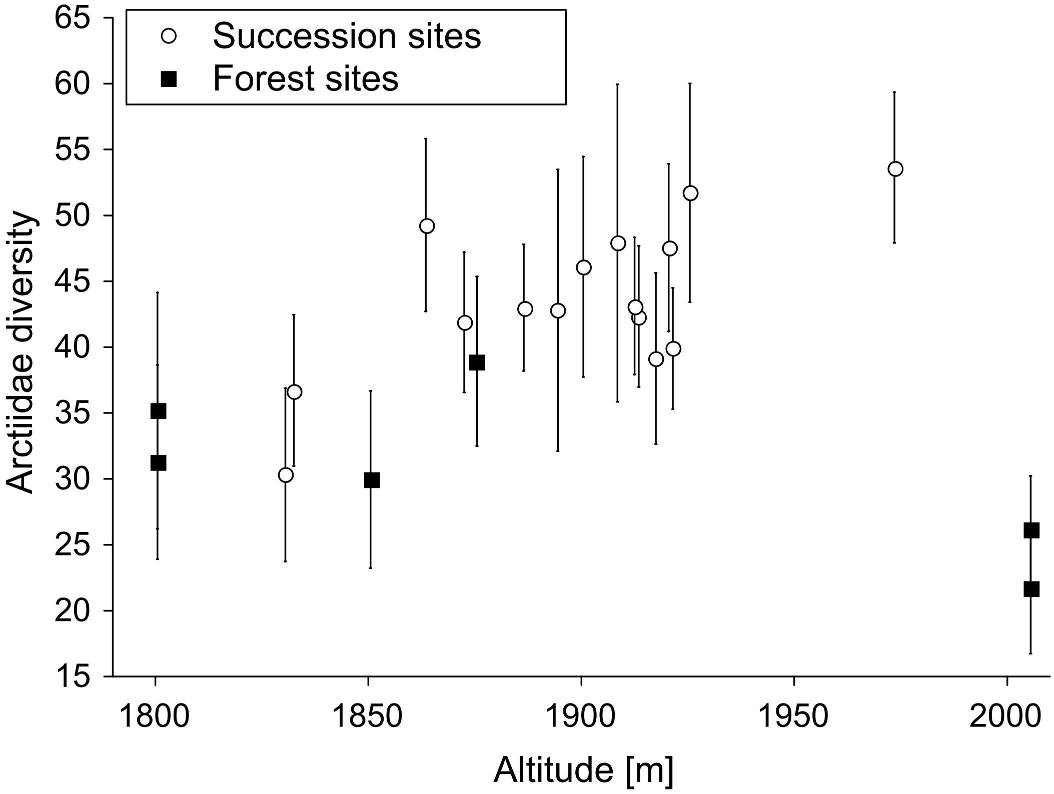


Figure 3: Arctiid diversity (Fisher's alpha, error bars: 95% confidence intervals) at the 21 individual sites, sorted according to altitude (open circles: succession sites, filled squares: natural forest understorey).

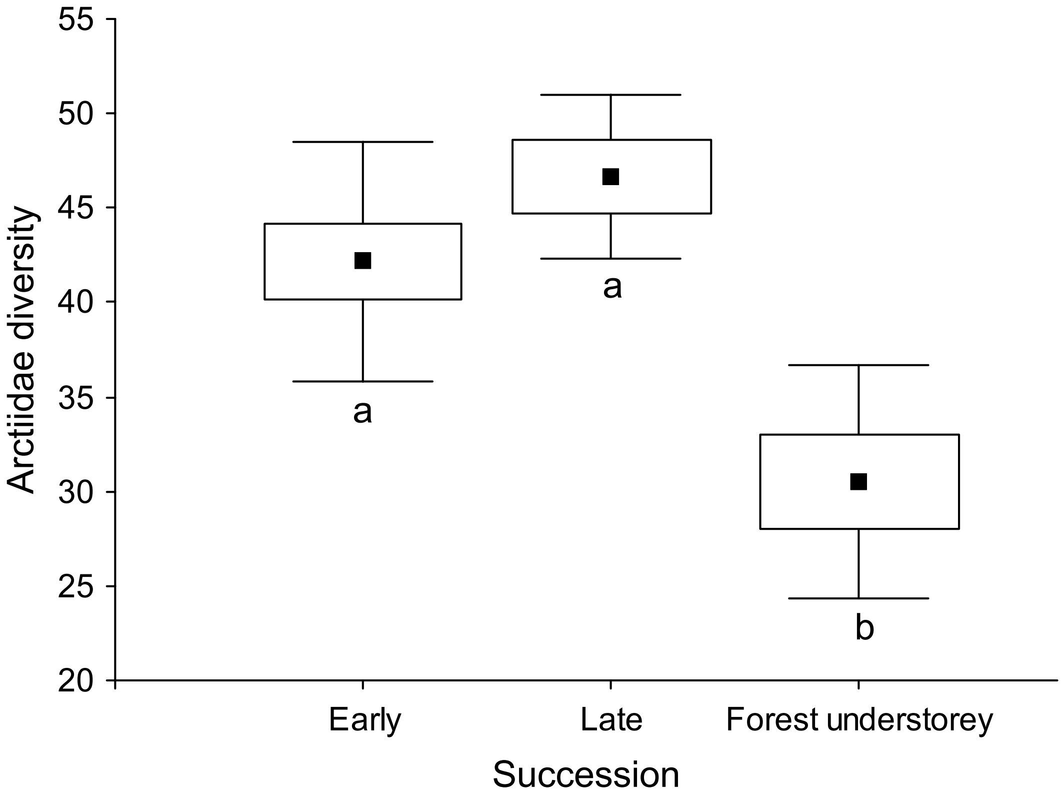


Figure 4: Mean Arctiid diversity (Fisher's alpha) in the three classes of succession habitat. Differences between groups are significant (ANOVA: $F_{2,18}$ = 11.65, $P<0.001$). Boxes labelled with different letters differ significantly at $P<0.05$ (Scheffé test). Symbols = means, boxes = ± 1 SE, whiskers = ± 1 SD.

Sixty-one species (21.3% of the species total) occurred as unique singletons. A comparison between the proportions of singletons in the succession sites (rarefaction analysis with 10 randomisations; mean value: 27% ± 2%) vs. the mature forest (41%) showed that singletons were much more numerous in natural forest understorey.

The fraction of local singletons relative to species numbers recorded per site varied between 35% (site G1) and 62% (site 3b). Mean proportions of local singletons differed significantly between the three succession classes (Figure 5). The highest contribution of singletons was found in natural forest understorey. Early succession habitats had lower proportions of singletons, and these were lowest at sites with more advanced forest regeneration.

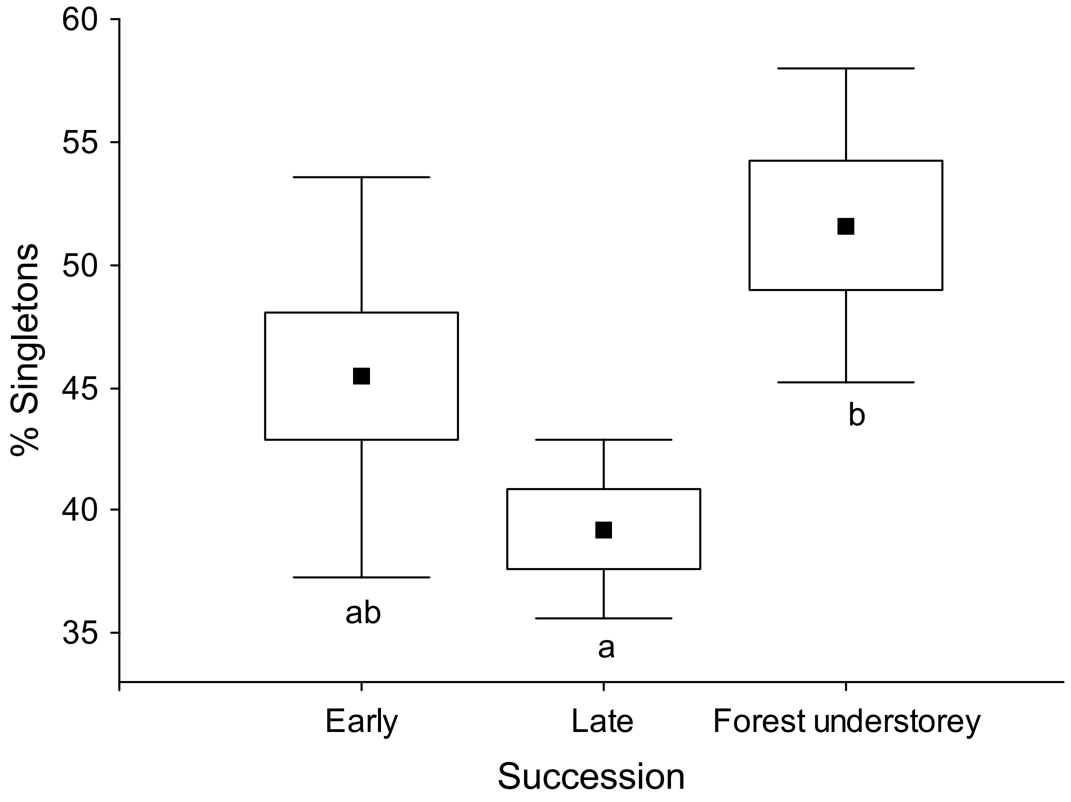


Figure 5: Mean proportion of local singletons (in % of species) in the three different succession classes (early with N=10, late with N=5 closed-canopy forest understory with N=6). Differences between groups are significant (ANOVA: $F_{2,18}$ = 4.39, $P<0.05$). Boxes labelled with different letters differ significantly at $P<0.05$ (Scheffé test). Symbols = means, boxes = ± 1 SE, whiskers = ± 1 SD.

The Berger-Parker index varied from 0.07 (site H1) to 0.34 (site 5a). Mean dominance values were similar in all three habitat groups (mean value ± 1 SD, **E**: 0.155 ± 0.04; **L**: 0.097 ± 0.02; **F**: 0.176 ± 0.09; ANOVA: *F*(2,18) = 2.74, *P*>0.05; Levene-Test *P*>0.05).

Species composition

We performed two- and three-dimensional NMDS ordinations of arctiid ensembles for the whole possible range of values of the sample size parameter, *m*. Stress (as a measure of poorness-of-fit between the original distance matrix and the final NMDS configuration) ranged between 0.13-0.17 for two-dimensional solutions and between 0.08-0.10 for three-dimensional ones.

Generally, model fit increased with higher *m* values, suggesting that rare species contain much of the faunal information (Figure 6). Here we figure only two-dimensional ordinations since these are visually more comprehensible and their stress values are still acceptable according to Clarke's (1993) guidelines.

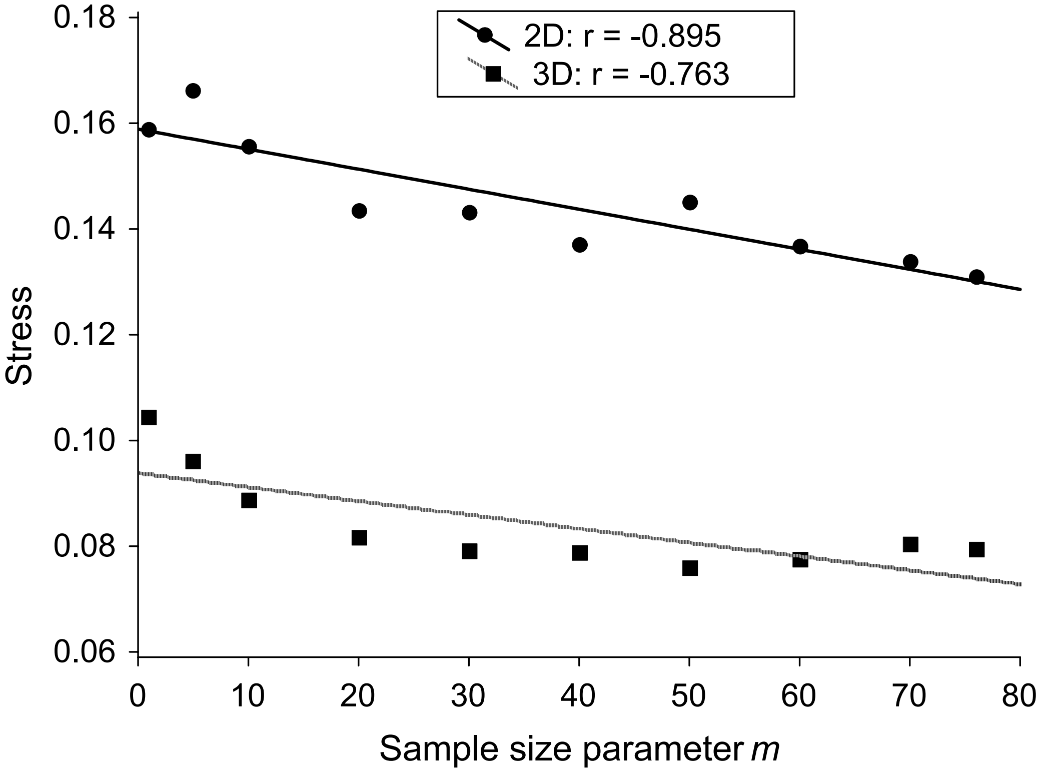


Figure 6: Correlation between the sample size parameter *m* of the CNESS index and stress values of 2D and 3D ordinations obtained by non-metric multidimensional scaling (2D: *r* = -0.895, *P*<0.001; 3D: *r* = -0.763, *P*<0.001).

An ordination of arctiid assemblages based on the CNESS index with *m* = 1 (Fig. 7), which emphasizes the abundant species, revealed a significant separation between the mature forest sites (3a, 3b, 4a, 4b, 5a, 5b) and the succession sites (ANOSIM with step-up FDR correction; **E** vs. **F**: *R* = 0.56, *P*<0.005; **L** vs. **F**: *R* = 0.421, *P*<0.005), and also a separation between the earlier and later succession sites (**E** vs. **L**: *R* = 0.551, *P*<0.005). Arctiid ensembles of abandoned pastures were segregated from the true succession sites, but fell in between the closed-canopy forest samples. The ensembles from the two forest sites at lowest elevation (3a, 3b) were quite distant to the remaining forest arctiid samples.

Ordinating the same samples with an intermediate value of the sample size parameter ($m_{\text{intermediate}} = 76$) revealed a slightly different structure (Fig. 7). There was a significant separation between arctiid ensembles from closed forest understorey and those from succession sites (**E** vs. **F**: $R = 0.664$, $P<0.005$; **L** vs. **F**: $R = 0.395$, $P<0.05$). Arctiid samples from natural forest sites formed a distinct group with a clear altitudinal gradient from the lower sites (3a, 3b) to the higher ones (5a, 5b). Succession sites formed two subclusters which, however, were not significantly different from each other (**E** vs. **L**: $R = 0.224$, $P>0.05$). Tiger moth ensembles from the two abandoned pastures were well separated from those of the other 19 sites, but due to the low number of replicates this difference cannot be assessed statistically. Ordinations based on CNESS matrices for higher m values (up to $m_{\text{max}} = 153$) revealed very similar configurations (not shown). A clear distinction between forest and succession arctiid ensembles was apparent only at $m>20$.

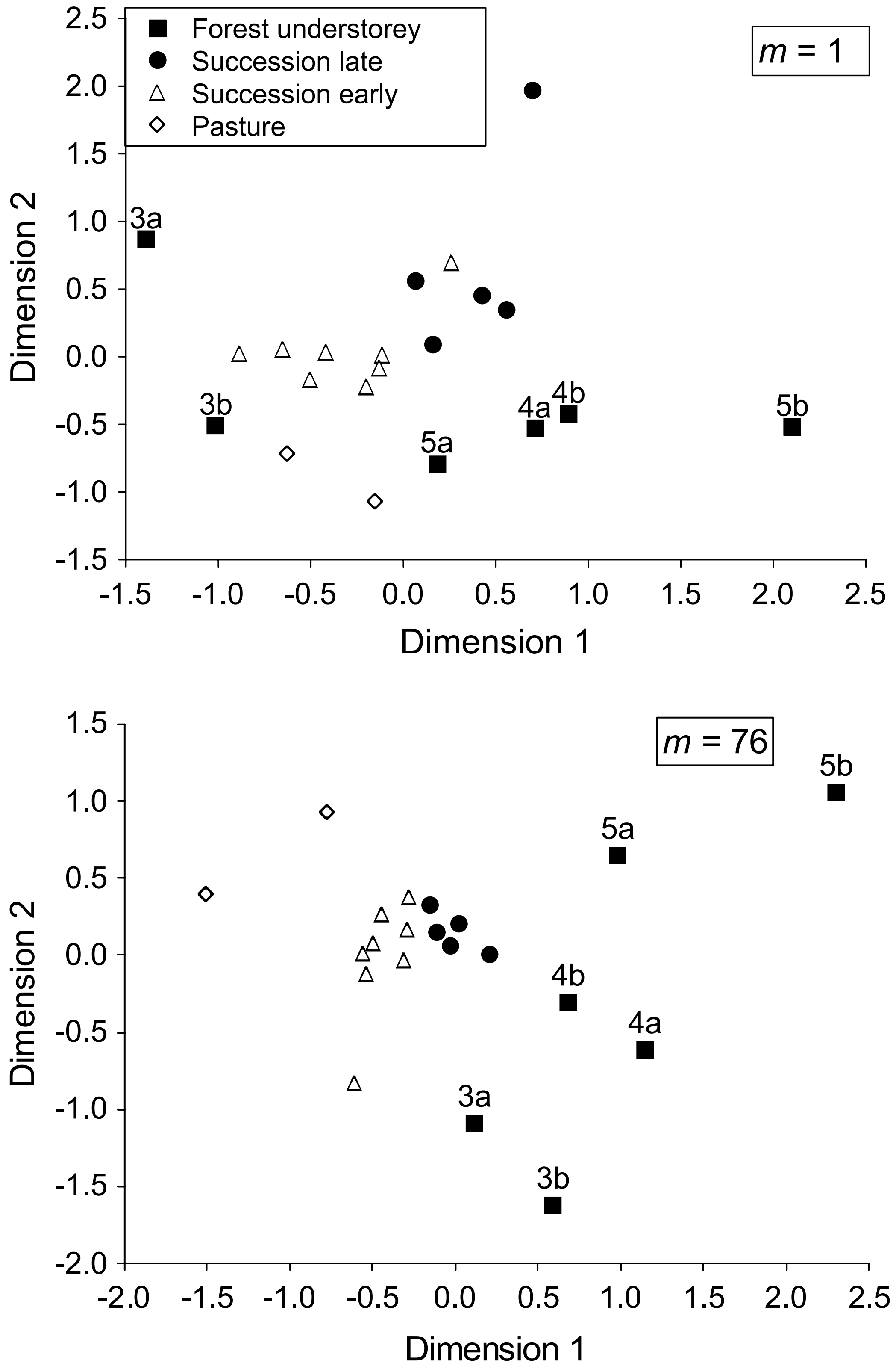


Figure 7: Ordination of 21 arctiid ensembles (non-metric two-dimensional scaling based on CNESS distances with *m* = 1, stress: 0.159 and *m* = 76, stress: 0.131) from a succession gradient in the montane forest zone of southern Ecuador.

Rank-based matrix correlation tests revealed significant relationships between faunal dissimilarity and the degree of habitat openness (Table 2) for all *m* values. Altitudinal effects were only significant at *m*>5 and were always much weaker. Even less pronounced relationships occurred between faunal dissimilarity and air temperature during sampling, and these were restricted to *m* values in the range between 10 and 50. Faunal dissimilarity was not at all related to the geographical distance between sampling sites. No significant matrix correlations were found with classical Mantel tests which assume linearity (results not shown, all *P*>0.05).

Table 2: Results of matrix rank correlations (based on Spearman coefficients, 1000 random permutations) between faunal dissimilarity (CNESS distances) and distance matrices for elevation, geographic position, temperature, and visible sky. For environmental variables, Euclidean distances between sites were used. Figures in bold: significant at a table-wide FDR of *P*<0.05. n.s.: not significant.

***m* value**	**Elevation**	**Geographic distance**	**Visible sky**	**Temperature**
1	n.s.	n.s.	**r = 0.455** ***P*<0.005**	n.s.
5	**r = 0.231** ***P*<0.05**	n.s.	**r = 0.54** ***P*<0.005**	n.s.
10	**r = 0.294** ***P*<0.01**	n.s.	**r = 0.587** ***P*<0.005**	r = 0.155 *P*<0.05
20	**r = 0.333** ***P*<0.005**	n.s.	**r = 0.614** ***P*<0.005**	r = 0.169 *P*<0.05
30	**r = 0.348** ***P*<0.005**	n.s.	**r = 0.618** ***P*<0.005**	r = 0.171 *P*<0.05
40	**r = 0.351** ***P*<0.005**	n.s.	**r = 0.621** ***P*<0.005**	r = 0.169 *P*<0.05
50	**r = 0.351** ***P*<0.005**	n.s.	**r = 0.619** ***P*<0.005**	r = 0.163 *P*<0.05
60	**r = 0.357** ***P*<0.005**	n.s.	**r = 0.615** ***P*<0.005**	n.s.
70	**r = 0.362** ***P*<0.005**	n.s.	**r = 0.613** ***P*<0.005**	n.s.
76	**r = 0.363** ***P*<0.005**	n.s.	**r = 0.61** ***P*<0.005**	n.s.

Exploration of possible relationships between axes in reduced space and environmental variables corroborated the ecological meaningfulness of the ordinations (Table 3). In the two-dimensional case, faunal segregation along with variables that are related to vegetation succession or disturbance was only significant for high *m* values. Visible sky had the strongest predictive quality. Elevation of sampling sites affected faunal similarity at low, intermediate and high *m* values, even though elevational differences between sites were small. In three-dimensional ordinations the effect of succession on arctiid ensembles was consistently significant, irrespective of the selected *m* value. Again visible sky emerged as the strongest predictor of faunal change, and altitude of sampling sites significantly influenced faunal similarity.

Table 3: Pearson's correlation coefficients between the axis scores of arctiid samples extracted from two- and three-dimensional NMDS ordinations and different environmental factors. *m* – sample size parameter of the CNESS index; Dim – dimension of ordination. Figures in bold: significant at a table-wide FDR of $P<0.05$. n.s.: not significant.

	Altitude	Temperature	Visible sky	Distance from forest	Degree of succession
***m* = 1**					
Dim 1	**r = 0.64** **$P<0.005$**	n.s.	n.s.	n.s.	n.s.
Dim 2	n.s.	n.s.	n.s.	n.s.	n.s.
***m* = 76**					
Dim 1	n.s.	r = 0.490 $P<0.05$	**r = 0.855** **$P<0.0001$**	**r = 0.710** **$P<0.0005$**	**r = 0.747** **$P<0.0005$**
Dim 2	**r = 0.829** **$P<0.0001$**	n.s.	n.s.	n.s.	n.s.
***m* = 1**					
Dim 1	**r = 0.475** **$P<0.05$**	n.s.	n.s	r = 0.438 $P<0.05$	**r = 0.584** **$P<0.01$**
Dim 2	n.s	n.s.	n.s	n.s	n.s
Dim 3	n.s	**r = 0.734** **$P<0.0005$**	**r = 0.734** **$P<0.001$**	**r = 0.608** **$P<0.005$**	**r = 0.478** **$P<0.05$**
***m* = 76**					
Dim 1	n.s	**r = 0.525** **$P<0.05$**	**r = 0.870** **$P<0.0001$**	**r = 0.710** **$P<0.0005$**	**r = 0.747** **$P<0.0005$**
Dim 2	**r = 0.850** **$P<0.0001$**	n.s.	n.s	n.s	n.s
Dim 3	n.s	n.s.	n.s	n.s	n.s

2.5 Discussion

Species richness, local diversity and abundance

Overall, diversity of tiger moths in our Andean study area was much higher than in Old World tropical regions (Schulze, 2000; Kitching *et al.*, 2000). This was expected since the Neotropical realm houses by far the largest fraction of the global Arctiidae fauna (Kitching & Rawlins, 1999). However, a record of 287 arctiid species sampled in an area of roughly 2 km² is amazingly high by all standards. This confirms that the East Andean slopes are probably one of the hotspots of moth diversity about the world (Brehm, 2002; Brehm *et al.*, 2005). However, contrary to our initial expectations, highest arctiid diversity was not recorded in natural forest but in advanced succession habitats in close proximity to such forest. This observation stands in stark contrast to the decrease in species diversity and structural complexity of the vegetation (especially with regard to epiphytes) when moving from natural forest to disturbed habitats (Paulsch *et al.*, 2001; Paulsch, 2002).

The intermediate disturbance hypothesis (Connell, 1978) might provide an explanatory framework for the pattern observed in Ecuador. According to this hypothesis species diversity is greatest in communities experiencing intermediate levels of disturbance, so both very early as well as very late stages of recovery from disturbance should exhibit lower diversity. Disturbance creates novel opportunities for species not found in undisturbed forest, and the habitat mosaic resulting from regeneration after patchy disturbance further increases the number of niches available. This model has been applied to different community types and a wide range of organisms (overview see Li *et al.*, 2004), including tropical montane forests (Kok *et al.*, 1995; Kessler, 1999). However, alternative models to the intermediate disturbance hypothesis may similarly explain effects of disturbance on community structure (Li *et al.,* 2004).

Responses of tropical arthropod communities to habitat disturbance or successional recovery vary across taxa, guilds, and regions (Basset *et al.*, 1998; Lawton *et al.*, 1998; Schulze *et al.*, 2004). Lepš *et al.* (2001) found an increase of leaf-chewing herbivore species numbers from early successional to mature vegetation. In a habitat gradient in Borneo canopy ant and beetle communities converged towards the pattern found in primary forest with progressing forest succession, and ant abundance as well as diversity increased concomitantly (Floren & Linsenmair, 2001). Liow *et al.* (2001) observed higher bee species richness in disturbed forests, whereas bee abundance was significantly higher in larger primary forests than in other types of forests. Moth diversity in Borneo generally declined with forest disturbance, but different moth taxa did not respond in a uniform manner (Beck *et al.*, 2002; Fiedler & Schulze, 2004). In montane forest on Mt. Kilimanjaro, however, moth diversity did not parallel plant diversity along a gradient of forest recovery (Axmacher *et al.*, 2004). At least some of these discrepancies between studies may depend on the spatial scale considered (Hamer & Hill, 2000; Hill & Hamer, 2004). At small scales (as in our present analysis) habitat disturbance indeed frequently increases diversity (Hill & Hamer, 2004).

Studies in SE Asia and Australia (Willott, 1999; Kitching *et al.*, 2000; Schulze, 2000) indicate that a substantial fraction of Arctiid ensembles benefit from habitat disturbance. Such species can even serve as disturbance indicators (Holloway, 1985; Kitching *et al.*, 2000; Summerville *et al.*, 2004). Our results suggest that this also applies, at least partially, to Neotropical tiger moths whose abundance and diversity were highest at advanced succession sites. This is not merely an effect of higher catch efficiency in open disturbed habitats, since in early succession stages and on pastures, where light-trap visibility was highest, numbers of moths attracted were low. It remains to be tested whether the diversity and abundance patterns seen in Arctiidae in response to habitat disturbance and forest recovery can be generalized to other insect groups.

Our sampling regime might have contributed to the lower (but still remarkably high) diversity of Arctiidae in natural forest as compared to succession habitats. Lacking access to the canopy, we restricted sampling to the understorey layer. Thus, species that predominantly or exclusively occur in the canopy are undersampled. The fraction of canopy specialists in tropical forest varies across moth taxa (Willott, 1999; Intachat & Holloway, 2000; Beck *et al.*, 2002; Schulze & Fiedler, 2003). In Borneo, nectar-feeding tiger moths are significantly more prevalent in the canopy than in the understorey (Schulze *et al.*, 2001), and observations from Costa Rica also suggest existence of a rich and distinct arctiid canopy fauna (G. Brehm, pers. comm.). Moreover, sampling efficiency at light traps was reduced in the dense forest vegetation. Therefore, we covered forest tiger moth ensembles probably less completely by our sampling than those from open habitats. However, using a sample-size independent diversity measure like Fisher's alpha (Hayek & Buzas, 1997) should minimize distortions of between-habitat comparisons.

Ensemble structure and species composition

Insect communities in tropical rainforests usually contain large numbers of rare species. Singletons often constitute more than half of the species total (Novotny & Basset, 2000). In our study the proportion of unique singletons was 21.3%, but fractions of local singletons mostly ranged around 50%. Singletons were more prevalent in the mature forest understorey. Ricketts *et al.* (2001) observed an even higher proportion of unique moth species (58%) in a forest sample compared to 30-46% in agricultural habitats in southern Costa Rica. Also Basset *et al*. (2001) found that, most insect herbivores species in a rainforest in Guyana were rare (38%). One plausible explanation for this high proportion is that species represented as singletons are “true forest species”, which occupy special niches and occur at low densities (Basset *et al.*, 1998, 2001; Novotny & Basset, 2000). However, as with most tropical insect species, data on life cycles and habitat requirements of Andean arctiids are presently too scant to allow for an assessment of that hypothesis. The fraction of local singletons was also high in early succession stages. Probably, many of these singletons must be regarded as colonists, which were sampled during dispersal flights from the nearby forest.

These dispersers also increase diversity estimates in the early succession stages.

While the proportion of rare species followed our expectations, this was not true for the extent of dominance. Overall, dominance of the commonest species per site was almost twice as high (mean: 0.147) as compared to Geometridae moths in the same area (Brehm, 2002; Brehm & Fiedler, 2005) and did not increase in early successional habitats. Rather, we paradoxically found highest dominance values in the forest understorey. Moreover, the same species *Macroptila laniata* (Dognin 1899; Lithosiinae) was the single most abundant species at 18 of 21 sites. Only sites H1, 4b and 5b had another dominant species. This does not support the idea that a few 'pioneer species' would disproportionately benefit from habitat disturbance. Floren & Linsenmair (2001) observed similar patterns of dominance with regard to Bornean canopy ants along a disturbance gradient.

In line with this conclusion, there was no radical change in species composition along the succession gradient. Despite large differences in sample sizes between forest (1,494 individuals) and disturbed sites (7,717 moths), almost half of the species observed were shared between these two habitat categories. With m = 1, which accentuates the abundant species, there was no clear separation between arctiid ensembles from forest and succession sites. When the more rare species were emphasized (i.e. increasing the sample size parameter m), the more distinct was faunal segregation between forest understorey and succession habitats. Differences between early and late succession habitats and an elevational gradient of arctiid species composition in natural forest also emerged only when emphasizing rare species. Arctiid ensembles in habitats dominated by grass vegetation (abandoned pastures D1, D2, site C near a river) turned out to be different from those at the remaining 12 succession sites. These three habitats also had the lowest arctiid abundance (<40 individuals per night) of all sites with open vegetation (i.e. where trap efficiency should be high). Only in dense forest understorey was the mean number of arctiids sampled per night similarly low. Collectively, these results underscore that much of the information about faunal differences rests on the rare species. As a corollary, if rare species are neglected (either by deliberately omitting them from ordination analyses, or due to insufficient sampling or identification effort), much information will be lost and the ecological significance of faunal comparisons becomes questionable.

Matrix rank correlation tests and explorations of axis scores extracted by ordination revealed that species composition of arctiid ensembles follows both the natural (altitude) and anthropogenic (disturbance) environmental gradients between the sites. Especially for high *m* values (i.e. emphasizing rare species: Brehm & Fiedler, 2004a) the first ordination axis depicts the degree of habitat disturbance, whereas the second axis reflects habitat elevation. Thus, for arctiids in the Ecuadorian montane forest zone the pattern of β-diversity, rather than α-diversity, mirrors changes in vegetation and climate along the habitat gradient under study. This segregation is largely due to the disproportionate loss of rare 'forest species' and to more subtle changes in abundance relationships among the more common species. We found only very limited evidence for abundant species characteristic of only one habitat type, which would qualify as indicators. For example, *Mesothen roseifemur* (Draudt 1915; Ctenuchini), *Correbia lycoides* (Walker 1854; Ctenuchini) and *Pelochyta* sp. (Phaegopterini) were the only relatively abundant species that we exclusively recorded in near-natural forest, whereas *Agylla argentifera* (Walker 1866; Lithosiinae), *Ischnocampa tristis* (Schaus 1889; Phaegopterini) and *Eucereon perstriatum* (Hampson 1909; Ctenuchini) appeared to be specific to disturbed, regenerating habitats. Apart from these few examples, most of the more common Arctiidae in our study area have a sufficient dispersal potential to enable recolonisation of succession habitats from intact forest at the small spatial scale of our study (Summerville & Crist, 2004).

In conclusion, despite the small distances between habitats studied, and the ample dispersal movements of mobile moths (Ricketts *et al*., 2001), local ecological processes were strong enough to allow for a differentiation between arctiid ensembles from mature forest and anthropogenically disturbed sites. At disturbed sites arctiid ensembles retained considerable diversity, partially even higher than in the forest, suggesting that landscape mosaics at the edge of nature reserves may support the survival of many of the more common tiger moth species. Such areas could play an important role as buffer zones around protected areas (Schulze, 2000). However, the impoverishment of arctiid ensembles at pastures only 400 m away from intact forest, and the drop-out of rare forest species at even smaller spatial scales, show that without preserving large blocks of natural montane forest as source areas it will be impossible to conserve these uniquely diverse moth communities in the long run.

Acknowledgments

We thank Dirk Süßenbach who provided data from his samples from the natural forest. Gunnar Brehm, Doreen Fetting, Claudia Ramenda, Anne Walter, Anna Spengler, Annick Servant and Caroline Schulze (all at University of Bayreuth) helped with sampling and processing moths. Giovanni Onore (Pontificia Universidad Católica del Ecuador, Quito) and Christoph L. Häuser (Staatliches Museum für Naturkunde, Stuttgart) supported the project logistically. C.L. Häuser, Martin Honey and Linda M. Pitkin (Natural History Museum, London) and Axel Hausmann (Zoologische Staatssammlung, Munich) provided access to reference collections under their care. Benoît Vincent (Paris) identified some species. Matthias Oesker (Bielefeld) assisted with measuring canopy closure. Ekkehard Jordan (Düsseldorf) kindly made available the aerial photograph that formed the basis for Fig. 1. The Ministerio del Medio Ambiente in Ecuador issued research permits (Nro. 002-PNP-DBAP-RLZCH/MA), and the foundation Nature and Culture International (Loja, Ecuador) allowed access to the study sites and their facilities. The Deutsche Forschungsgemeinschaft financed our work (FOR 402/1-1 TP15, FOR 402/2-1 TP A3). Special thanks go to John Sloggett, Gunnar Brehm and two anonymous reviewers for helpful comments on the manuscript.

2.6 References

Axmacher, J.C., Tünte, H., Schrumpf, M., Müller-Hohenstein, K., Lyaruu, H.V.M. & Fiedler, K. (2004) Diverging diversity patterns of vascular plants and geometrid moths during forest regeneration on Mt. Kilimanjaro, Tanzania. *Journal of Biogeography*, **31**, 895-904.

Basset, Y., Charles, E., Hammond, D.S. & Brown, V.K. (2001) Short-term effects of canopy openness on insect herbivores in a rain forest in Guyana. *Journal of Applied Ecology*, **38**, 1045-1058.

Basset, Y., Novotny, V., Miller, S.E. & Springate, N.D. (1998) Assessing the impact of forest disturbance on tropical invertebrates: some comments. *Journal of Applied Ecology*, **35**, 461-466.

Beck, J., Schulze, C.H., Linsenmair, K.E. & Fiedler, K. (2002) From forest to farmland: diversity of geometrid moths along two habitat gradients on Borneo. *Journal of Tropical Ecology*, **17**, 33-51.

Bendix, J. & Lauer, W. (1992) Die Niederschlagsjahreszeiten in Ecuador und ihre klimadynamische Interpretation. *Erdkunde*, **46**, 118-134.

Benjamini, Y. & Hochberg, Y. (1995) Controlling the false discovery rate: a pratical and powerful approach to multiple testing. *Journal of the Royal Statistical Society, B* **57**, 289-300.

Boesch, D.F. (1977) Application of numerical classification in ecological investigations of water pollution. *Special Scientific Report*, Institute of Marine Science, Virginia.

Brehm, G. (2002) *Diversity of geometrid moths in a montane rainforest in Ecuador*. Ph.D. thesis, University of Bayreuth. URL: http://opus.ub.uni-bayreuth.de/volltexte/2003/20/

Brehm, G. & Fiedler, K. (2003) Faunal composition of geometrid moths changes with altitude in an Andean montane rainforest. *Journal of Biogeography* **30**, 431-440.

Brehm, G. & Fiedler, K. (2004) Ordinating tropical moth ensembles from an elevational gradient: a comparison of common methods. *Journal of Tropical Ecology* **20**, 165-172.

Brehm, G. & Fiedler, K. (2005) Diversity and community structure of geometrid moths of disturbed habitat in a montane area in the Ecuadorian Andes. *Journal of Research on the Lepidoptera*, **38**, 1-14.

Brehm, G., Homeier, J. & Fiedler, K. (2003a) Beta diversity of geometrid moths (Lepidoptera: Geometridae) in an Andean montane rainforest. *Diversity and Distributions*, **9**, 351-366.

Brehm, G., Pitkin, L.M., Hilt, N. & Fiedler, K. (2005) Montane Andean rain forests are a global diversity hotspot of geometrid moths. *Journal of Biogeography*, **32**, 1621-1627.

Brehm, G., Süssenbach, D. & Fiedler, K. (2003b) Unique elevational diversity patterns of geometrid moths in an Andean montane rainforest. *Ecography*, **26**, 456-466.

Brummitt, N. & Lughadha, E.N. (2003) Biodiversity: Where’s hot and where’s not. *Conservation Biology*, **17**, 1442-1448.

Bussmann, R. (2001) The montane forest of Reserva Biologica San Francisco (Zamora-Chinchipe, Ecuador). *Die Erde*, **132**, 9-25.

Chey, V.K., Holloway, J.D. & Speight, M.R. (1997) Diversity of moths in forest plantations and natural forests in Sabah. *Bulletin of Entomological Research*, **87**, 371-385.

Clarke, K.R. (1993) Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, **18**, 117-143.

Clarke, K.R. & Warwick, R.M. (2001) *Change in marine communities: an approach to statistical analysis and interpretation*. Primer-E, Plymouth.

Connell, J.H. (1978) Diversity in tropical rain forests and coral reefs. *Science*, **199**, 1302-1310.

Delta, T. & Devices (1999) *Hemiview Canopy Analysis Software*, Version 2.1. Burwell, Cambridge.

DeVries, P.J., Murray, D. & Lande, R. (1997) Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. *Biological Journal of the Linnean Society*, **62**, 343-364.

Doumenge, C., Gilmour, D., Ruiz-Perez, M. & Blockhus, J. (1995) Tropical montane cloud forests: conservation status and management issues. In: *Tropical montane cloud forests. Ecological Studies*, vol. 110 (eds. L.S. Hamilton, J.O. Juvik and F.N. Scatena), pp. 24-37. Springer, New York.

Engen, S. & Lande, R. (1996) Population dynamic models generating species abundance distributions of the gamma type. *Journal of Theoretical Biology*, **178**, 325-331.

Fauth, J.E., Bernardo, J., Camara, M., Resetarits, W.J., Van Buskirk, J. & McCollum, S.A. (1996) Simplifying the jargon of community ecology: a conceptual approach. *The American Naturalist,* **147**, 282-286.

Fiedler, K. & Schulze, C.H. (2004) Forest modification affects diversity (but not dynamics) of speciose tropical pyraloid moth communities. *Biotropica,* **36**: 615-627.

Floren, A. & Linsenmair, K.E. (2001) The influence of anthropogenic disturbances on the structure of arboreal arthropod communities. *Plant Ecology*, **153**, 153-167.

Gotelli, N.J. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**, 379-391.

Grassle, J.F. & Smith, W. (1976) A similarity measure sensitive to the contribution of rare species and its use in investigation of variation n marine benthic communities. *Oecologia*, **25**, 13-22.

Hamer, K.C. & Hill, J.K. (2000) Scale-dependent effects of habitat disturbance on species richness in tropical forests. *Conservation Biology*, **14**, 1435-1440.

Hamilton, L.S., Juvik, J.O. & Scatena, F.N. (1995) The Puerto Rico cloud forest symposium: introduction and workshop synthesis. In: *Tropical montane cloud forests. Ecological Studies*, vol. 110 (eds. L.S. Hamilton, J.O. Juvik and F.N. Scatena), pp. 1-19. Springer, New York.

Hartig, K. & Beck, E. (2003) The bracken fern (*Pteridium arachnoideum* (Kaulf.) Maxon) dilemma in the Andes of Southern Ecuador. *Ecotropica*, **9**, 3-13.

Hayek, L.-A. & Buzas, M.A. (1997) *Surveying natural populations*. Columbia University Press, New York.

Henderson, P.A. & Seaby, R.M.H. (1998) *Species diversity and richness*. Version 2.62. Pennington: Pisces Conservation Ltd.

Hill, J.K. & Hamer, K.C. (2004) Determining impacts of habitat modification on diversity of tropical forest fauna: the importance of spatial scale. *Journal of Applied Ecology*, **41**, 744-754.

Holloway, J.D. (1985) Moths as indicator organisms for categorising rain forest and monitoring changes and regenerating processes. In: *Tropical Rain-Forest: The Leeds Symposium* (eds. A.C. Chadwick and S.L. Sutton), pp. 235-242. Philisophical and Literary Society, Leeds, UK.

Holloway, J.D. (1998) The impact of traditional and modern cultivation practices, including forestry, on Lepidoptera diversity in Malaysia and Indonesia. In: *Dynamics of Tropical Communities* (eds. D.M. Newbery, H.H.T. Prins and N.D. Brown), pp. 567-597. The 37th Symposium of the British Ecological Society, London

Holloway, J.D., Kibby, G. & Peggie, D. (2001) *The families of Malesian Moths and Butterflies*. Fauna Malesiana Handbooks. Brill, Leiden.

Homeier, J., Dalitz, H. & Breckle, S.-W. (2002) Waldstruktur und Baumartendiversität im montanen Regenwald der Estación Científica San Francisco in Südecuador. *Berichte der Reinhold-Tüxen-Gesellschaft,* **14**, 109-118.

Hubbell, S.P. (2001) *The unified neutral theory of biodiversity and biogeography.* Princeton University Press, Princeton.

Intachat, J. & Holloway, J.D. (2000) Is there stratification in diversity or preferred flight height of geometroid moths in Malaysian lowland tropical forest? *Biodiversity and Conservation*, **9**, 1417-1439.

Kessler, M. (1999) Plant species richness and endemism during natural landslide succession in a perhumid montane forestin the Bolivian Andes. *Ecotropica*, **5**, 123-136.

Kessler, M. (2001) Maximum plant-community endemism at intermediate intensities of anthropogenic disturbance in Bolivian montane forests. *Conservation Biology*, **15**, 634-641.

Kitching, R.L., Orr, A.G., Thalib, L., Mitchell, H., Hopkins, M.S. & Graham, A.W. (2000) Moth assemblages as indicators of environmental quality in remnants of upland Australian rain forest. *Journal of Applied Ecology*, **37**, 284-297.

Kitching, I.J. & Rawlins, J.E. (1999) The Noctuoidea. In: *Handbook of Zoology. Lepidoptera, Moths and Butterflies,* vol. 1 (ed. N.P. Kristensen), pp. 355-401. Berlin, New York, Walter de Gruyter.

Kok, K., Verweij, P.A. & Beukema, H. (1995) Effects of cutting and grazing on Andean treeline vegetation. In: *Biodiversity and conservation of neotropical montane forests* (eds. S.P. Churchill, H. Balslev, E. Forero and J. L. Luteyn), pp. 527-539. The New York Botanical Garden, New York.

Lawton, J.H., Bignell, D.E., Bolton, B., Bloemers, G.F., Eggleton, P., Hammond, P.M., Hodda, M., Holt, R.D., Larsen, T.B., Mawdsley, N.A., Stork, N.E., Shrivastava, D.S. & Watt, A.D. (1998) Biodiversity inventories, indicator taxa and effects of habitat modification in tropical rain forest. *Nature*, **391**, 72-76.

Lepš, J., Novotny, V. & Basset, Y. (2001) Habitat and successional status of plants in relation to the communities of their leaf-chewing herbivores in Papua New Guinea. *Journal of Ecology*, **89**, 186-199.

Li, J., Loneragan, W.A., Duggin, J.A. & Grant, C.D. (2004) Issues affecting the measurement of disturbance response patterns in herbaceous vegetation – A test of the intermediate disturbance hypothesis. *Plant Ecology*, **172**, 11-26.

Liow, L.H., Sodhi, N.S. & Elmqvist, T. (2001) Bee diversity along a disturbance gradient in tropical lowland forests of south-east Asia. *Journal of Applied Ecology*, **38**, 180-192.

Magurran, A.E. (1988) *Ecological diversity and its measurement*. Croom Helm, London.

McGeachie, W.J. (1989) The effects of moonlight illuminance, temperature and wind speed on light-trap catches of moths. *Bulletin of Entomological Research*, **79**, 185-192.

Mittermeier, R.A., Myers, N., Thomsen, J.B., da Fonseca, G.A.B. & Olivieri, S. (1998) Biodiversity hotspots and major tropical wilderness areas: Approaches to setting conservation priorities. *Conservation Biology*, **12**, 516-520.

Muirhead-Thomson, R.C. (1991) *Trap responses of flying insects*. London: Academic Press.

Myers, N. (2003) Conservation of biodiversity: How are we doing? *The Environmentalist*, **23**, 9-15.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Fonseca, G.A.B., & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853-858.

Novotny, V. & Basset, Y. (2000) Rare species in communities of tropical insect herbivores: pondering the mystery of singletons. *Oikos*, **89**, 564-572.

Novotny, V., Basset, Y., Miller, S.E., Weiblen, G.D., Bremer, B., Cizek, L. & Drozd, P. (2002) Low host specificity of herbivorous insects in a tropical forest. *Nature*, **416**, 841-844.

Ødegaard, F. (2000) How many species of arthropods? Erwin's estimate revised. *Biological Journal of the Linnean Society*, **71**, 583-597.

Ohl, C. & Bussmann, R. (2004) Recolonisation of natural landslides in tropical mountain forests of Southern Ecuador. *Feddes Repertorium*, **115**, 248-264.

Paulsch, A. (2002) *Development and application of a classification system for undisturbed and disturbed tropical montane forest based on vegetation structure*. Ph.D. thesis, University of Bayreuth. URL: http://opus.ub.uni-bayreuth.de/volltexte/2002/1/

Paulsch, A., Schneider, R. & Hartig, K. (2001) Land-use induced vegetation structure in a mountain region of South Ecuador. *Die Erde*, **132**, 93-102.

Piñas Rubio, F.S.J. & Manzano, I. (1997) *Mariposas del Ecuador. Vol. 1 Géneros*. Quito, Ecuador: Pontificia Universidad Católica del Ecuador.

Piñas Rubio, F.S.J. & Manzano, I. (2003) *Mariposas del Ecuador. Vol. 21b. Arctiidae. Subfamilia: Ctenuchinae.* Quito, Ecuador: Compañía de Jesús.

Piñas Rubio, F.S.J., Raab-Green, S., Onore, G. & Manzano, I. (2000) *Mariposas del Ecuador. Butterflies & Moths of Ecuador. Vol. 20: Familiy: Arctiiade.* Quito, Ecuador: Pontificia Universidad Católica del Ecuador.

Richter, M. (2003) Using epiphytes and soil temperatures for eco-climate interpretations in southern Ecuador. *Erdkunde*, **57**, 161-181.

Ricketts, T.H., Daily, G.C., Ehrlich, P.R. & Fay, J.P. (2001) Countryside biogeography of moths in a fragmented landscape: biodiversity in native and agricultural habitats. *Conservation Biology*, **15**, 378-388.

Schulze, C.H. (2000) *Auswirkungen anthropogener Störungen auf die Diversität von Herbivoren – Analysen von Nachtfalterzönosen entlang von Habitatgradienten in Ost-Malaysia*. Ph.D. thesis, University of Bayreuth.

Schulze, C.H. & Fiedler, K. (2003) Vertical and temporal diversity of a species-rich moth taxon in Borneo. In: *Arthropods of tropical forests: spatio-temporal dynamics and resource use in the canopy* (eds. Y. Basset, V. Novotny, S. Miller and R.L. Kitching), pp. 69-85. Cambridge University Press, Cambridge.

Schulze, C.H., Linsenmair, K.E. & Fiedler, K. (2001) Understorey versus canopy: patterns of vertical stratification and diversity among Lepidoptera in a Bornean rain forest. *Plant Ecology*, **153**, 133-152.

Schulze, C.H., Waltert, M., Kessler, P.J.A., Pitopang, R., Shahabuddin, Veddeler, D., Mühlenberg, M., Gradstein, S.R., Leuschner, C., Steffan-Dewenter, I. & Tscharntke, T. (2004) Biodiversity indicator groups of tropical land-use systems: comparing plants, birds, and insects. *Ecological Applications,* **14**, 1321–1333.

Scoble, M.J. (1992) *The Lepidoptera: Form, Function, and Diversity*. Oxford University Press, New York.

Southwood, T.R.E. & Henderson, P.A. (2000) *Ecological methods*, Blackwell Science Publishers, Oxford.

StatSoft, Inc. (2004) STATISTICA für Windows [Software-System für Datenanalyse] Version 6. www.statsoft.com

Süßenbach, D. (2003) *Diversität von Nachtfaltergemeinschaften entlang eines Höhengradienten in Südecuador (Lepidoptera: Pyraloidea, Arctiidae)*. Ph.D thesis, University of Bayreuth. URL: http://opus.ub.uni-bayreuth.de/volltexte/2003/33/

Summerville, K.S. & Crist, T.O. (2004) Contrasting effects of habitat quantity and quality on moth communities in fragmented landscapes. *Ecography*, **27**, 3-12.

Summerville, K.S., Ritter, L.M. & Crist, T.O. (2004) Forest moth taxa as indicators of lepidopteran richness and habitat disturbance: a preliminary assessment. *Biological Conservation*, **116**, 9-18.

Thomas, A.W. & Thomas, G.M. (1994) Sampling strategies for estimating moth species diversity using a light trap in a notheastern softwood forest. *Journal of the Lepidopterists' Society,* **48**, 85-105.

Trueblood, D.D., Gallagher, E.D. & Gould, D.M. (1994) Three stages of seasonal succession on the Savin Hill Cove mudflat, Boston Harbor. *Limnology and Oceanography*, **39**, 1440-1454.

Watson, A. & Goodger, D.T. (1986) Catalogue of the Neotropical tiger-moths. *Occasional Papers on Systematic Entomology*, **1**, 1-71.

Willott, S. (1999) The effects of selective logging on the distribution of moths in a Bornean rainforest. *Philosophical Transactions of the Royal Society of London B*, **354**, 1783-1790.

Wolda, H. (1983) Diversity, diversity indices and tropical cockroaches. *Oecologia*, **58**, 290-298.

Wolda, H. (1987) Altitude, habitat and tropical insect diversity. *Biological Journal of the Linnean Society*, **30**, 313-323.

Yela, J.L. & Holyoak, M. (1997) Effects of moonlight and meterological factors on light and bait trap catches of noctuid moths (Lepidoptera: Noctuidae). *Environmental Entomology*, **26**, 1283-1290.

3 Arctiid moth ensembles along a successional gradient in the Ecuadorian montane rainforest zone: how different are subfamilies and tribes?

Nadine Hilt[1)]*, Konrad Fiedler [1), 2)]

[1)] Department of Animal Ecology I, University of Bayreuth, Bayreuth, Germany

[2)] present address: Department of Population Ecology, Faculty of Life Sciences, University of Vienna, Althanstrasse 14, A-1090 Vienna, Austria

* Correspondence: Nadine Hilt, Department of Animal Ecology I, Universitätsstrasse 30, University of Bayreuth, D-95440 Bayreuth Germany. E-mail: nadine.hilt@uni-bayreuth.de

Published in Journal of Biogeography, (2006), **33**, 108-120

3.1 Abstract

We examined changes in species diversity and faunal composition of arctiid moths along a successional gradient at a fine spatial scale in one of the world's hotspots for moths, the Andean montane rainforest zone. We specifically study whether moth groups with divergent life-histories respond differentially to forest recovery. The study was carried out in Southern Ecuador along a successional gradient (between 1,800 and 2,005 m a.s.l.). Moths were sampled with weak light-traps at 21 sites representing three habitat categories (early and late succession, mature forest understorey), and were analysed at species level. Relative proportions were calculated from species numbers as well as from specimen numbers. Fisher's α were used as a measure of local diversity and for ordination analyses non-metric multidimensional scaling (NMDS) have been carried out. Proportions of higher arctiid taxa changed distinctly along the successional gradient. Ctenuchini contributed more strongly to ensembles in natural forest, whereas Lithosiinae numerically decreased with forest recovery. Arctiid species diversity was high in all habitats sampled. The three larger subordinated taxa contributed differentially to richness: Phaegopterini were always the most diverse clade, followed by Ctenuchini and Lithosiinae. Local species diversity was higher in successional habitats than in forest understorey, and this was most pronounced for the Phaegopterini. NMDS revealed a significant segregation between ensembles from successional sites and from forest understorey for all larger subordinated taxa (Phaegopterini, Ctenuchini, Lithosiinae). Abandoned pastures held an impoverished, distinct fauna. Faunal segregation was more pronounced for rare species. Ordination axes primarily reflected the degree of habitat disturbance (e.g. openness of vegetation, distance of the sites to mature forest) and to a lesser extent altitude, but not distance between sampling sites. Despite the geographical proximity of the 21 sites and the pronounced dispersal abilities of adult arctiid moths, local ecological processes were strong enough to allow for a differentiation between ensembles from mature forest and disturbed sites, even at the level of subfamilies and tribes. Differences in morphology and life-history characteristics of higher arctiid taxa were reflected in their differential representation (proportions of species and individuals) at the sites, whereas patterns of alpha- and beta-diversity were concordant. However, concordance was too low to allow for reliable extrapolation, in terms of biodiversity indication, from one tribe or subfamily to the entire family Arctiidae. Phaegopterini (comprising more putative generalist feeders during the larval stages) benefited from habitat disturbance, whereas Ctenuchini (with host-specialist larvae) were more strongly affiliated with forest habitats.

Keywords Alpha-diversity, Arctiidae, beta-diversity, biodiversity indicators, Ecuador, montane rainforest, moths, successional gradient, taxonomic levels

3.2 Introduction

A growing number of studies have investigated the diversity of insects along altitudinal gradients in species-rich tropical regions (Brühl *et al.*, 1999; Schulze, 2000; Brehm & Fiedler, 2003; Axmacher *et al.*, 2004a; Brehm & Fiedler, 2004). There is also an extensive literature on the effects of forest disturbance and fragmentation on tropical arthropod communities (overview: Basset *et al.*, 1998; Hamer & Hill, 2000; Basset *et al.*, 2001; Tscharntke *et al.*, 2002). Yet studies on insect diversity along tropical successional gradients are scarce (Chey *et al.*, 1997; Willot, 1999; Schulze, 2000; Beck *et al.*, 2002), particularly for montane areas (Davis *et al.*, 1999; Axmacher *et al.*, 2004b; Brehm & Fiedler, 2005).

Studies on different taxa along elevational gradients have revealed that there is variation in diversity patterns (Rahbek, 2005). Even though diversity generally decreases at higher elevations in plants and animals, various plant and animal taxa exhibit a diversity peak at mid-elevations (Zapata *et al.*, 2003; Axmacher *et al.*, 2004a; McCain, 2004).

Contrasting results have also been found for disturbance effects: some studies recorded a reduction in diversity following habitat disturbance or fragmentation, whereas others concluded that disturbance results in an increase in diversity (Hamer & Hill, 2000). Hill & Hamer (2004) have shown that spatial scale also affects the response of insects to disturbance.

Insect herbivores represent one of the most speciose components of tropical arthropod faunas (Basset *et al.*, 2001). Among insects, few groups contain species as readily identifiable and as well known as the Lepidoptera (Scoble, 1992). Furthermore, Lepidoptera are critical to the functioning of many ecosystems, with species having functional roles as selective herbivores, pollinators and prey (Summerville *et al.*, 2004).

We here investigate responses (e.g. in terms of local diversity and species composition) of the moth family Arctiidae along a successional gradient in the Ecuadorian montane rainforest zone. Species richness of arctiids in the Andean montane forest zone is high compared to other regions worldwide (Schulze, 2000; Süßenbach, 2003; chapter 2). Nevertheless, Ecuadorian Arctiidae (tiger, lichen, and wasp moths) are sufficiently well known to allow for taxonomic identification in the majority of cases. Results from lowland habitats in Old World tropical regions suggest that Arctiidae may even benefit from anthropogenic habitat disturbance (Holloway, 1998; Kitching *et al.*, 2000; Schulze, 2000). This response has been linked to the high degree of polyphagy shown by the larvae of many arctiid species (Kitching & Rawlins, 1999; Holloway *et al.*, 2001; Süßenbach, 2003), although this remains to be tested for the far more speciose Neotropical fauna.

According to Watson and Goodger (1986), the Arctiidae include about 11,000 species worldwide; more than half of these occur in the Neotropics. Here, arctiid moths fall into two subfamilies, viz. Lithosiinae and Arctiinae, and the latter are subdivided into four major tribes (Arctiini, Phaegopterini, Pericopini, and Ctenuchini: Jacobson & Weller, 2002).

We have recently analyzed diversity patterns of arctiid moths from the same study area at the level of the entire family (chapter 2). In the present paper we are interested in within-family comparisons, i.e. whether different subfamilies or tribes show contrasting responses to forest disturbance. Due to the pronounced morphological and ecological differences between higher arctiid taxa (Kitching & Rawlins, 1999), we expected that **(a)** they would also respond differentially in their species diversity to changes in vegetation in the course of forest regeneration. Kitching *et al.* (2000) observed that Arctiinae are particularly abundant at more disturbed sites, whereas Syntominae (the Palaeotropical ecological analogue to Neotropical Ctenuchini) show the reverse pattern. Furthermore, we **(b)** analyze beta diversity of arctiid species along the succession gradient at the taxonomic levels of subfamilies and tribes. We expected that life-history differences between taxa would lead to discordances in the dynamics of species composition during succession. Finally, we **(c)** searched for correlations between faunal data and abiotic environmental factors as candidates for causal factors that govern faunal change.

3.3 Material and Methods

Study sites and environmental variables

The study area in southern Ecuador (Reserva Biológica San Francisco, 3°58' S, 79°5' W) is situated within the Eastern Cordillera of the Andes at the northern border of the Podocarpus National Park (see Brehm & Fiedler, 2003). There are 10-11 humid months per year (Richter, 2003). At 1,950 m elevation mean annual air temperature is 15.5 °C, and mean annual precipitation amounts to ~ 2,000 mm with a maximum in June and July and a short dry season termed veranillo in October and November (Bendix & Lauer, 1992).

The natural vegetation of the area at altitudes from 1,800-2,800 m is montane forest (Homeier *et al.*, 2002; Paulsch, 2002). At anthropogenically disturbed sites this is replaced by pastures, thickets of bracken (Paulsch *et al.*, 2001; Hartig & Beck, 2003), shrub encroachment, or regenerating forest (Paulsch, 2002).

We selected 15 sites at altitudes between 1,822 to 1,973 m a.s.l. (labelled A to I; Fig. 1 and chapter 2) representing seven different stages of vegetation succession and including two abandoned pastures. For most of these stages two replicate sites could be found in sufficient proximity, but with a distance between the sites of at least 100 m. In addition, six sites situated in the understorey of natural forest (labelled 3a to 5b; altitude: 1,800 to 2,005 m a.s.l.; see Brehm & Fiedler, 2005) were chosen (two replicate sites at every 100 m elevation). Collectively, these 21 sites (Fig. 1) depict a successional gradient of forest recovery after a landslide as well as some of the most relevant types of habitats due to human land use practices such as bracken thicket, abandoned pastures. Altitude and geographical coordinates of sampling sites were measured with the Global Positioning System (GPS) using a Garmin GPS III instrument (Garmin Instruments Inc., Olathe, KS, USA).

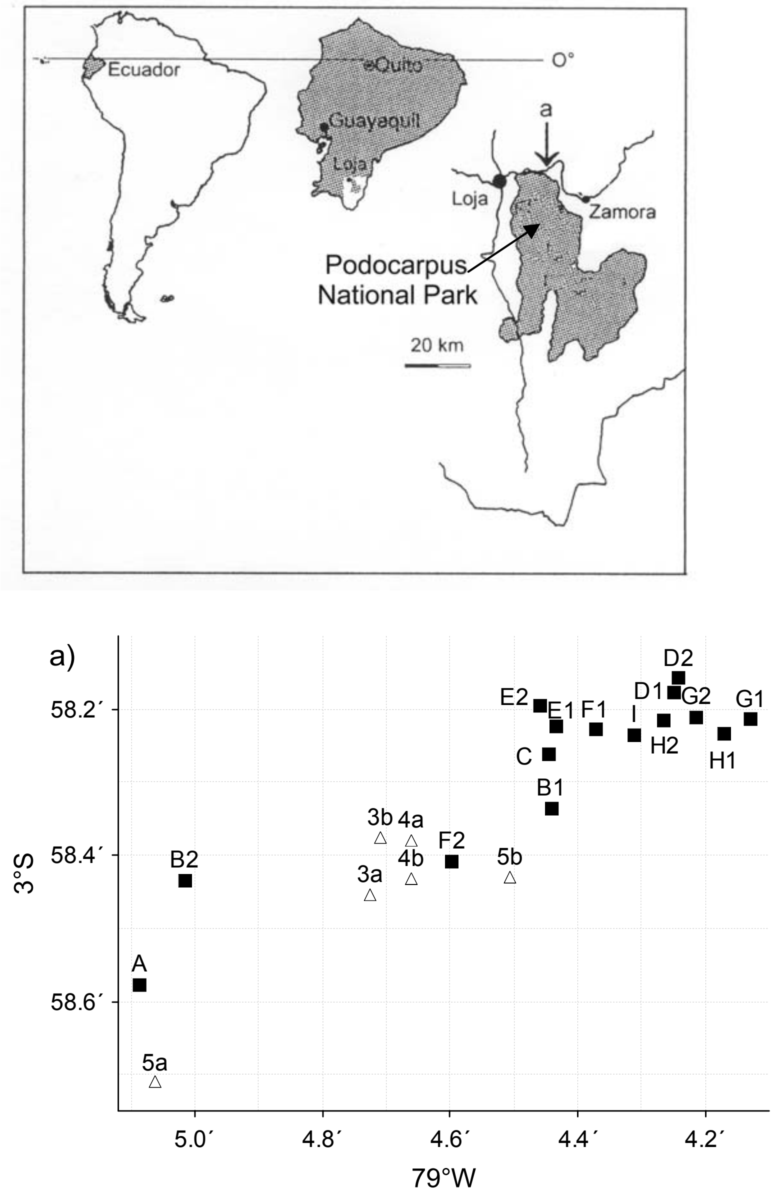


Figure 1: Geographical positions of the 21 sampling sites in South America and Ecuador at the northern border of the Podocarpus National Park, Province Zamora-Chinchipe (map from G. Brehm, 2002). Top: overview, a) sites in the area of the Estación Científica San Francisco. A to I are the succession sites; 3a to 5b are the mature forest understorey sites. All sites range between 1,800 m above sea level and 2,005 m.

Depending on the type of analysis, the degree of succession was either scored on a rank scale from 1 (young landslide with sparse vegetation) to 7 (mature forest), according to the proportion of woody plants, or sampling sites were grouped into three categories according to their successional stage (early [E] without woody vegetation: N=8 sites; late [L] with shrubs or young secondary forest: N=5; abandoned pastures [P]: N=2; understorey of closed-canopy forest [F]: N=6).

Air temperature during moth sampling was measured every 30 min during each catch unit with an electronic thermometer (TFA, Dostmann, Wertheim, Germany) 1.60 m above ground (on top of the light trap). For analyses, temperature readings were averaged over all catch nights per site. To measure canopy cover, one hemispherical photograph was taken per site with a Nikon Coolpix 990 with an 8mm lens and an additional 180° hemispheric lens (fisheye lens). From these pictures, the 'visible sky' value was calculated with the HemiView program (Delta-T & Devices, 1999; Brehm *et al.*, 2003a).

Moth sampling and identification

Arctiid moths were sampled with weak light traps (2 x 15 W tubes, Sylvania black light-blue, F 15 W/BLB-TB and Philips TLD 15 W 05) in a white gauze cylinder (height 1.6 m, diameter 0.6 m) operated at ground level. Trap positions were at least 100 m apart from each other, and all trap positions were selected so that within a radius of 50 m around the trap the vegetation appeared homogeneous. We used only weak light sources to increase the probability of the majority of the catch belonging to the resident fauna rather than being stray individuals attracted from outside. Earlier studies with similar light sources revealed that spatial resolution of the resulting catches is high enough to link moth samples with the surrounding vegetation (Schulze & Fiedler, 2003; Fiedler & Schulze, 2004), even though all samples may contain a few strays that originate from more distant habitats. We restricted sampling to the evening hours between 18:30 and 21:30 h (closed-canopy forest) or 18:45-21:45 h (successional habitats without closed canopy). These hours encompass the time of maximum activity for moths in the study area (Brehm, 2002; Süßenbach, 2003; pers. observation). Specimens were collected manually during three field periods in 1999 (April-May and October-December) and 2000 (September) (natural forest), and three periods in 2002 (March-April and October-November) and 2003 (August-October) (successional sites). At each site six to nine nightly trappings were performed until at least 150 arctiid individuals had been assembled. Trapping was restricted to periods without strong moonlight (McGeachie, 1989).

Since we found little evidence of seasonal changes in the moth ensembles (Süßenbach, 2003), we collated all catches from a site into one sample to obtain an integrated view of the local moth community. Sampling period had less influence on the moth communities than the habitat category. There were significant changes in abundance for only a very few common arctiid species, but the number of individuals caught per night was slightly, but not significantly higher in the more humid periods than in the drier period (veranillo). Species diversity (measured as Fisher's alpha) showed no seasonal trends in the Arctiidae, and 52% of all recorded species representing 93.8% of all individuals caught were found in all three sampling periods (see chapter 6). Specimens were taxonomically identified as far as possible using published literature (Watson & Goodger, 1986; Piñas Rubio & Manzano, 1997, 2003; Piñas Rubio *et al.*, 2000) and reference collections (see acknowledgements). Vouchers of all species are deposited in the State Museum of Natural History, Stuttgart, Germany. For checking arctiid species names we used the global Lepidoptera names index (http://internt.nhm.ac.uk/jdsml/perth/lepindex/) from the Natural History Museum, London.

Quantitative analyses

Relative proportions were calculated from species numbers as well as from individual numbers. For calculation of Fisher's alpha and ordination analyses we used only the subfamily Lithosiinae and the tribes Phaegopterini and Ctenuchini. The remaining tribes (Arctiini and Pericopini) were ignored because of their small numbers (seven and nine species respectively).

Andean arctiid ensembles are very rich and were not completely covered by our sampling regime. Under such circumstances species numbers are poor descriptors of diversity (Gotelli & Colwell, 2001). We therefore calculated Fisher's alpha of the log series as a measure of local diversity using a program developed by Henderson and Seaby (1998). Fisher's alpha has been used extensively in many other arthropod and especially moth studies, thus facilitating comparisons between studies (e.g. Thomas & Thomas, 1994; Beck *et al.*, 2002; Brehm *et al.*, 2003b).

Insect communities in tropical rainforests usually contain large numbers of rare species (Novotny & Basset, 2000). We calculated the proportion of singletons and doubletons for every sampling site and separately for the subfamily and accordingly tribes. Dominance of the commonest species was expressed through the Berger-Parker index (Southwood & Henderson, 2000).

To study species composition of local ensembles we ordinated moth samples, separately for Phaegopterini, Ctenuchini and Lithosiinae, by non-metric multidimensional scaling (NMDS: Clarke, 1993; Brehm & Fiedler, 2004) of the chord-normalized expected species shared (CNESS) index of dissimilarity (Trueblood *et al.*, 1994). We calculated CNESS distances using the updated version of the COMPAH program (Boesch, 1977), provided by Gallagher at UMASS/Boston (http://www.es.umb.edu/edgwebp.htm) for a small (m = 1) and the optimal ($m = m_{\text{optimal}}$) value of the sample size parameter m. The optimal m value was determined after Trueblood *et al.* (1994). Low values of m emphasize the role of common species, whereas at higher m values successively more weight is given to the rare species. Ordinations were performed with the Statistica 6.1 package (StatSoft, 2004). We present only two-dimensional ordinations, which are easiest to interpret and most readily compared visually (Shepard, 1974; Jackson & Somers, 1991). All two-dimensional scaling plots had acceptably low stress values between 0.13 and 0.19 (a measure of poorness-of-fit between the distances in reduced ordination space and original distance matrices: Clarke, 1993). The significance of faunal differences between predefined groups of sites was assessed using ANOSIM (Clarke & Warwick, 2001) with 1,000 random permutations. We investigated the association between distance matrices using a rank test based on Spearman coefficients, as implemented in PRIMER v5 (Clarke & Warwick, 2001) with 1,000 random permutations. We searched for possible relationships between ordination axes and environmental factors using Pearson's correlation coefficient. Where necessary, multiple tests of significance were corrected for a table-wide false discovery rate (FDR) of $P<0.05$ according to the step-up procedure developed by Benjamini and Hochberg (1995).

3.4 Results

Proportions of subordinated taxa

We recorded 287 species, of which 135 belong to the tribe Phaegopterini (47%), followed by Ctenuchini (82; 29%), Lithosiinae (54; 19%), Pericopini (9; 3%), and Arctiini (7; 2%). An overview of the distribution of species and individuals per site is given in Table 1.

The majority of arctiid moths could be identified to species (Total Arctiidae: 70.4% of species and 76.1% of individuals; Phaegopterini: 69.6 and 81.0%; Ctenuchini: 73.2 and 64.7%; Lithosiinae: 63.0 and 79.8%). The remaining moths were sorted and analyzed using a morphospecies approach.

Table 1: Number of arctiid moths (Arctiini, Pericopini, Phaegopterini, Ctenuchini, Lithosiinae) species (S) and individuals (N) at 21 sampling sites. S: species total; N: individuals total.

Site	S	Arctiini (S)	Pericopini (S)	Phaegopterini (S)	Ctenuchini (S)	Lithosiinae (S)	N	Arctiini (N)	Pericopini (N)	Phaegopterini (N)	Ctenuchini (N)	Lithosiinae (N)
A	119	4	3	49	30	33	646	10	9	120	161	346
B1	117	3	2	49	30	33	642	8	12	113	111	398
B2	109	2	2	48	30	27	374	7	12	81	79	195
C	62	0	0	29	18	15	204	0	0	49	49	106
D1	67	1	2	21	27	16	162	2	3	27	57	73
D2	71	1	1	23	22	24	163	1	1	35	59	67
E1	91	1	1	30	28	31	401	1	1	68	87	244
E2	124	2	3	47	34	38	561	2	11	123	181	244
F1	90	3	3	37	21	26	351	7	9	103	89	143
F2	123	3	2	51	29	38	830	10	11	131	179	499
G1	132	4	1	55	39	33	882	9	5	232	257	379
G2	124	2	2	47	41	32	721	5	3	124	213	376
H1	92	1	2	39	30	20	293	2	5	92	101	93
H2	121	3	3	47	37	31	558	7	8	110	156	277
I	156	6	5	63	43	39	929	28	16	243	261	381
3a	59	0	2	16	25	16	175	0	5	28	77	65
3b	59	0	0	25	21	13	153	0	0	35	60	58
4a	60	1	2	20	24	13	192	1	2	44	87	58
4b	90	1	2	29	32	26	354	1	9	74	156	114
5a	75	0	0	28	22	25	434	0	0	75	89	270
5b	49	1	0	25	13	10	186	1	0	86	51	48

A – F2 are early succession sites; G1 – I are later succession sites; 3a – 5b are mature forest understorey. All sites range between 1,800 and 2,005 m a.s.l.

Representation of the subfamily Lithosiinae and the tribes Phaegopterini, Arctiini, Pericopini and Ctenuchini in terms of species richness changed between the three habitat categories (two-way ANOVA; taxon: $F_{2,54} = 31.64$, $P<0.001$; habitat category: $F_{2,54} = 0.095$, $P=0.91$; interaction term: $F_{4,54} = 2.58$, $P<0.05$; Fig. 2a). Phaegopterini always accounted for the largest species share (37-40%), but slightly decreased towards more forested habitats. Ctenuchini had the second rank (28-35%) and tended to increase with forest recovery, whereas Lithosiinae were the third-richest group (25-29%) and tended to decrease. Arctiini and Pericopini occurred sparsely throughout. These differences were far more pronounced when considering the representation of higher taxa by individuals (two-way ANOVA; taxon: $F_{2,54} = 32.93$, $P<0.001$; habitat category: $F_{2,54} = 0.016$, $P=0.98$; interaction term: $F_{4,54} = 4.63$, $P<0.005$; Fig. 2b). The proportion of Phaegopterini remained largely unchanged (20-25%). However, the proportions of Ctenuchini (26-37%) increased, and those of Lithosiinae (38-51%) decreased, with forest recovery.

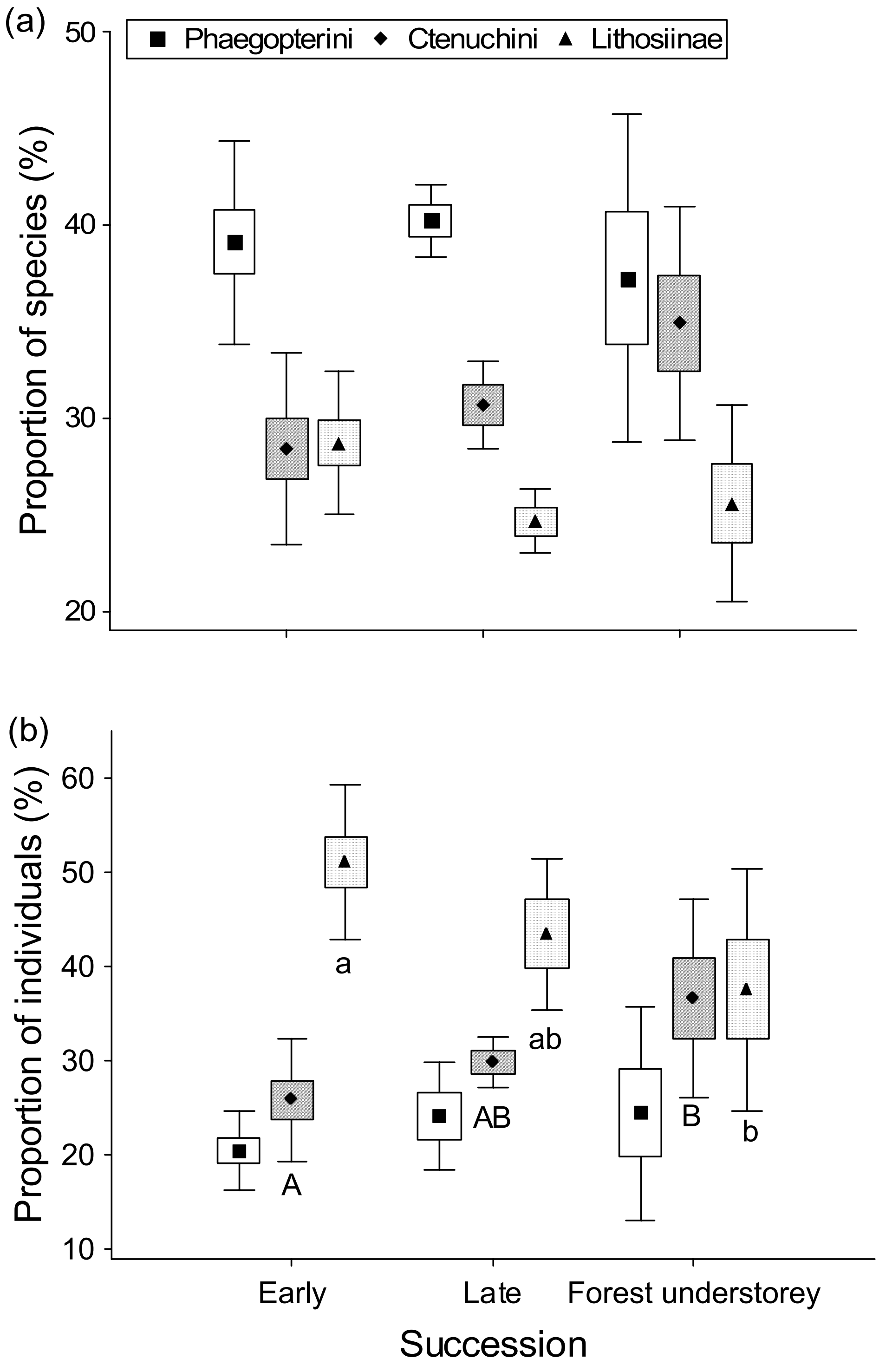


Figure 2: Relative proportions of one subfamily and two tribes of arctiid moths, based on species (a) and individual (b) numbers, in the three different habitat types. Boxes labelled with different letters differ significantly at *P*<0.05 (one-way ANOVA for each taxon followed by Scheffé test). Symbols = means, boxes = ± 1 SE, whiskers = ± 1 SD.

Local diversity

Species diversity of the entire family Arctiidae was high with a maximum in the later successional stages (mean α = 46.7; L: N=5) and a minimum in mature forest understorey (α = 30.5; chapter 2). When viewed separately at lower systematic levels, diversity (Fisher's alpha, mean ±1 SD) was highest among Phaegopterini (α = 26.9 ± 9.6, range 18.9-31.0), followed by Ctenuchini (α = 12.8 ± 3.1) and Lithosiinae (α = 8.3 ± 2.5). For Arctiini and Pericopini no values of Fisher's alpha could be calculated due to the small sample sizes.

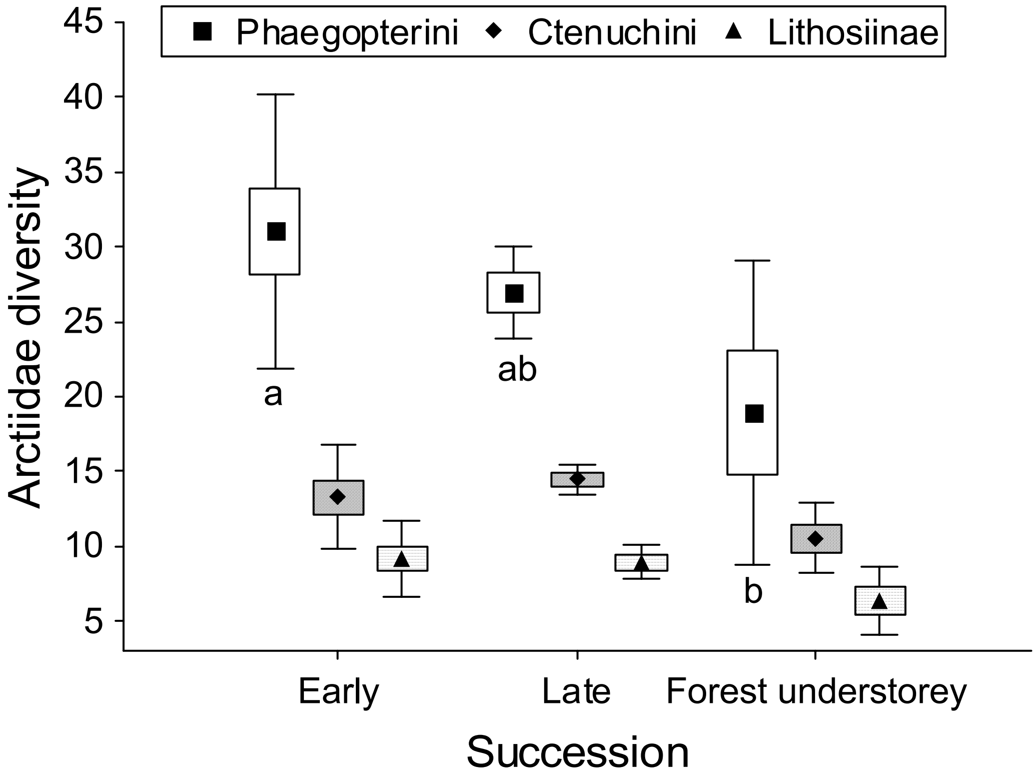


Figure 3: Diversity (Fisher's alpha) of arctiid moth subtaxa (Phaegopterini, Ctenuchini and Lithosiinae) in the three different habitat types. Boxes labelled with different letters differ significantly at *P*<0.05 (one-way ANOVA for each taxon followed by Scheffé test). Symbols = means, boxes = ± 1 SE, whiskers = ± 1 SD.

Fig. 3 illustrates the mean values of Fisher's alpha for Phaegopterini, Ctenuchini and Lithosiinae classified into the three habitat categories. Within Phaegopterini, diversity significantly decreased from early successional stages to mature forest understorey (one-way ANOVA: $F_{2,18} = 3.81$, $P<0.05$). Patterns for Ctenuchini and Lithosiinae were similar, but did not attain significance (Ctenuchini: $F_{2,18} = 3.00$, $P=0.075$; Lithosiinae $F_{2,18} = 3.12$, $P=0.069$). Alpha diversity at the family level correlated quite strongly with that at the subfamilial or tribal level, whereas among subordinated arctiid taxa a significant relationship in alpha diversity values was found only between Phaegopterini and Ctenuchini (Table 2).

Table 2: Correlation between alpha diversity of Arctiidae and various subordinated taxa. Significant correlations (FDR-corrected) are shown in bold. n.s.: *P*> 0.05. All *n* = 21.

	Lithosiinae	**Phaegopterini**	**Ctenuchini**
Arctiidae	***r* = 0.74** ***P*<0.001**	***r* = 0.63** ***P*<0.001**	***r* = 0.65** ***P*<0.001**
Lithosiinae		*r* = 0.15 n.s.	*r* = 0.21 n.s.
Phaegopterini			***r* = 0.68** ***P*<0.001**

Among Phaegopterini, Ctenuchini and Lithosiinae, dominance of the commonest species was higher in mature forest than at successional sites (Kruskal-Wallis ANOVA; Phaegopterini: H(2, N=21) = 2.79, $P>0.05$; Ctenuchini: H(2, N=21) = 6.63, $P<0.05$; Lithosiinae: H(2, N=21) = 13.15, $P<0.005$; Fig. 4a). Proportions of singletons differed strongly between taxa and much less so among habitat classes (two-way ANOVA; taxon: $F_{2,54} = 44.83$, $P<0.001$; habitat category: $F_{2,54} = 3.59$, $P<0.05$; interaction term: $F_{4,54} = 0.53$, $P=0.72$; Fig. 4b).

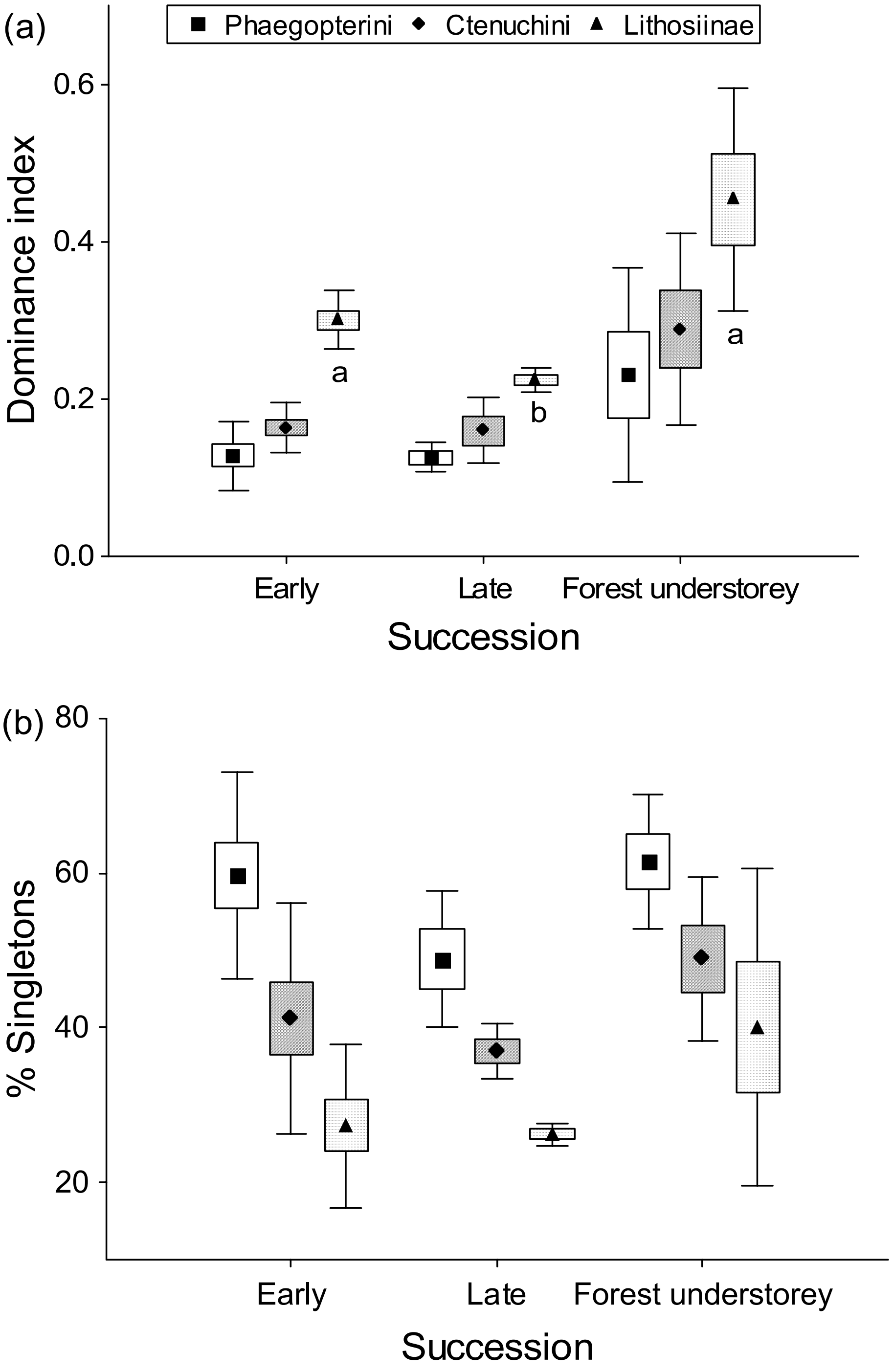


Figure 4: Berger-Parker index (a) and proportion of local singletons (in % of species) (b) for Phaegopterini, Ctenuchini and Lithosiinae in the three different habitat classes. Boxes labelled with different letters differ significantly at *P*<0.05 (Kruskal-Wallis ANOVA for each taxon followed by post hoc test). Symbols = means, boxes = ± 1 SE, whiskers = ± 1 SD.

Species composition

Ordinations generally revealed a significant segregation between moth ensembles of successional sites and the mature forest understorey for Phaegopterini, Ctenuchini and Lithosiinae (Figs. 5 and 6). However, ensembles of Ctenuchini showed a clear separation between early and later succession sites vs. mature forest understorey only, if rare species were weighted more strongly, i.e. at high *m* values. With $m = 1$, Ctenuchini ensembles from successional sites were placed between the mature forest understorey samples in the ordination. Analysis of similarity (ANOSIM) reveals that segregation of moth communities between successional sites and natural forest was in most cases statistically significant, whereas the two abandoned pastures could be separated only for the subordinated taxa with larger sample sizes and when emphasizing rare species (Table 3).

Table 3: Analysis of similarity (ANOSIM, with 1,000 permutations) for Phaegopterini, Ctenuchini and Lithosiinae ensembles compared between habitat types (E: early succession, L: late succession, P: pasture, F: mature forest understorey). Results are presented for CNESS distances with $m = 1$ and $m = m_{\text{optimal}}$. Only significant results after FDR-correction are shown.

	m value	habitat type	*r*	*P*
Phaegopterini	1	**E** vs. **F**	0.74	0.001
		L vs. **F**	0.48	0.006
	27	**E** vs. **F**	0.62	0.001
		L vs. **F**	0.35	0.009
		E vs. **P**	0.83	0.022
Ctenuchini	1	**E** vs. **F**	0.33	0.012
	10	**E** vs. **F**	0.55	0.002
		L vs. **F**	0.28	0.017
Lithosiinae	1	**E** vs. **L**	0.58	0.001
		E vs. **F**	0.41	0.001
		L vs. **F**	0.62	0.002
	18	**E** vs. **F**	0.53	0.001
		E vs. **L**	0.45	0.002
		L vs. **F**	0.54	0.004
		E vs. **P**	0.88	0.022

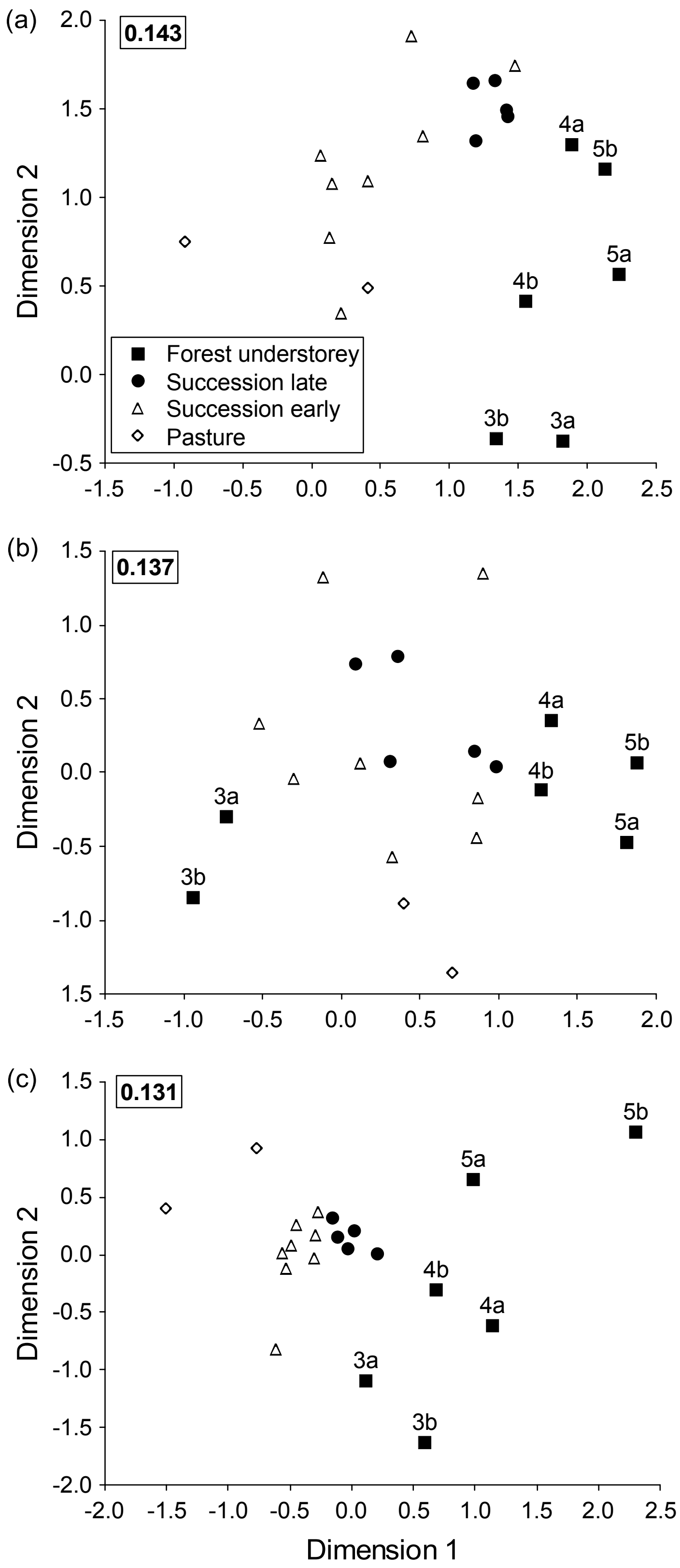


Figure 5: Nonlinear two-dimensional scaling plots of the CNESS dissimilarity matrix for Phaegopterini (a), Ctenuchini (b) and Lithosiinae (c) with sample-size parameter *m* = 1 for all 21 sites. Stress values of ordinations are given as insets in boxes.

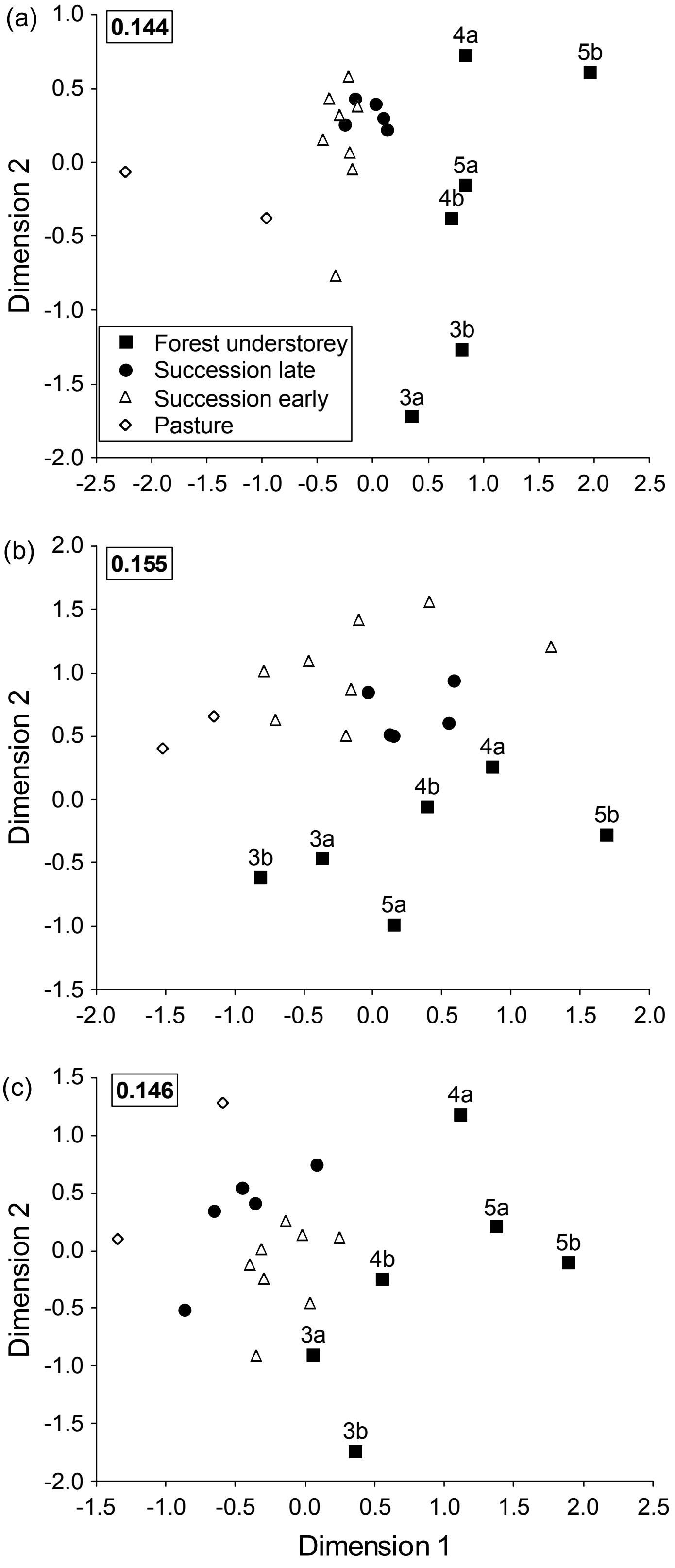


Figure 6: Nonlinear two-dimensional scaling plots of the CNESS dissimilarity matrix for Phaegopterini [$m_{optimal}$ = 27] (a), Ctenuchini [$m_{optimal}$ = 10] (b) and Lithosiinae [$m_{optimal}$ = 18] (c). Stress values of ordinations are given in boxes.

Rank-based matrix correlation tests revealed significant relationships between faunal dissimilarity and the degree of habitat openness as well as elevation (Euclidean distances) for almost every *m* value (Table 4). Differences in habitat openness always correlated much more strongly with faunal differentiation than did differences in habitat elevation. Faunal dissimilarity was not at all related to the geographic distance between sampling sites, nor to the air temperature during sampling (all $r<0.14$, $P>0.1$, data not shown).

Table 4: Matrix rank correlations *r* (based on Spearman coefficients, 1,000 random permutations) between faunal dissimilarity (CNESS distances) and distance matrices for habitat openness, elevation and geographic position. For environmental variables, Euclidean distances between sites are used.

Taxon	Sample size parameter *m*	Habitat openness	Elevation	Geographic position
Phaegopterini	1	0.45**	0.25*	0.03 n.s.
	27	0.50**	0.28*	-0.18 n.s.
Ctenuchini	1	0.32*	0.21*	-0.14 n.s.
	10	0.50**	0.26*	-0.10 n.s.
Lithosiinae	1	0.29*	0.13 n.s.	0.19 n.s.
	18	0.53**	0.33**	-0.03 n.s.

n.s., not significant; * $P<0.05$; ** $P<0.005$. All results remain significant after FDR correction.

Patterns of faunal differentiation were significantly more similar between Phaegopterini, Ctenuchini and Lithosiinae at high *m* values (Table 5), while relationships were much less similar when emphasizing the dominant moth species.

Table 5: Matrix rank correlations *r* (based on Spearman coefficients, 1,000 random permutations) between the faunal dissimilarity (CNESS distances) of the three subordinated arctiid moth taxa and for different *m* values.

	Ctenuchini	Lithosiinae	Arctiidae
$m = 1$			
Phaegopterini	0.50**	0.32*	0.52**
Ctenuchini		0.16 n.s.	0.43**
Lithosiinae			0.69**
$m = m_{opt}$			
Phaegopterini m=27	0.70**	0.70**	0.76**
Ctenuchini m=10		0.59**	0.80**
Lithosiinae m=18			0.84**

n.s., not significant; * $P<0.05$; ** $P<0.005$. All results remain significant after FDR correction.

For Phaegopterini and Lithosiinae the first ordination axis depicted the successional gradient, whereas the second ordination axis correlated with habitat elevation (Table 6). This pattern was observed with high and low values of the sample size parameter *m*. For Ctenuchini, ecological correlates of the ordination axes were less distinct. At *m* = 1 the first axis depicted elevational divergence, whereas at *m* = 24 both ordination axes correlated with the successional gradient.

Table 6: Pearson's correlation coefficients between the axis scores of arctiid samples extracted from two-dimensional NMDS ordinations and different environmental factors. *m* - Sample size parameter of the CNESS index; DIM - dimension of ordination.

	Axis	Altitude	Temperature	Habitat openness	Distance from forest	Degree of succession
Phaegopterini *m* = 1	DIM1	-0.27 n.s.	-0.41 n.s.	0.76***	0.81***	-0.84***
	DIM2	-0.54*	0.51*	-0.39 n.s.	0.08 n.s.	0.23 n.s.
Phaegopterini *m* = 27	DIM1	-0.18 n.s.	*-0.47**	0.82***	0.80***	-0.67***
	DIM2	0.55*	*-0.45**	0.25 n.s.	-0.03 n.s.	-0.12 n.s.
Ctenuchini *m* = 1	DIM1	-0.59*	-0.06 n.s.	0.28 n.s.	0.13 n.s.	-0.13 n.s.
	DIM2	0.01 n.s.	0.15 n.s.	0.04 n.s.	0.32 n.s.	-0.06 n.s.
Ctenuchini *m* = 10	DIM1	-0.24 n.s.	-0.13 n.s.	0.50*	0.54*	-0.41 n.s.
	DIM2	0.11 n.s.	0.67***	-0.74***	-0.42 n.s.	0.67***
Lithosiinae *m* = 1	DIM1	0.30 n.s.	*0.49**	-0.86***	-0.72***	0.76***
	DIM2	0.83***	-0.42 n.s.	0.30 n.s.	0.32 n.s.	-0.21 n.s.
Lithosiinae *m* = 18	DIM1	0.34 n.s.	0.37 n.s.	-0.75***	-0.62**	0.49*
	DIM2	0.48*	-0.48*	0.26 n.s.	0.23 n.s.	-0.04 n.s.

n.s., not significant; * *P*<0.05; ** *P*<0.005; *** *P*<0.001. Results printed in italics are not significant after FDR-correction.

3.5 Discussion

Proportional contributions of subfamilies and tribes

Proportions of higher arctiid taxa changed distinctly along the successional gradient in the montane forest zone of southern Ecuador. Ctenuchini contributed more strongly to ensembles in natural forest, whereas Lithosiinae decreased with forest recovery. These observations can be linked to life-history characters of both moth groups. Many Ctenuchini larvae are host plant specialists (e.g. on Apocynaceae plants that contain pyrrolizidine alkaloids (PAs): Kitching & Rawlins, 1999; Holloway *et al.*, 2001), and adult moths are often pharmacophagous on PA plants as well (Boppré, 1995; Häuser & Boppré, 1997; Kreusel & Häuser, 1998). Natural candidate PA sources in the study area (*Mesechites*, *Pelastes*, *Mandevilla* (Apocynaceae); *Tournefortia* (Boraginaceae), *Eupatorium* (Asteraceae); *Crotalaria* (Fabaceae): J. Homeier & S. Matezki, pers. comm.; http://www.visualplants.de/) occur predominantly in the forest and are less prevalent at open sites. Most Ctenuchini are also small and delicate (Kreusel & Häuser, 1998), which suggests that their dispersal capacities are limited. Lithosiinae larvae are suspected to feed, at least in part, on lichens (Jacobson & Weller, 2002), which grow abundantly already in early succession stages of tropical montane habitats. Hence their numerical prevalence at disturbed sites is not surprising.

Species of the large tribe Phaegopterini, in contrast, are more frequently polyphagous as larva, and the adult moths of many species are robust good flyers (Kitching & Rawlins, 1999; Solis & Pogue, 1999). Representatives of this clade were almost equally prevalent across the succession gradient. Thus, the changes in relative contributions of arctiid subtaxa to the local communities can at least partially be explained by characters of larval host plant use and adult dispersal capacity.

Local diversity

Arctiid species diversity was high in all habitats sampled, but the three larger subordinated taxa contributed differentially to this diversity. Phaegopterini were always the most diverse clade. Their local diversity clearly declined from the early successional stages to the forest sites. Studies on Old World Arctiinae revealed similar results. There, Arctiinae moths are particularly abundant at more disturbed sites and are usually thought of as species associated with ruderal situations, with larvae feeding on a wide range of herbaceous species. Also they are likely to have wider host-plant ranges and may not even be forest species as such (Holloway, 1998; Kitching *et al.*, 2000; Ricketts *et al.*, 2001). Ctenuchini and Lithosiinae always had a lower local diversity and showed much less marked changes of species diversity along the successional gradient. Notably, their diversity also did not increase with forest recovery.

In recent years, many authors have proposed that the diversity of entire species-rich groups can be estimated by sampling a subset of the fauna that is easily collected and readily identifiable (biodiversity indicators or ‘focal taxa’: Beccaloni & Gaston, 1995; Schulze *et al.*, 2004; Summerville *et al.*, 2004). In our data set, however, correlations between diversity measures of subordinated taxa, or between the entire family and subordinated taxa, were rather low. Lithosiinae are particularly poor predictors of Ctenuchini or Phaegopterini diversity, even though they correlate quite well with the diversity of the total Arctiidae. Overall, these results leave little scope for the use of small manageable subsets of Neotropical arctiid moths as diversity indicators for this large, prominent moth family in Andean habitats (Brehm & Fiedler, 2003).

Changes in community structure and species composition

Contrary to expectation, the highest dominance values of individual species were found in the mature forest sites for all three taxa (Phaegopterini, Ctenuchini and Lithosiinae). Moreover, dominance values were generally high comparable with other tropical moth communities (e.g. geometrid moths in the same study area: Brehm, 2002). High dominance of few species is often viewed as an effect of anthropogenic habitat disturbance (e.g. Beck *et al.*, 2002), but recent studies have called this generalization into question (Nummelin & Kaitala, 2004). Apparently, a few arctiid moth species find particularly suitable habitat conditions in natural montane forests, which allow them to attain higher relative abundances than do these same species or other ‘pioneer species’ at disturbed sites.

Insect samples from tropical rainforests usually contain large numbers of rare species (Novotny & Basset, 2000). While this was true also for the family Arctiidae as a whole (chapter 2), the pattern was remarkably different at lower systematic levels. Singletons were most prevalent among robust Phaegopterini, and much less numerous among smaller sized and more slender-built Ctenuchini and Lithosiinae. We suggest that the flight capacity of the adult moths might explain much of the incidence of singletons in our data. Among the Phaegopterini, activity ranges are likely to be larger (Kitching *et al.*, 2000), which would increase the likelihood of sampling dispersing or ‘tourist’ individuals. Differences between habitat types with regard to the proportion of singletons were much smaller for all three taxa. Hence, the progress of succession had little impact on the numerical contribution of such rare species to local moth samples.

Ordinations and subsequent statistical analyses revealed a significant segregation between ensembles of successional sites and the mature forest understorey for all three larger subordinated arctiid moth taxa. Thus, despite smaller sample sizes (Phaegopterini: 135 spp., 1,998 individuals; Ctenuchini: 82 spp., 2,555 ind.; Lithosiinae: 54 spp., 4,434 ind.) these subsets of data were sufficient to recover the same patterns of faunal differentiation across the successional gradient as found at the family level (chapter 2). Ecological patterns became more distinct in the Phaegopterini when using higher *m* values for calculating CNESS distances, i.e. when giving more emphasis to less abundant species. This underscores that in tropical insect communities, with their many rare species; much relevant information is often contained in these rare taxa (chapter 2). Similar conclusions were drawn by Brehm and Fiedler (2004) for geometrid moths from an extended elevational gradient in the same study area. In contrast, emphasis on rare species did not yield much additional information for the segregation of Lithosiinae ensembles.

Phaegopterini and Lithosiinae ensembles responded sensitively to habitat changes related to the progress of forest recovery (habitat openness, degree of succession, and distances of the sites from natural forest), whereas elevational effects (in the narrow belt covered by our sampling design) were minor.

Patterns of faunal change were less distinct among Ctenuchini. When emphasizing dominant species, there was not even a clear distinction between Ctenuchini ensembles from forest and successional habitats, respectively. This is not surprising; since the same two species dominated at all sites. Yet, when accentuating rare species, Ctenuchini samples did show a clear split into successional stages vs. mature forest, but neither reflected the stage of succession more precisely, nor was there a pronounced segregation between abandoned pastures and other successional sites. This suggests that there are only a few species of Ctenuchini that are abundant and behave as relative habitat generalists in the study area, whereas most wasp moths occur at generally low abundances and appear to be forest specialists.

Phaegopterini, Ctenuchini and Lithosiinae differ from each other in many ecological and life-history characters and their proportional contributions to local arctiid ensembles changed accordingly. Nevertheless, patterns of faunal change were significantly correlated across these taxa. This indicates that the mode of species turnover along the succession gradient is to some degree concordant between the taxa, but correlations are not particularly close and partly lacking when dominant species are emphasized. Thus, as with correlations of alpha-diversity between subordinated arctiid taxa, the pattern of species turnover also does not allow us to make strong inferences from one group to the next. This again undermines the applicability of the use of biodiversity indicators in the case of Neotropical arctiid moths.

In our analyses, only habitat openness, degree of succession, the distance of sites from natural forest, or elevation and temperature were significantly associated with species turnover between sites; all these factors are strongly interrelated with each other. Other studies have also shown that distance between study sites may affect faunal turnover. For example, species turnover of litter beetles and ants with distance explained a small, but significant part of the variance in species distributions among fragmented forest remnants in Amazonia (Basset *et al.*, 2001). Arctiid moths are more mobile than litter beetles and ants, and spatial autocorrelation is more likely to occur in less dispersive organisms. On the other hand, despite their dispersal capacities, patterns in arctiid moth communities along the successional gradient were strong and significant. Hence, these patterns reflect shaping of moth communities by local ecological factors and are obviously not swamped by massive dispersal.

Many environmental factors concomitantly change along successional gradients. In the absence of a forest canopy, the microclimatic conditions are significantly altered, resulting in higher insolation, lower humidity, more rapid temperature decrease after sunset and generally a higher variance of microclimatic parameters (Murcia, 1995; Basset *et al.*, 2001; Toral *et al.*, 2002). We cannot presently assess which of these factors are primarily responsible for the observed changes in faunal composition. Much more life-history information on individual species will be required to establish causal links between observed responses and specific predictor variables.

Although there was substantial species turnover along the successional gradient, a considerable fraction of species occurred in natural forest as well as at successional sites. For the entire family Arctiidae, 49% of the species were shared. The respective figures for subordinated taxa were 45% in Phaegopterini, 50% in Ctenuchini, and 61% in Lithosiinae (N. Hilt & K. Fiedler, unpublished). The intact forest provides a reservoir of species with the potential to spread into adjacent successional sites and exploit suitable resources at the fine spatial scale of our study. Davis (1993) found the same result for dung beetles in Sabah (Malaysia), where species of primary forest overlapped spatially with species of disturbed sites. Large blocks of primary forest in close proximity to disturbed sites may act initially as a refuge and later as a source for populations (Willot, 1999). Even strongly modified habitat remnants, such as secondary forest, contain significant fractions of regional biodiversity and therefore have important value as sources for recolonization of disturbed habitats (Kitching *et al.*, 2000; Schulze, 2000). This also applies to the arctiid moths in the landscape mosaic around Podocarpus National Park in southern

Ecuador, where we observed diverse, but distinct moth communities in successional habitats in close proximity to remaining montane forest.

In conclusion, despite the small distances between the habitats studied here, and the substantial dispersal movements of mobile moths (Ricketts *et al.*, 2001), local ecological processes were strong enough to allow for a differentiation between arctiid ensembles from mature forest and anthropogenically disturbed sites. However, even though strong ecological differentiation exists between the major clades within the Neotropical Arctiidae (mostly Phaegopterini, Ctenuchini, and Lithosiinae), the responses of these taxa in the successional gradient surprisingly revealed more parallels than differences.

Acknowledgements

We thank Dirk Süßenbach who provided data on his samples from the natural forest. Gunnar Brehm, Doreen Fetting, Claudia Ramenda, Anne Walter, Katja Temnow, Anna Spengler, Georg Petschenka, Annick Servant and Caroline Schulze (all at University of Bayreuth) helped with sampling and processing moths. Giovanni Onore (Pontificia Universidad Católica del Ecuador, Quito) and Christoph L. Häuser (Staatliches Museum für Naturkunde, Stuttgart) supported the project logistically. Martin R. Honey and Linda M. Pitkin (Natural History Museum, London) and Axel Hausmann (Zoologische Staatssammlung, Munich) provided access to reference collections under their care. Suzanne Rab-Green (American Museum of Natural History, New York) and Benoît Vincent (Paris) kindly identified some species. Matthias Oesker (Bielefeld) assisted with measuring canopy closure, Gunnar Brehm for the general map from Ecuador, and Stefan Dötterl determined optimal m values. Special thanks go to John Sloggett, Klaus Fischer, Gunnar Brehm, Phil DeVries and one anonymous reviewer for helpful comments on this manuscript. The Ministerio del Medio Ambiente in Ecuador issued research permits (Nro. 002-PNP-DBAP-RLZCH/MA), and the foundation Nature and Culture International (Loja, Ecuador) allowed access to the study sites and their facilities. The Deutsche

Forschungsgemeinschaft financed our work (FOR 402/1-1 TP15, FOR 402/2-1 TP A3).

3.6 References

Axmacher, J.C., Holtmann, G., Scheuermann, L., Brehm, G., Müller-Hohenstein, K. & Fiedler, K. (2004a) Diversity of geometrid moths (Lepidoptera: Geometridae) along an Afrotropical elevational rainforest transect. *Diversity and Distributions*, **10**, 293-302.

Axmacher, J.C., Tünte, H., Schrumpf, M., Müller-Hohenstein, K., Lyaruu, H.V.M. & Fiedler, K. (2004b) Diverging diversity dynamics of vascular plants and moths during forest regeneration on Mt. Kilimanjaro, Tanzania. *Journal of Biogeography*, **31**, 895-904.

Basset, Y., Charles, E., Hammond, D.S. & Brown, V.K. (2001) Short-term effects of canopy openness on insect herbivores in a rain forest in Guyana. *Journal of Applied Ecology*, **38**, 1045-1058.

Basset, Y., Novotny, V., Miller, S.E. & Springate, N.D. (1998) Assessing the impact of forest disturbance on tropical invertebrates: some comments. *Journal of Applied Ecology*, **35**, 461-466.

Beccaloni, G.W. & Gaston, K.J. (1995) Predicting the species richness of Neotropical forest butterflies: Ithomiinae (Lepidoptera: Nymphalidae) as indicators. *Biological Conservation*, **71**, 77-86.

Beck, J., Schulze, C.H., Linsenmair, K.E. & Fiedler, K. (2002) From forest to farmland: diversity of geometrid moths along two habitat gradients on Borneo. *Journal of Tropical Ecology*, **17**, 33-51.

Bendix, J. & Lauer, W. (1992) Die Niederschlagsjahreszeiten in Ecuador und ihre klimadynamische Interpretation. *Erdkunde,* **46**, 118-134.

Benjamini, Y. & Hochberg, Y. (1995) Controlling the false discovery rate: a pratical and powerful approach to multiple testing. *Journal of the Royal Statistical Society*, B **57**, 289-300.

Boesch, D.F. (1977) Application of numerical classification in ecological investigations of water pollution. *Special Scientific Report*, Institute of Marine Science, Virginia.

Boppré, M. (1995) Pharmakophagie: Drogen, Sex und Schmetterlinge. *Biologie in unserer Zeit*, **25**, 8-17.

Brehm, G. (2002) *Diversity of geometrid moths in a montane rainforest in Ecuador.* Ph.D. thesis, University of Bayreuth. URL: http://opus.ub.uni-bayreuth.de/volltexte/2003/20/

Brehm, G. & Fiedler, K. (2003) Faunal composition of geometrid moths changes with altitude in an Andean montane rain forest. *Journal of Biogeography*, **30**, 431-440.

Brehm, G. & Fiedler, K. (2004) Ordinating tropical moth ensembles from an elevational gradient: a comparison of common methods. *Journal of Tropical Ecology*, **20**, 165-172.

Brehm, G. & Fiedler, K. (2005) Diversity and community structure of geometrid moths of disturbed habitat in a montane area in the Ecuadorian Andes. *Journal of Research on the Lepidoptera*, **38**, 1-14.

Brehm, G., Homeier, J. & Fiedler, K. (2003a) Beta diversity of geometrid moths (Lepidoptera: Geometridae) in an Andean montane rainforest. *Diversity and Distributions*, **9**, 351-366.

Brehm, G., Süssenbach, D. & Fiedler, K. (2003b) Unique elevational diversity patterns of geometrid moths in an Andean montane rainforest. *Ecography*, **26**, 456-466.

Brühl, C.A., Mohamed, M. & Linsenmair, K.E. (1999) Altitudinal distribution of leaf litter ants along a transect in primary forest on Mount Kinabalu, Sabah, Malaysia. *Journal of Tropical Ecology*, **15**, 265-277.

Chey, V.K., Holloway, J.D. & Speight, M.R. (1997) Diversity of moths in forest plantations and natural forests in Sabah. *Bulletin of Entomological Research*, **87**, 371-385.

Clarke, K.R. (1993) Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, **18**, 117-143.

Clarke, K.R. & Warwick, R.M. (2001) *Change in marine communities: an approach to statistical analysis and interpretation*. 2nd edition: Primer-E, Plymouth, UK, 172 pp.

Davis, A.J. (1993) *The ecology and behaviour of rainforest dung beetles in Northern Borneo*. Ph.D. thesis. University of Leeds.

Davis, A.L.V., Scholtz, C.H. & Chown, S.L. (1999) Species turnover, community boundaries and biogeographical composition of dung beetle assemblages across an altitudinal gradient in South Africa. *Journal of Biogeography*, **26**, 1039-1055.

Delta, T. & Devices (1999) *Hemiview Canopy Analysis* Software, Version 2.1. Burwell, Cambridge.

Fiedler, K. & Schulze, C.H. (2004) Forest modification affects diversity (but not dynamics) of speciose tropical pyraloid moth communities. *Biotropica*, **36**, 615-627.

Gotelli, N.J. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**, 379-391.

Hamer, K.C. & Hill , J.K. (2000) Scale-dependent effects of habitat disturbance on species richness in tropical forests. *Conservation Biology*, **14**, 1435-1440.

Hartig, K. & Beck, E. (2003) The bracken fern (Pteridium arachnoideum (Kaulf.) Maxon) dilemma in the Andes of Southern Ecuador. *Ecotropica*, **9**, 3-13.

Häuser, C.L. & Boppré, M. (1997) Pyrrolizidine alkaloid-related pharmacophagy in neotropical moths (Lepidoptera). In: *Tropical biodiversity and systematic. Proceedings of the International Symposium on Biodiversity and Systematics in Tropical Ecosystems*, Bonn, 1994 (ed. H. Ulrich), pp. 291-296. Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn.

Henderson, P.A. & Seaby, R.M.H. (1998) *Species diversity and richness*. Version 2.62. Pennington: Pisces Conservation Ltd.

Hill, J.K. & Hamer, K.C. (2004) Determining impacts of habitat modification on diversity of tropical forest fauna: the importance of spatial scale. *Journal of Applied Ecology*, **41**, 744-754.

Holloway, J.D. (1998) The impact of traditional and modern cultivation practices, including forestry, on Lepidoptera diversity in Malaysia and Indonesia. In: *Dynamics of Tropical Communities* (eds. D.M. Newbery, H.H.T. Prins and N.D. Brown), pp. 567-597. The 37th Symposium of The British Ecological Society, London.

Holloway, J.D., Kibby, G. & Peggie, D. (2001) *The families of Malesian Moths and Butterflies*. Fauna Malesiana Handbooks. Brill, Leiden.

Homeier, J., Dalitz, H. & Breckle, S.-W. (2002) Waldstruktur und Baumartendiversität im montanen Regenwald der Estación Científica San Francisco in Südecuador. *Berichte der Reinhold-Tüxen-Gesellschaft*, **14**, 109-118.

Jackson, D.A. & Somers, K.M. (1991) Putting things in order: the ups and downs of detrended correspondence analysis. *American Naturalist*, **137**, 704-712.

Jacobson, N.L. & Weller, S.J. (2002) *A cladistic study of the Arctiidae (Lepidoptera) by using characters of immatures and adults*. Thomas Say Publications in Entomology: Monographs. Lanham, Maryland: Entomological Society of America. 98 pp.

Kitching, R.L., Orr, A.G., Thalib, L., Mitchell, H., Hopkins, M.S. & Graham, A.W. (2000) Moth assemblages as indicators of environmental quality in remnants of upland Australian rain forest. *Journal of Applied Ecology*, **37**, 284-297.

Kitching, I.J. & Rawlins, J.E. (1999) The Noctuoidea. In: *Handbook of Zoology. Lepidoptera, Moths and Butterflies, vol. 1* (ed. N.P. Kristensen), pp. 355-401. Berlin, New York, Walter de Gruyter.

Kreusel, B. & Häuser, C.L. (1998) Morphological diversity of the tympanal organ in Wasp Moths (Arctiidae: Ctenuchinae) and its systematic importance. *Memoires de la Societe Royale Belge d'Entomologie*, **38**, 13-23.

McCain, C.M. (2004) The mid-domain effect applied to elevational gradients: species richness of small mammals in Costa Rica. *Journal of Biogeography*, **31**, 19-31.

McGeachie, W.J. (1989) The effects of moonlight illuminance, temperature and wind speed on light-trap catches of moths. *Bulletin of Entomological Research*, **79**, 185-192.

Murcia, C. (1995) Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution*, **10**, 58-62.

Novotny, V. & Basset, Y. (2000) Rare species in communities of tropical insect herbivores: pondering the mystery of singletons. *Oikos*, **89**, 564-572.

Nummelin, M. & Kaitala, S. (2004) Do species dominance indices indicate rain forest disturbance by logging? *Biotropica*, **36**, 628-632.

Paulsch, A. (2002) *Development and application of a classification system for undisturbed and disturbed tropical montane forest based on vegetation structure.* Ph.D. thesis, University of Bayreuth. URL: http://opus.ub.uni-bayreuth.de/volltexte/2002/1/

Paulsch, A., Schneider, R. & Hartig, K. (2001) Land-use induced vegetation structure in a mountain region of South Ecuador. *Die Erde*, **132**, 93-102.

Piñas Rubio, F.S.J. & Manzano, I. (1997) *Mariposas del Ecuador. Vol. 1 Géneros*. Quito, Ecuador: Pontificia Universidad Católica del Ecuador.

Piñas Rubio, F.S.J. & Manzano, I. (2003) *Mariposas del Ecuador. Vol. 21b. Arctiidae. Subfamilia: Ctenuchinae*. Quito, Ecuador: Compañía de Jesús.

Piñas Rubio, F.S.J., Raab-Green, S., Onore, G. & Manzano, I. (2000) *Mariposas del Ecuador. Butterflies & Moths of Ecuador. Vol. 20: Familiy: Arctiiade*. Quito, Ecuador: Pontificia Universidad Católica del Ecuador.

Rahbek, C. (2005) The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters*, **8**, 224-239.

Richter, M. (2003) Using epiphytes and soil temperatures for eco-climate interpretations in southern Ecuador. *Erdkunde*, **57**, 161-181.

Ricketts, T.H., Daily, G.C., Ehrlich, P.R. & Fay, J.P. (2001) Countryside biogeography of moths in a fragmented landscape: biodiversity in native and agricultural habitats. *Conservation Biology*, **15**, 378-388.

Schulze, C.H. (2000) *Auswirkungen anthropogener Störungen auf die Diversität von Herbivoren – Analyse von Nachtfalterzönosen entlang von Habitatgradienten in Ost-Malaysia*. Ph.D. thesis, University of Bayreuth, Bayreuth.

Schulze, C.H. & Fiedler, K. (2003) Vertical and temporal diversity of a species-rich moth taxon in Borneo. In: *Arthropods of tropical forests: spatio-temporal dynamics and resource use in the canopy* (eds. Y. Basset, V. Novotny, S. Miller and R.L. Kitching), pp. 69-85. Cambridge University Press, Cambridge.

Schulze, C.H., Waltert, M., Kessler, P.J.A., Pitopang, R., Shahabuddin, Veddeler, D., Mühlenberg, M., Gradstein, S.R., Leuschner, C., Steffan-Dewenter, I. & Tscharntke, T. (2004) Biodiversity indicator groups of tropical land-use systems: comparing plants, birds, and insects. *Ecological Applications*, **14**, 1321–1333.

Scoble, M.J. (1992) *The Lepidoptera: Form, Function, and Diversity*. Oxford University Press, Oxford, UK. 404 pp.

Shepard, R.N. (1974) The analysis of proximities: multidimensional scaling with an unknown distance function. *Psychometrika*, **39**, 373-421.

Solis, M.A. & Pogue, M.G. (1999) Lepidopteran biodiversity: patterns and estimators. *American Entomologist*, **45**, 206-212.

Southwood, T.R.E. & Henderson, P.A. (2000) Ecological methods, Blackwell Science Publishers, Oxford.

Süßenbach, D. (2003) *Diversität von Nachtfaltergemeinschaften entlang eines Höhengradienten in Südecuador (Lepidoptera: Pyraloidea, Arctiidae)*. Ph.D. thesis, University of Bayreuth. URL: http://opus.ub.uni-bayreuth.de/volltexte/2003/33/

StatSoft (2004) STATISTICA for Windows, Version 6.0. www.statsoft.com

Summerville, K.S., Ritter, L.M. & Crist, T.O. (2004) Forest moth taxa as indicators of lepidopteran richness and habitat disturbance: a preliminary assessment. *Biological Conservation*, **116**, 9-18.

Thomas, A.W. & Thomas, G.M. (1994) Sampling strategies for estimating moth species diversity using a light trap in a northeastern softwood forest. *Journal of the Lepidopterists' Society*, **48**, 85-105.

Toral, E.C., Feinsinger, P. & Crump, M.L. (2002) Frogs and a cloud-forest edge in Ecuador. *Conservation Biology*, **16**, 735-744.

Trueblood, D.D., Gallagher, E.D. & Gould, D.M. (1994) Three stages of seasonal succession on the Savin Hill Cove mudflat, Boston Harbor. *Limnology and Oceanography*, **39**, 1440-1454.

Tscharntke, T., Steffan-Dewenter, I., Kruess, A. & Thies, C. (2002) Characteristics of insect populations on habitat fragments: A mini review. *Ecological Research*, **17**, 229-239.

Watson, A. & Goodger, D.T. (1986) Catalogue of the Neotropical tiger-moths. *Occasional Papers on Systematic Entomology*, **1**, 1-71.

Willot, S.J. (1999) The effects of selective logging on the distribution of moths in a Bornean rainforest. *Philosophical Transactions of the Royal Society London* B, **354**, 1783-1790.

Zapata, F.A., Gaston, K.J. & Chown, S.L. (2003) Mid-domain models of species richness gradients: assumptions, methods and evidence. *Journal of Animal Ecology*, **72**, 677-690.

4 Morphological traits of arctiid moths along a succession gradient in southern montane Ecuador: clades differ more than habitats

Nadine Hilt[*, 1], Konrad Fiedler[2]

[1] Department of Animal Ecology I, Universitätsstraße 30, University of Bayreuth, D-95440 Bayreuth, Germany

[2] Department of Population Ecology, Faculty Centre of Ecology, University of Vienna, Althanstrasse 14, A-1090 Vienna, Austria

[*] Correspondence: Nadine Hilt, Department of Animal Ecology I, University of Bayreuth, Germany. E-mail: nadine.hilt@uni-bayreuth.de or n-hilt@gmx.de

4.1 Abstract

Body size, flight-related traits, proboscis length and external appearance of arctiid moths were examined along a succession gradient in southern Ecuador. Forewing length, body length, wing surface area, wing load, and aspect ratio all showed strong taxon specific variation. However, arctiid species did not differ consistently in any body-size related traits along the succession gradient. Only analyses on subfamily/tribe level, and individual rather than species-based comparisons, revealed subtle differences in size distributions along the succession gradient. Arctiids with reduced proboscis overall constituted a minority (8.4% of species, 5.3% of individuals), but occurred twice as frequently at succession sites than in mature forest understorey. We scored all 287 species according to their external appearance as either cryptic (dull or unicoloured wing colours: 49.5% of species) or aposematic (brightly coloured wings and/or abdomen: 39.7%; Hymenoptera mimicry: 6.6%; metallic shine:

4.2%). Overall the relative incidence of aposematism in arctiid moths did not change along the succession gradient. However, such patterns became apparent at lower systematic levels: Aposematic species and especially individuals among Phaegopterini and Lithosiinae were more prevalent at succession sites, whereas Ctenuchini showed the reverse pattern. Collectively, variation in morphological traits related to dispersal (size, wing load) or the strength of biotic interactions (uptake of nectar, aposematism, mimicry) was much greater between arctiid clades than between habitats.

Keywords: aposematism, Arctiidae, body size, external appearance, proboscis length, succession gradient, wing characters

4.2 Introduction

Variation in morphological traits of organisms is shaped by natural selection (i.e. adaptation to given environments) and historical legacy (i.e. phylogenetic constraints that limit the scope of evolutionary change possible within groundplans). Community-wide multispecies comparisons between habitats with different environmental conditions allow for assessing the relative strength of these two opposing forces on certain traits. If actual ecological effects dominate, this should result in clear predictable shifts of trait distributions. In contrast, if phylogenetic constraints are more prevalent, then communities from different habitats should share common trait distributions. We here address if and how a set of morphological traits varies along a tropical successional gradient in a very speciose insect ensemble. We selected the moth family Arctiidae as a target for that analysis, since species of this group display a startling diversity of trait combinations (Kitching & Rawlins, 1999). Arctiid body size ranges from small to large, wing shapes and colour patterns are highly variable, and there is tremendous variation as to the importance of adult resource requirements.

In macroecological studies, body size distributions are often used to characterize and compare communities in response to the influence of abiotic or biotic factors (Blackburn *et al.*, 1990; Lawton, 1991). Studies, which explore relationships between different disturbance intensity and body size, found generally a decrease in body size in the more acutely disturbed areas (see Braun *et al.*, 2004).

For insects capable of flight, wing morphology and the relationship between wing size, wing shape and body mass essentially determine maneuverability, strength of flight, and thus dispersal capacity (Chai & Srygley, 1990; Hall & Willmott, 2000; Malmqvist, 2000; Rydell & Lancaster, 2000; Braun *et al.*, 2004). Frequently, traits such as wing load or aspect ratio that can be derived from morphometric data are used as proxies to compare communities, species or populations with regard to flight-related issues, since such data are easier to obtain than direct physiological measures of flight performance (Kutsch *et al.*, 2002; see Agosta & Janzen, 2005). Recent studies in the Lepidoptera, for example, revealed that even on the level of populations and individuals slight variation in such characters can occur that have a direct meaning with regard to dispersal capacity or flight behaviour (Gaston, 1994; Thomas *et al.*, 1998; Siemann *et al.*, 1999; Braun *et al.*, 2004). One should therefore expect that recolonisation processes in the course of succession after habitat disturbance might result in changes of the frequency distribution of body size or flight-related traits on the community level. For example, species with morphological traits related to good dispersal are expected to be more prevalent in pioneer faunas.

Another feature of high relevance related to dispersal and recolonisation is the ability to obtain nutrients. In adult Lepidoptera, a functional proboscis is necessary for taking up food resources such as nectar or rotting fruits. In certain Lepidoptera, including many Arctiidae, the proboscis is also essential for obtaining pyrrolizidine alkaloids (PAs; pharmacophagy: Boppré, 1990; Häuser & Boppré, 1997). However in the Old World, many species of the tribe Arctiini have a rudimentary or non-functional proboscis (Schulze *et al.*, 2001). This raises the question whether arctiids with non-functional mouthparts may gain selective advantages in certain habitats, e.g. as colonists during early succession.

Lepidopteran wing colour patterns often play a role in defence and predator avoidance (aposematism, mimicry, mimetic camouflage). Most nocturnal moths have dull wing colours that make them inconspicuous during day-time when they hide in the vegetation (Turner, 1984). Striking examples of background matching include the well known peppered moth *Biston betularia* (Geometridae) with light vs. melanic forms that are cryptic under unpolluted vs. polluted environmental conditions (‘industrial melanism’: e.g. West, 2003). Far fewer moth species are aposematically coloured. Aposematism (Poulton, 1890) is an anti-predator defence, combining a warning signal, most often black in combination with yellow, orange, or red or other bright coloration, with unpalatability or toxicity (Merilaita & Kaitala, 2002). Aposematic colouration is a visual cue that acts to alert predators that a species is chemically defended and unpalatable (Talianchich *et al.*, 2003).

Insects with aposematic colouration are often part of co-evolved Müllerian or Batesian mimicry systems (Turner, 1984; Mallet & Gilbert, 1995; Joron & Mallet, 1998; Simmons & Weller, 2002). Both such interactions are common among Lepidoptera in Neotropical forests (Mallet & Gilbert, 1995; Cardoso, 1997; Joron & Mallet, 1998). Within the Lepidoptera one unusual case of mimicry is found in moths that imitate aculeate hymenopterans. Apart from the Sesiidae and a few Sphingidae, this trait is most strikingly developed within the Ctenuchini clade of the Arctiidae (Kitching & Rawlins, 1999; Simmons & Weller, 2002).

In moths and butterflies, unpalatability or toxicity to predators is usually mediated by secondary plant metabolites which the larvae sequester from their food plants (Nishida, 2002). Many aposematic species of Arctiidae sequester and store plant-derived secondary compounds, such as pyrrolizidine alkaloids (PAs) (Hartmann *et al.*, 2004). PAs play essential roles for chemical defence, as precursors of male sex pheromones, as regulators of morphogenesis, and in the evolution of mating systems (Kitching & Rawlins, 1999; Weller *et al.*, 1999).

When tropical forests are cut down, abiotic factors such as temperature regimes, wind speed and humidity change dramatically (Murcia, 1995; Toral *et al.*, 2002). Moreover, many biotic interactions between species are affected. For example, the impact and identity of insectivorous birds and bats may differ between forest and open landscape (e.g. Dale *et al.*, 2000; Medellín *et al.*, 2000; Schulze *et al.*, 2004), and the availability of host plants (Dale *et al.*, 2000; Brehm & Fiedler, 2005) and the risk of parasitoid infestation (Jactel *et al.*, 2002) may be altered. Also the availability and abundance of models and mimics may change, thus interfering with the stability and function of mimicry rings (Turner, 1984; Joron & Mallet, 1998). When disturbed habitats are subsequently left to natural regeneration, one expects that with ongoing succession the original conditions in a forest might re-establish with time. Disturbance and succession processes may, therefore, leave a signature, on the community level, in morphological features that are related to dispersal or are altered biotic interactions.

We have recently analyzed in detail the diversity patterns of Arctiidae moths in a succession gradient in the montane forest zone of the Ecuadorian Andes, a global hotspot of moth diversity (e.g. Brehm *et al.*, 2005; chapters 2, 5). We here extend these analyses to the morphological features of these moths on the ensemble level (Fauth *et al.*, 1996). In particular, we address the following questions:

(1) Do body size distributions within arctiid moths differ along the succession gradient? Several studies have found a decrease in body size in more acutely disturbed areas (see Braun *et al.*, 2004). Therefore we expected a decrease in body size towards earlier stages of succession.

(2) Do wing-to-body size ratios vary with the progress of succession? We expected that in open habitats strong fliers would predominate, because of the increasing presence of enemies and thus a higher predation pressure. As a corollary, with increasing density of the vegetation in the course of forest recovery slender moths with higher maneuverability should be at an advantage.

(3) Does the incidence of a functional proboscis change with forest recovery? We expected that the proportion of species with functional proboscis should be higher in the mature forest understorey where selection should favour longer-lived income breeders (Tammaru &

Haukioja, 1996) that depend on nectar, and possibly PA pharmacophagy, for reproduction. In early succession habitats, in contrast, colonist and pioneer species might be at an advantage which may not need fully functional mouthparts.

(4) Does the proportion of aposematic moths change with succession? We expected that in intact forest with its more intricate biotic interactions the incidence of arctiids with aposematic colours, or embedded into mimicry rings should be higher.

4.3 Material and Methods

Arctiid moths were quantitatively sampled by light-trapping at 21 sites in the montane forest zone (1,800-2,005 m a.s.l.) of the eastern cordillera of the Ecuadorian Andes (see chapters 2 and 3 for a map). These sites represent a succession gradient from early stages of vegetation recovery (no woody vegetation, 10 sites, termed ‘early succession’ hereafter), across secondary shrub and forest vegetation (5 sites, ‘late succession’), to natural closed-canopy forest understorey (6 sites, ‘forest understorey’). Altogether, 9,211 arctiid individuals representing 287 species form the basis for the subsequent analyses. The study area and sampling methods were described in detail in chapter 2. Alpha- and beta-diversity of arctiid moths as a whole were analysed in chapter 2, and for the subordinated taxa in chapter 3.

There are various ways to quantify body size in arthropods. In the order Lepidoptera three measures are generally used, viz. body length, forewing length, and wing span (e.g. Siemann *et al.*, 1999; Rydell & Lancaster, 2000; Brehm, 2002). Usually these measures are highly interrelated to each other (e.g. Bishop & Armbruster, 1999; Koh *et al.*, 2004). We measured (a) the forewing length (distance from wing base to apex), (b) maximum forewing width, (c) body length (distance from frons to tip of the abdomen), and (d) maximum thorax width/ body width (see Fig.1). We took measurements from scaled digital photographs of specimens set in standard manner (wings spread at a right angle to the body axis). Photographs were taken with a Nikon Coolpix 995 camera at a resolution of 2,048x1,536 pixels and measurements were performed using the program ImageJ 1.33u (free software: http://rsb.info.nih.gov/ij/).

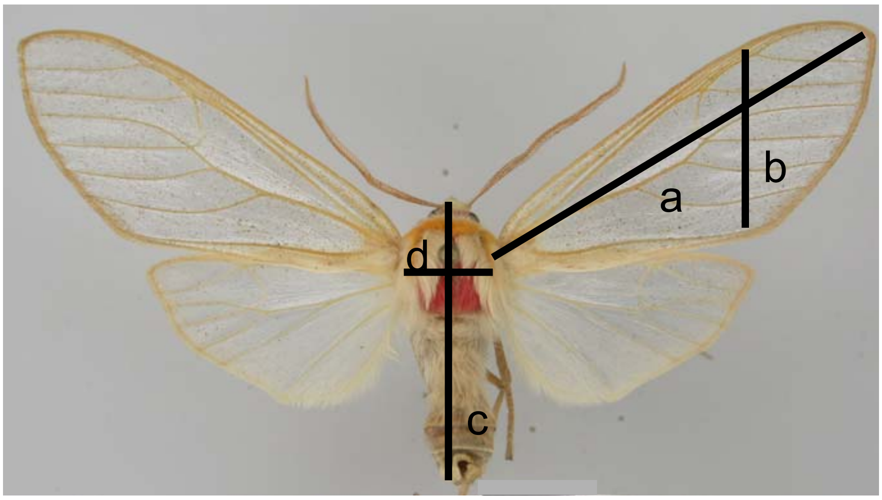


Figure 1: Photograph of an arctiid moth (*Amastus* sp nr *erganoides* (Subfamily: Phaegopterini)) and the measured morphometric parameters. (a) forewing length, (b) maximum forewing width, (c) total body length, (d) maximum thorax width.

Body length and thorax width were used to calculate an index of body stoutness (ratio of body length to thorax width; e.g. Schulze *et al.*, 2001). Slender-built species reach higher values, and low values characterize stoutly built species.

To assess the flight and dispersal abilities of the moths, the following parameters were calculated (all approximate values): (1) wing surface area of the forewing (wing surface area = [forewing length * maximum forewing width]/2), (2) body volume as a proxy of body mass ($V = \frac{4}{3}\pi l r^2$ with *l* = body length/2 and *r* = body width/2), the wing load (*WL* = body mass/wing area), and the aspect ratio (*AR* = forewing length/forewing width). A high wing load means that only a small wing area is available for swaying body mass, whereas low wing load means that the moth moves little mass per wing area. Moths with a high wing load are mostly robust with small wings and a high wing beat frequency, whereas the others have a slow flapping or rather a gliding flight (Rydell & Lancaster, 2000). Moths with high values of the aspect ratio have long, small wings, whereas moths with low values have broad and rounded wings.

In 95% of all 287 arctiid species sampled, males were measured. One photo of each species was analyzed. In the other cases (5%) females were taken, because no males were available. This was the case in the tribes Ctenuchini (7 spp.), Phaegopterini (7 spp.) and Pericopini (1 sp.). In most arctiid species in our samples there is no distinctive sexual dimorphism (N. Hilt, pers. obs.), thus the error introduced by this approach should be negligible.

We examined the mouthparts of all species and categorized their character states as 0 (no functional proboscis), 1 (rudimentary or reduced proboscis, length < 5 mm, can probably not be used for nectar uptake from flowers), or 2 (functional proboscis, length > 5 mm, coiled in usual manner and suitable for access to floral nectar). To avoid statistical problems of the standard χ^2 statistics due to small observation numbers in some cells of the resulting 3x3 and 3x2 contingency tables (moths with reduced mouthparts were generally rare), we used a generalized version of Fisher's 'Exact test' to compare the distribution of different proboscis states across habitats. We report results as χ^2 statistics based on Monte Carlo simulations with 10,000 permutations.

We scored all 287 species according to their external appearance as either cryptic (dull or unicoloured wing colours) or aposematic. White Lithosiinae species were scored as cryptic, because they do not exhibit display behaviours as typical for aposematic moths. Aposematic moths were further subdivided into species with brightly coloured wings and/or abdomen, those with distinct hymenopteran mimicry (as judged by a human observer), and species with a metallic shine on wings and body. It must be noted that any such classification based on human vision needs further validation once information is available on the visual capacities and prey selection behaviour of the relevant natural predators (e.g. Lyytinen *et al.*, 2001; Endler & Mappes, 2004). At present, the visually hunting predators of moths in Andean montane forests are too poorly known to allow for such an approach.

Morphological characters such as body size, general shape or wing pattern are not independent between species, but rather are connected by phylogenetic legacy (Harvey & Pagel, 1991; Bishop & Armbruster, 1999; Simmons & Weller, 2002). However, the current state of phylogenetic research on Arctiidae (Jacobsen & Weller, 2002) precludes comparative analyses controlling for phylogeny in a strict sense. To provide at least a partial control for phylogenetic effects, we carried out analyses at the level of the entire family Arctiidae and separately for the subordinated taxa (subfamily Lithosiinae; and tribes Pericopini, Arctiini, Phaegopterini and Ctenuchini nested within subfamily Arctiinae). Statistical analyses were performed using Statistica 6.1 (StatSoft, Tulsa, USA). Analyses were calculated on the level of species as well as individuals, respectively.

4.4 Results

Body size and wing shape – comparisons between habitat classes and arctiid clades

Size distributions of all arctiids combined (Fig. 2) were unimodal with regard to forewing length in all three habitat classes. This applied to species as well as individuals. Only minor differences were observed between the three habitat classes. Very large arctiid species with a forewing length greater than 42 mm and a body length greater than 30 mm were restricted to mature forest understorey, but were overall rare. In contrast, the smallest size classes (forewing length 8-12 mm) were more strongly represented in succession habitats, especially with regard to numbers of individuals. Size distributions of the three larger subordinated taxa (Ctenuchini, Phaegopterini, Lithosiinae: Fig. 3a-c) revealed distinct taxon-specific syndromes, but only minor shifts across the three habitat classes. Ctenuchini had a narrow range of body size (forewing length: 12 to 28 mm). The size class from 16-18 mm was dominantly represented in all three habitat categories. While in Phaegopterini modal body size was largest and size variation was also highest, the largest proportion of species had a forewing length of 18-20 mm in mature forest understorey, but

22-24 mm at succession sites. Very large Phaegopterini (> 34 mm) were most frequently collected in the mature forest understorey. The subfamily Lithosiinae showed the clearest picture. Size distribution was bimodal with a first maximum in the class 10-12 mm and a second peak at larger sizes (14-16 and 16-18 mm). This second peak was far more pronounced in the forest understorey, whereas the smaller species (10-12 mm) were most prevalent in succession habitats.

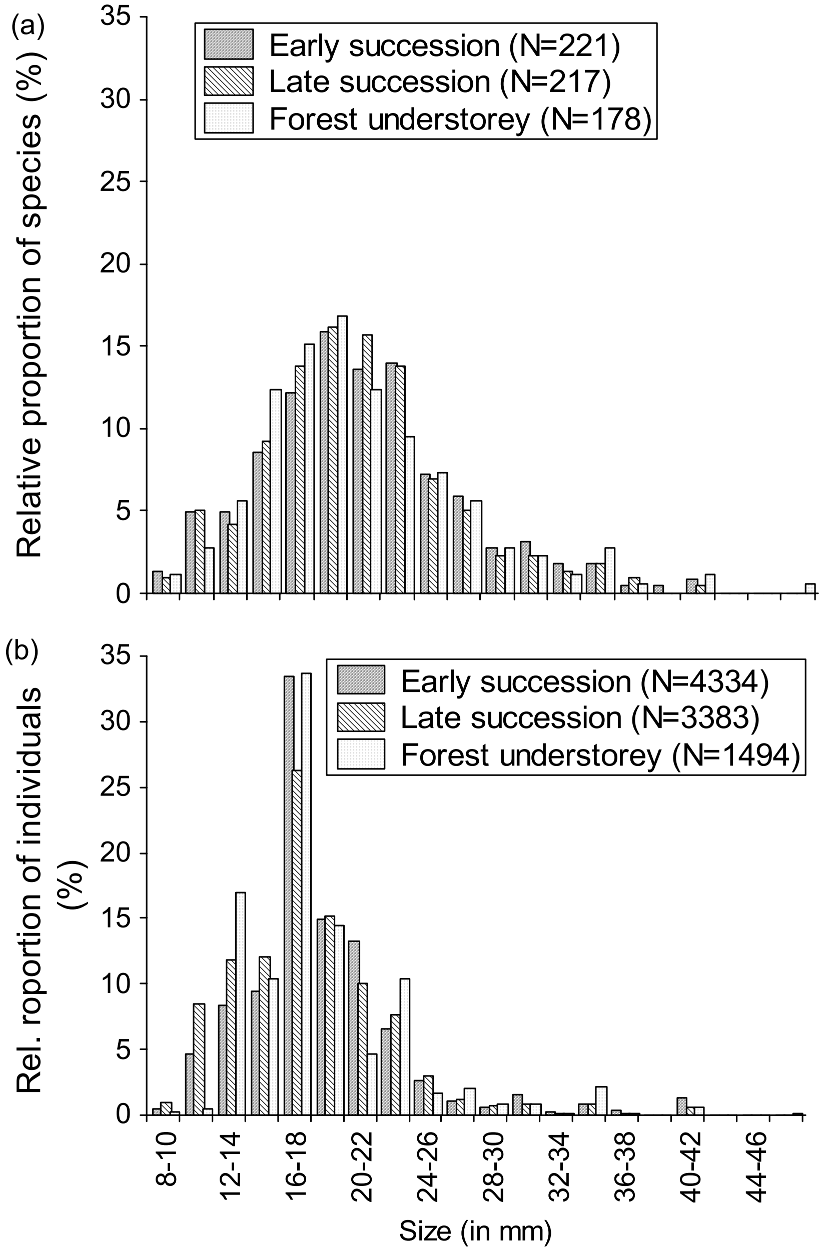


Figure 2: Distribution of the forewing length of all arctiid moth species (a) and individuals (b) collected along a succession gradient in southern Ecuador. Size classes were defined in 2 mm steps. Relative proportions sum up to 100% for each habitat category. N means species total and accordingly individuals total per habitat category.

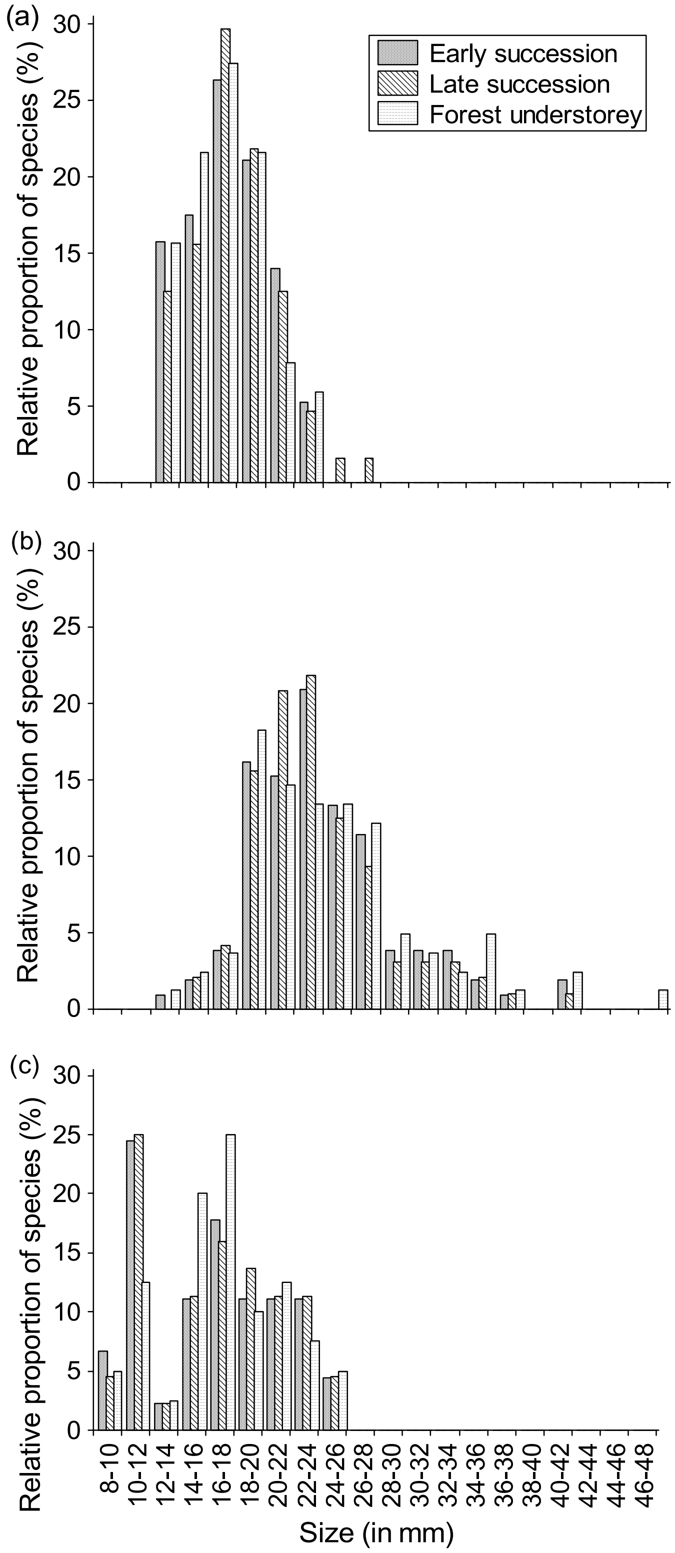


Figure 3: Distributions of the forewing length of species from (a) the tribe Ctenuchini (total 82 spp.), (b) Phaegopterini (135 spp.) and (c) the subfamily Lithosiinae (54 spp.) along the succession gradient with the three different habitat categories. Size classes were defined in 2 mm steps. Relative proportions sum up to 100% for each habitat category.

Statistical comparisons revealed that all body size-related parameters varied very strongly across the taxa (Table 1, Figs. 4-5). This was equally valid for analyses on species as well as individual level (results not shown).

Table 1: Results of two-way analyses of variance on individuals and species of arctiid moths for the different morphological traits. Categorical variables were taxon (Arctiini, Pericopini, Ctenuchini, Phaegopterini and Lithosiinae) and habitat (early, late succession, and forest understorey). F and P values (in parentheses) are given when significance was detected at the *P*<0.05 level. NS indicates non-significance.

Dependent variable	*F*(Taxon)	*F*(Habitat)	*F*(Interaction)
Forewing length (species)	99.8 (0.001)	NS	NS
Forewing length (individuals)	1458.9 (0.001)	6.87 (0.005)	12.1 (0.001)
Maximum forewing width (species)	178.5 (0.001)	NS	NS
Maximum forewing width (individuals)	2085.3 (0.001)	7.86 (0.001)	11.32 (0.001)
Body length (species)	98.6 (0.001)	NS	NS
Body length (individuals)	1407.0 (0.001)	4.83 (0.01)	16.94 (0.001)
Thorax width (species)	114.8 (0.001)	NS	NS
Thorax width (individuals)	1770.9 (0.001)	6.07 (0.005)	14.69 (0.001)
Ratio (species)	51.3 (0.001)	NS	NS
Ratio (individuals)	412.1 (0.001)	NS	7.90 (0.001)
Wing area of forewing (species)	127.4 (0.001)	NS	NS
Wing area of forewing (individuals)	1819.2 (0.001)	7.74 (0.001)	12.89 (0.001)
Body mass (species)	59.4 (0.001)	NS	NS
Body mass (individuals)	1034.2 (0.001)	5.78 (0.005)	21.8 (0.001)
Wing load (species)	50.3 (0.001)	NS	NS
Wing load (individuals)	944.4 (0.001)	3.05 (0.05)	14.03 (0.001)
Aspect ratio (species)	65.1 (0.001)	NS	NS
Aspect ratio (individuals)	137.4 (0.001)	NS	7.50 (0.001)

Moths of the tribe Pericopini were always the largest, followed by Phaegopterini, Arctiini, Ctenuchini and Lithosiinae (Fig. 4).

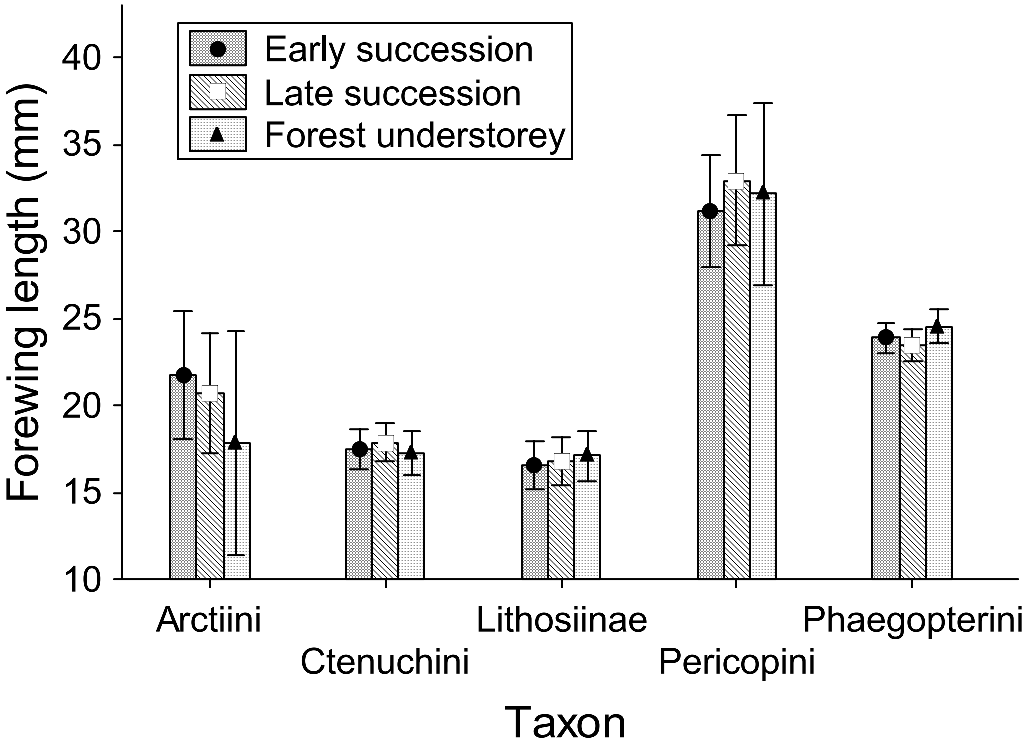


Figure 4: Forewing length (mean ± 95% confidence intervals) of arctiid moth species across the subordinated taxa (Arctiini, Ctenuchini, Lithosiinae, Pericopini, Phaegopterini) and the three different habitat categories.

Wing loads were highest in Arctiini and Phaegopterini, which are robust moths with broad wings, in contrast to the Lithosiinae and Ctenuchini, which are slender built and small. Pericopini were intermediate in that respect. Lithosiinae had highest aspect ratios and body-to-thorax ratios (Figs. 5a and 5b). Arctiini and Phaegopterini had low body-to-thorax ratios. Table 2 gives an overview over the major arctiid taxa and their morphometric traits.

When analysed on species level, there were no differences in body-size related traits between three classes of habitat (see Tab. 1). Also habitat x taxon interactions were absent. Only when viewed on individual level, arctiid ensembles regularly showed weak, but significant differences in these traits along the succession gradient. There was a decrease of the body mass, forewing length, wing surface area of the forewing as well as the body length of the moths with forest recovery. In contrast, wing load did not vary consistently over the whole gradient.

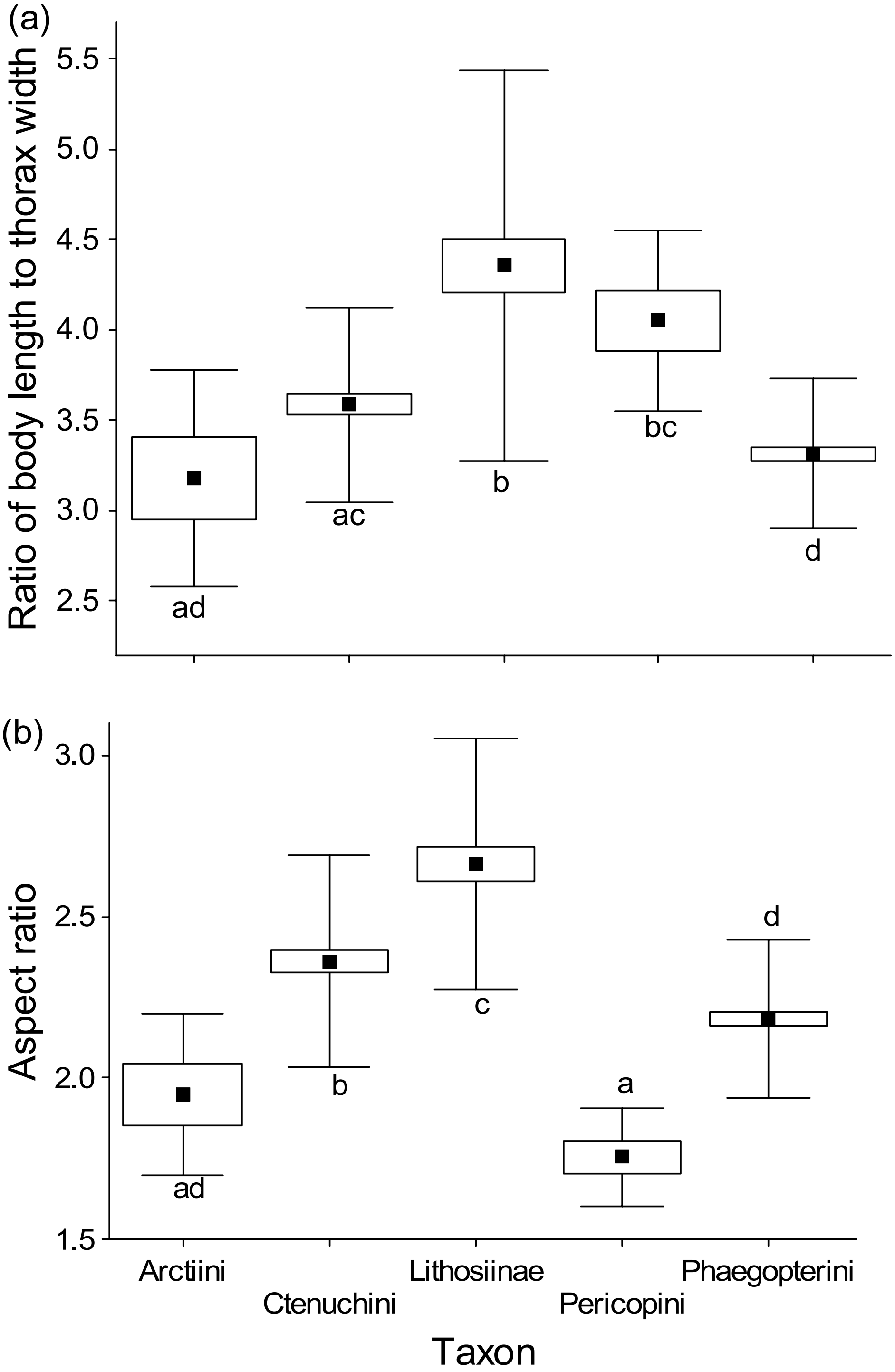
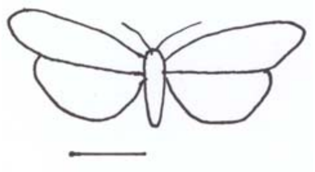
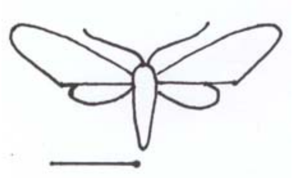
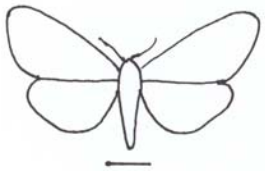
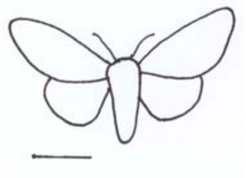
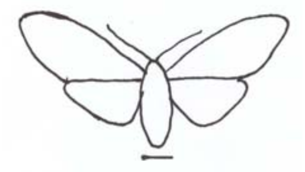


Figure 5: Ratio of body length to maximum thorax width (a) and aspect ratio (b) for species in five arctiid taxa (Arctiini N=7 species; Ctenuchini N=82; Lithosiinae N=54; Pericopini N=9; Phaegopterini N=135). Boxes labelled with different letters differ significantly at *P*<0.05 (Kruskal-Wallis ANOVA; body/thorax ratio: H(4, N=287) = 79.1, *P*<0.0001; aspect ratio: H(4, N=287) = 93.2, *P*<0.0001, followed by post hoc test: all *P*<0.05). Symbols = means, boxes = ± 1 SE, whiskers = ± 1 SD.

Table 2: Overview among the five major arctiid taxa (line drawings of typical representative) and their morphological characters. Black bar = 1cm.

	Taxon	**General shape**	**Wing load**	**Aspect ratio**	**Body-to-thorax ratio**	**Body volume**
	Lithosiinae	Small, slender and narrow wings	Low	High	High	Low
	Ctenuchini	Small, narrow wings	Intermediate	High	Intermediate	Low
	Pericopini	Large, slender, broad winged	Intermediate	Low	High	High
	Arctiini	Medium sized, robust	High	Low	Low	Intermediate
	Phaegopterini	Medium sized, robust	High	Intermediate	Low	Intermediate

Mouthpart functionality

91.6% of the species (94.7% of individuals) had a functional proboscis, whereas only 5.2% (individuals: 2.3%) had a rudimentary proboscis and 3.2% (individuals: 3.0%) had no apparent proboscis at all. Cases of proboscis reduction were not uniformly distributed across the arctiid subfamilies and tribes (Fisher's generalized exact test: $\chi^2_{Df8} = 63.2$, $P<0.0001$; if both categories of proboscis reduction were aggregated: $\chi^2_{Df4} = 59.8$, $P<0.0001$). All Ctenuchini studied had a functional proboscis, and in the Phaegopterini and Lithosiinae reductions of the proboscis were rare. In contrast, all Arctiini and half of the sampled Pericopini species had no functional or a rudimentary proboscis (Tab. 3).

Table 3: Distribution of reductions in proboscis functionality across the major arctiid taxa and the three succession habitat classes. Given are absolute numbers and percentages of row totals (in parentheses). Upper table: species; lower table: individuals as units of analysis.

	Functional proboscis	Reduced proboscis	No proboscis
Lithosiinae	52 (96.3%)	2 (3.7%)	0 (0%)
Arctiini	0 (0%)	5 (71.4%)	2 (28.6%)
Ctenuchini	82 (100%)	0 (0%)	0 (0%)
Pericopini	4 (44.5%)	2 (22.2%)	3 (33.3%)
Phaegopterini	125 (92.6%)	6 (4.4%)	4 (3.0%)
all Arctiidae	263	15	9

	Functional proboscis	Reduced proboscis	No proboscis
Early succession	4205 (94.7%)	93 (2.2%)	136 (3.1%)
Late succession	3169 (93.7%)	106 (3.1%)	108 (3.2%)
Forest understorey	1451 (97.1%)	15 (1.0%)	28 (1.9%)

The proportion of moths with various stages of proboscis development varied also significantly along the succession gradient (χ^2_{Df4} = 29.68, $P<0.001$). Species with reduced proboscis and those with no proboscis at all were similarly distributed along the succession gradient (χ^2_{Df2} = 5.18, $P>0.05$). When pooling all cases of proboscis reduction, a significant difference emerged between the three different succession stages (χ^2_{Df2} = 24.65, $P<0.001$). Moths with reduced mouthparts showed a higher incidence at succession sites (early succession: 5.3%, later succession: 6.3%) than in the mature forest understorey (2.9%). Also, when the proportion of individuals with reduced proboscis per site was compared across the three succession stages (mean values: early succession = 4.9%; late succession = 6.3%; forest understorey = 2.9%), we found a significant decrease with forest recovery (one-way ANOVA: $F(2,18)$ = 4.24, $P<0.05$; Levene test: $P>0.05$).

Aposematic vs. cryptic appearance

Overall, according to their external appearance we scored 49.5% of all 287 species and 64.2% of all 9,211 individuals as cryptic. Correspondingly, a substantial fraction of arctiids in our samples were scored as aposematic (brightly coloured wings and/ or abdomen: 39.7% of species, 22.7% of individuals; Hymenoptera mimicry: 6.6%, 9.2%; metallic shine: 4.2%, 3.9%). The relative incidence of aposematism in arctiid moths did not change along the succession gradient (Kruskal-Wallis ANOVA: species H(2,N=21) = 3.61, $P>0.16$; individuals: H(2,N=21) = 3.81, $P>0.14$; Fig. 6).

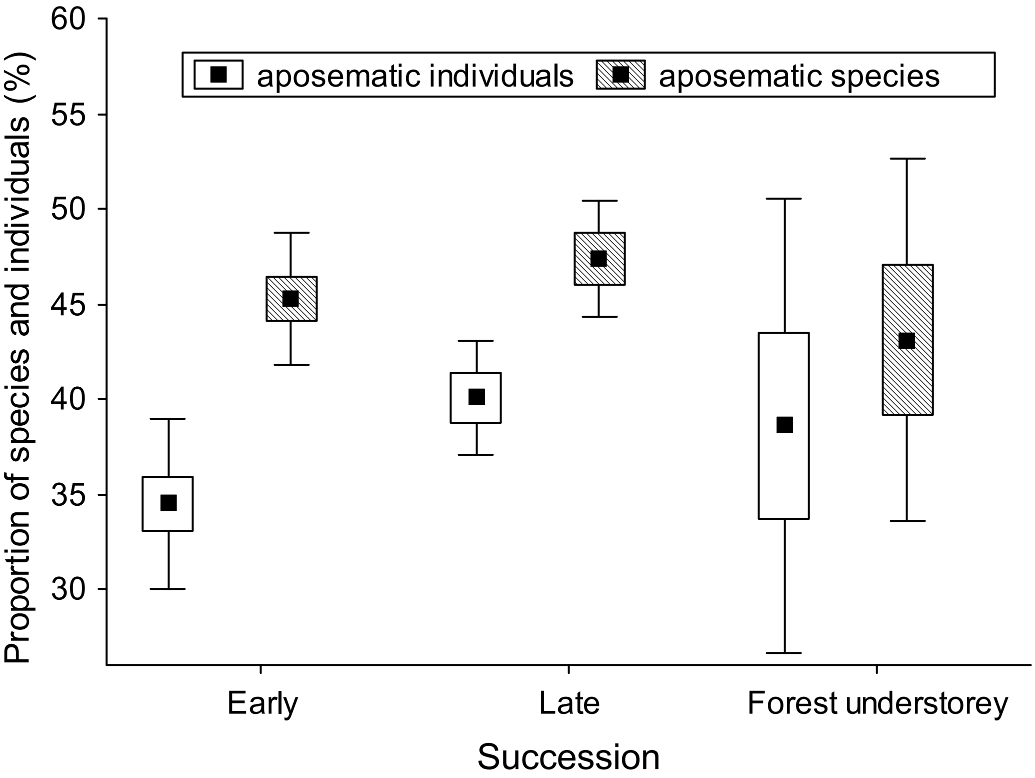


Figure 6: Proportion of aposematic arctiid moth species and individuals, relative to total samples, in three classes of succession habitats. Differences between groups are not significant. The box-whisker plot presents means as well as their standard errors (box) and standard deviations (whisker).

However, such patterns became apparent at lower systematic levels. Aposematic species among Phaegopterini showed a slight decrease along the succession gradient and aposematic Lithosiinae were significantly more prevalent at succession sites than in mature forest, whereas Ctenuchini showed a slight increase (tendency) with forest recovery (Fig. 7a). When analysed on individual rather than species level, these trends (decrease of aposematic Phaegopterini and Lithosiinae, as well as an increase of aposematic Ctenuchini with forest recovery) became more distinct (Fig. 7b).

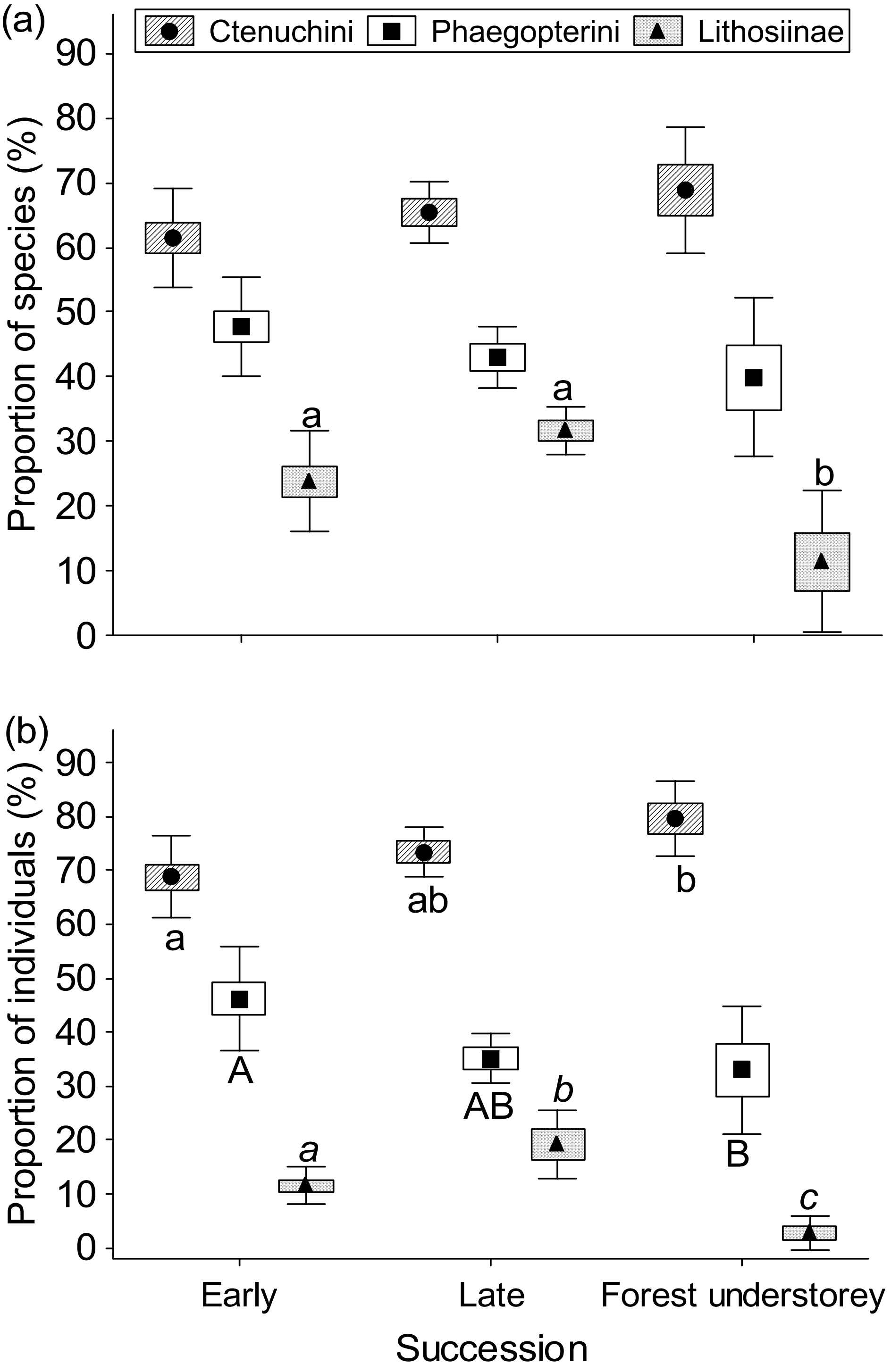


Figure 7: Proportion of aposematic (a) species and (b) individuals of Arctiidae in three classes of succession habitats. Differences between habitats are significant only once in the analysis of species (a) for Lithosiinae (ANOVA: F(2,18) = 8.73, *P*<0.005), but are significant for all three taxa in the analysis of individuals (b) (Ctenuchini: F(2,18) = 4.72, *P*<0.05; Phaegopterini: F(2,18) = 4.44, *P*<0.05; Lithosiinae: F(2,18) = 20.80, *P*<0.001). Given are means (symbols), standard errors (boxes) and standard deviations (whiskers). Within each taxon, boxes accompanied by different letters differ at *P*<0.05 (Scheffé post hoc test).

The major clades differed significantly in their proportions of aposematic and cryptic species (χ^2_{Df9} = 20.38, *P*<0.05) and individuals (χ^2_{Df9} = 129.87, *P*<0.001), respectively (see also Tab. 4). In general, aposematic moths were disproportionally common in the Ctenuchini and rare in the Lithosiinae and Arctiini. Table 4 shows a further breakdown of the aposematic category into five subgroups (aposematic or 'crazy colour' at thorax, abdomen and wings; only abdomen coloured; only brightly coloured wings; hymenopteran mimicry; and metallic shine on wings and body). Hymenopteran mimicry was restricted to the tribe Ctenuchini. Pericopini showed a higher proportion of aposematic and metallic-coloured species than expected, whereas Lithosiinae had an increased proportion of cryptic species. Phaegopterini and Arctiini contained a high proportion of species with only a warningly coloured abdomen.

Table 4: Distribution of arctiid species (bold) and individuals (italics) across the different external appearance classes. Percentages relative to the species total in the respective taxon are given in parentheses. Results of χ² tests for homogeneity of the external appearance across taxa are reported separately for species and individuals, based on observed vs. expected frequencies.

Taxon	Aposematic ('crazy coloured')	Abdomen coloured	Brightly coloured wings	Hymenopteran mimicry	Metallic shine	Cryptic
Arctiini	**1** /*1* (14.3%)	**2** /*13* (28.6%)	**1** /*16* (14.3%)	**0**	**0**	**3** /*72* (42.8%)
Ctenuchini	**5** /*168* (6.1%)	**16** /*607* (19.5%)	**7** /*240* (8.5%)	**19** /*843* (23.2%)	**7** /*9* (8.5%)	**28** /*688* (34.2%)
Pericopini	**3** /*4* (33.3%)	**0**	**1** /*92* (11.1%)	**0**	**1** /*1* (11.1%)	**4** /*25* (44.5%)
Phaegopterini	**20** /*169* (14.8%)	**48** /*586* (35.5%)	**2** /*42* (1.5%)	**0**	**0**	**65** /*1201* (48.2%)
Lithosiinae	**3** /*31* (5.6%)	**5** /*212* (9.3%)	**7** /*222* (13.0%)	**0**	**4** /*346* (7.4%)	**35** /*3623* (64.8%)
Proportion of total arctiid	11.1%	24.7%	6.3%	6.6%	4.2%	47.1%
χ² test for species	37.4 *P*<0.001	111.3 *P*<0.001	10.9 *P*<0.05	76.0 *P*<0.001	15.5 *P*<0.005	96.8 *P*<0.001
χ² test for individuals	401.3 *P*<0.001	1251.1 *P*<0.001	346.9 *P*<0.001	3372.0 *P*<0.001	1326.6 *P*<0.001	7804.9 *P*<0.001

4.5 Discussion

Body size and flight morphology: strong historical legacy vs. weak ecological pattern

Several studies have found a decrease in insect body size in more acutely disturbed areas (Braun *et al.*, 2004). In arctiid moths from the montane zone in southern Ecuador, however, there was no consistent difference in body size from early succession stages to the mature forest understorey. Separate analyses on lower systematic levels (subfamilies and tribes) also revealed but subtle differences in the size distributions of moth species and individuals along the succession gradient. The clearest differences were found in the subfamily Lithosiinae with larger species in the mature forest than at the succession sites forming the modal class. However, lichen moth species with forewing lengths greater than 20 mm were similarly distributed along the succession gradient. Phaegopterini showed also two different maxima for the forest and the succession sites in their size distributions, but here with a higher modal value for the succession habitats. This might indicate that dispersal capacities of some pioneer Phaegopterini species are indeed related to body size. In general, however, the lack of clear shifts in the geometry of body size distributions along the succession gradient was surprising. Similarly, we failed to detect major shifts along the successional gradient with all other morphological traits that we analysed (e.g. wing load, aspect ratio, ratio of body length to thorax width). This absence of clear ecological patterns stands in stark contrast to the prominent differences between arctiid clades. These differences underscore phylogenetic constraints on flight-related traits and are primarily a legacy of phylogeny.

Wing load is a good predictor for flight speed (Rydell & Lancaster, 2000) and thus for dispersal ability of the moths. Low wing load values, as found among Lithosiinae, usually indicate slow flight. In contrast, high wing load facilitates high flight speed such as in moths of the tribe Phaegopterini, which are large and robust animals. Larger insects have often been thought to be more mobile and hence being better capable of covering larger distances and colonizing (new) sites (Merckx & Van Dyck, 2002). We also used the ratio of body length to thorax width as an indicator for flight characteristics (see Schulze *et al.*, 2001).

Species with lower ratios and, therefore, sturdier bodies predominate in the tribes Arctiini and Phaegopterini. In contrast, slender-built species with higher ratio values prevailed in the Ctenuchini and Pericopini. Usually such slender-built insects do not reach high flight speeds, but may have a superior maneuverability (Chai, 1990). With regard to their aspect ratio, the arctiid taxa likewise fall into two major groups. High values characterize species with narrow, small wings such as most Lithosiinae and Ctenuchini, whereas low values indicate moths with broad, rounded wings such as Pericopini and Arctiini. Phaegopterini occupy intermediate values in this respect. Our morphometric analyses therefore qualify Ecuadorian Phaegopterini and to a lesser extent Arctiini as robust moths with strong flight capacity, whereas most Lithosiinae, Ctenuchini and also Pericopini would be expected to show less strong flight capacities.

Generally in the Lepidoptera a positive association seems to exist between larval niche breadth and adult body size. Polyphagous species tend to be larger than monophagous ones (overview in Komonen *et al.*, 2004). However, little is known about the host plants of Neotropical arctiids, and the issue of polyphagy vs. monophagy in tropical herbivores remains controversial overall (Novotny & Basset, 2005). From our size measurements we would predict that Phaegopterini and Arctiini tend to be more polyphagous than Lithosiinae and Ctenuchini. This is in agreement with tentative assessments based on the very incomplete host plant data for tropical Arctiidae (e.g. Süßenbach, 2003). However, the large-sized Pericopini would also be predicted to be host plant generalists, whereas in reality these moths – where known – are host specialists with a complex chemical ecology (e.g. Kitching & Rawlins, 1999; Weller *et al.*, 1999).

The presence of functional mouthparts

In the Old World, the arctiid tribe Arctiini contains a large proportion of species without a functional proboscis (Schulze *et al.*, 2001). Therefore, many Arctiini species are capital breeders, where the adult moths are independent of the availability of any food resources like nectar (Tammaru & Haukioja, 1996). Relatively few representatives of this tribe have retained functional mouthparts and visit flowers for nectar-feeding. Contrary to the arctiid ensembles in a Bornean rainforest (Schulze *et al.*, 2001), over 90% of the arctiid moth species had functional mouthparts in the Ecuadorian study area. Likewise, among arctiid ensembles sampled in a Costa Rican lowland rain forest, Brehm (2005) detected a proboscis in almost all studied species. Our analyses revealed that arctiid clades differ significantly in the functionality of their proboscis. Hence, the discrepancy between the findings in Ecuador, Costa Rica and Borneo can be related to differences in the clade composition of Neotropical vs. Palaeotropical arctiid ensembles. In the Neotropical samples all studied Ctenuchini had a functional proboscis. Ctenuchini moths often take up PAs pharmacophagously (Häuser & Boppré, 1997; Kreusel & Häuser, 1998; Brehm *et al.*, *submitted*) and therefore require a functional proboscis. In contrast, all Ecuadorian Arctiini such as the genus *Hypercompe,* and half of the Pericopini species such as *Dysschema semirufa* (Druce 1818), had no functional proboscis (see Appendix 1). Among the largest clade in our Ecuadorian samples, the tribe Phaegopterini, reductions of the proboscis occurred in but 7.4% of the species and 8.6% of the individuals. Thus, most Phaegopterini are income breeders, in contrast to the Arctiini which have rather similar wing traits (see above).

Apart from these clade differences, which again hint to strong phylogenetic constraints, the proportion of moths with a reduced proboscis differed significantly along the succession gradient. Moths with reduced mouthparts were twice as common in earlier (5.3%) and later succession stages (6.3%) vs. the mature forest understorey (2.9%). This suggests that indeed capital breeders among the Arctiidae have an advantage in colonizing succession habitats, even though overall moths with a reduced proboscis made up but 5.3% of all arctiid individuals sampled in our study area.

Aposematism

Aposematism is defined as the combination of an anti-predator defence with an outward signal that indicates unpalatability. Visually hunting vertebrate predators are regarded as the major selective agents for the evolution of aposematic colouration in Lepidoptera (e.g. Pinheiro, 1996; Cardoso, 1997). In most aposematic Lepidoptera, unpalatability is mediated by secondary plant metabolites that are sequestered from larval or adult resources (Nishida, 2002). In the Arctiidae chemical defence is derived from various substance classes such as pyrrolizidine alkaloids (PAs), iridoid glycosides, histamines and others (Boppré, 1990; Cardoso, 1997; Weller *et al.*, 1999; Hartmann *et al.*, 2004). Aposematic arctiid moths accounted for about half of the species and one third of the individuals in our study, which emphasizes the significance of chemical defence and aposematism in that moth family. Overall the incidence of aposematism in arctiids did not change along the succession gradient, but such patterns became apparent at lower systematic levels. Moreover, the proportion of aposematic moths differed strikingly between the arctiid clades.

Hymenopteran mimicry was found exclusively in the tribe Ctenuchini (19 species). The most extreme forms of Hymenoptera mimicry are exhibited by ctenuchines such as *Pseudosphex*, in which the basal abdominal segments are constricted to form a ‘wasp-waist’, and in species where longitudinal wing folding resembles the condition in vespid wasps (Kitching & Rawlins, 1999). Metallic shiny species were rare, but occurred predominantly among Ctenuchini (7 species), Lithosiinae (4 species) and also in one Pericopini species.

Within the Ctenuchini with their complex but largely unknown chemical ecology (pharmacophagy, sequestration of host plant alkaloids: Boppré, 1990; Häuser & Boppré, 1997; Brehm *et al.*, *submitted*) the incidence of aposematic species and individuals increased from earlier succession stages to natural forest understorey. This might indicate that a richer natural forest vegetation offers more resources for these putative host plant specialists. Moreover, the Batesian mimicry rings that involve many Ctenuchini species obviously are more strongly developed in natural forest. In contrast, Phaegopterini and

Lithosiinae showed a decrease in the proportion of aposematic species, and especially aposematic individuals, with forest recovery. Apparently for these moths defense against visually hunting predators is relatively more important in the open vegetation of earlier succession stages, whereas a cryptic appearance is favoured in the dense forest understorey. Similar patterns of the micro-distribution of conspicuously coloured Lepidoptera have been found in other studies. In a Bornean rainforest cryptic large-bodied fruit-feeders among butterflies were more prevalent in the understorey whereas brightly coloured nectar-feeders with high maneuverability were more abundant in the canopy (Schulze *et al.*, 2001). Brehm (2005) found an increase in conspicuously coloured arctiid species from the understorey (36.6%) to the canopy (52.0%) in a Costa Rican lowland forest.

In conclusion, we found surprisingly little evidence for shifts along a succession gradient in character distributions such as body size, dispersal-related traits, functionality of mouthparts, and external appearance of the Arctiidae. In contrast, we observed strong differences between the major arctiid clades with regard to all traits studied. This suggests that phylogenetic constraints and historical legacy are of overriding importance in shaping character distributions in this speciose moth clade, whereas ecological shifts are far less obvious, at least on the small spatial scale of our study.

Acknowledgments

We thank Dirk Süßenbach and Gunnar Brehm who provided data of moths sampled from natural forest. Giovanni Onore (Pontifícia Universidad Católica del Ecuador, Quito) and Christoph L. Häuser (Staatliches Museum für Naturkunde, Stuttgart) supported the project logistically. Special thanks go to John Slogett and Gunnar Brehm for helpful comments on this manuscript. The Ministerio del Medio Ambiente in Ecuador issued research permits (Nro. 002-PNP-DBAP-RLZCH/MA). The foundation Nature and Culture International (Loja, Ecuador) allowed access to the study sites and their facilities. The Deutsche

Forschungsgemeinschaft financed our work (FOR 402/1-1 TP15, FOR 402/2-1 A3).

4.6 References

Agosta, S. J. & Janzen, D.H. (2005) Body size distributions of large Costa Rican dry forest moths and the underlying relationship between plant and pollinator morphology. *Oikos*, **108**, 183-193.

Bishop, J.A. & Armbruster, W.S. (1999) Thermoregulatory abilities of Alaskan bees: effects of size, phylogeny and ecology. *Functional Ecology*, **13**, 711-724.

Blackburn, T.M., Harvey, P.H. & Pagel, M.D. (1990) Species number, population density and body size relationships in natural communities. *Journal of Animal Ecology*, **59**, 335-345.

Boppré, M. (1990) Lepidoptera and pyrrolizidine alkaloids: exemplification of complexity in chemical ecology. *Journal of Chemical Ecology*, **16**, 165-185.

Braun, S.D., Jones, T.H. & Perner, J. (2004) Shifting average body size during regeneration after pollution – a case study using ground beetle assemblages. *Ecological Entomology*, **29**, 543-554.

Brehm, G. (2002) *Diversity of geometrid moths in a montane rainforest in Ecuador*. Ph.D. thesis, University of Bayreuth. URL: http://opus.ub.uni-bayreuth.de/volltexte/2003/20

Brehm, G. (2005) Contrasting patterns of vertical stratification in two moth families in a Costa Rican lowland rain forest. *Basic and Applied Ecology*, in press.

Brehm, G. & Fiedler, K. (2005) Diversity and community structure of geometrid moths of disturbed habitat in a montane area in the Ecuadorian Andes. *Journal of Research on the Lepidoptera,* **38**, 1-14.

Brehm, G., Pitkin, L.M., Hilt, N. & Fiedler, K. (2005) Montane Andean rain forests are a global diversity hotspot of geometrid moths. *Journal of Biogeography*, **32**, 1621-1627.

Brehm, G., Hartmann, T., Willmott, K.W. (*submitted July 2005*) Pyrrolizidine alkaloids and pharmacophagous Lepidoptera visitors of *Prestonia amabilis* (Apocynaceae) in a montane rain forest in Ecuador. *Annals of the Missouri Botanical Garden.*

Cardoso, M.Z. (1997) Testing chemical defence based on pyrrolizidine alkaloids. *Animal Behaviour*, **54**, 985-991.

Chai, P. (1990) Relationships between visual characteristics of rain forest butterflies and responses of a specialized insectivorous birds. In: *Adaptive coloration in invertebrates* (ed. M. Wickstein), pp. 31-60. Proceedings of Symposium sponsored by American Society of Zoologists Galveston: Seagrant College, Program, Texas A & M University.

Chai, P. & Srygley, R.B. (1990) Predation and the flight, morphology, and temperature of Neotropical rain forest butterflies. *The American Naturalist*, **135**, 748-765.

Dale, S., Mork, K., Solvang, R. & Plumptre, A.J. (2000) Edge effects on the understory bird community in a logged forest in Uganda. *Conservation Biology*, **14**, 265-276.

Endler, J.A. & Mappes, J. (2004) Predator mixes and the conspicuousness of aposematic signals. *The American Naturalist*, **163**, 532-547.

Fauth, J.E., Bernardo, J., Camara, M., Resetarits, W.J., Van Buskirk, J. & McCollum, S.A. (1996) Simplifying the jargon of community ecology: a conceptual approach. *The American Naturalist*, **147**, 282-286.

Gaston, K.J. (1994) *Rarity. Population and Community Biology Series 13*. Chapman & Hall, London. 220 pp.

Häuser, C.L. & Boppré, M. (1997) Pyrrolizidine alkaloid-related pharmacophagy in neotropical moths (Lepidoptera). In: *Tropical biodiversity and systematics, Proceedings of the International Symposium on Biodiversity and Systematics in Tropical Ecosystems* (ed. H. Ulrich), pp. 291-296, Museum Alexander Koenig, Bonn.

Hall, J.P.W. & Willmott, K.R. (2000) Patterns of feeding behaviour in adult male riodinid butterflies and their relationship to morphology and ecology. *Biological Journal of the Linnean Society*, **69**, 1-23.

Hartmann, T., Theuring, C., Beuerle, T., Ernst, L., Singer, M.S. & Bernays, E.A. (2004) Acquired and partially *de novo* synthesized pyrrolizidine alkaloids in two polyphagous arctiids and the alkaloid profiles of their larval food-plants. *Journal of Chemical Ecology*, **30**, 229-254.

Harvey, P.H. & Pagel, M.D. (1991) *The comparative method in evolutionary biology*. Oxford: Oxford University Press. 248 pp.

Jacobson, N.L. & Weller, S.J. (2002) *A cladistic study of the Arctiidae (Lepidoptera) by using characters of immatures and adults.* Thomas Say Publications in Entomology: Monographs. Lanham, Maryland: Entomological Society of America. 98 pp.

Jactel, H., Goulard, M., Menassieu, P. & Goujon, G. (2002) Habitat diversity in forest plantations reduces infestations of the pine stem borer *Dioryctria sylvestrella*. *Journal of Applied Ecology*, **39**, 618-628.

Joron, M. & Mallet, J.L.B. (1998) Diversity in mimicry: paradox or paradigm? *Trends in Ecology and Evolution*, **13**, 461-466.

Kitching, I.J. & Rawlins, J.E. (1999) The Noctuoidea. In: *Handbook of Zoology. Lepidoptera, Moths and Butterflies,* vol. 1 (ed. N.P. Kristensen), pp. 355-401. Berlin, New York, Walter de Gruyter.

Koh, L.P., Sodhi, N.S. & Brook, B.W. (2004) Ecological correlates of extinction proneness in tropical butterflies. *Conservation Biology*, **18**, 1571-1578.

Komonen, A., Grapputo, A., Kaitala, V., Kotiaho, J.S. & Päivinen, J. (2004) The role of niche breadth, resource availability and range position on the life history of butterflies. *Oikos*, **105**, 41-54.

Kreusel, B. & Häuser, C.L. (1998) Morphological diversity of the tympanal organ in Wasp Moths (Arctiidae: Ctenuchinae) and its systematic importance. *Memoires de la Societe Royale Belge d'Entomologie*, **38**, 13-23.

Kutsch, W., Martz, H. & Gäde, G. (2002) Flight capability and flight motor pattern in a sedentary South African grasshopper, *Phymateus morbillosus* – a comparison with migratory species. *Physiological Entomology*, **27**, 39-50.

Lawton, J.H. (1991) Species richness, population abundances, and body size in insect communities: tropical versus temperate comparisons. In: *Plant-animal Interactions: Evolutionary ecology in tropical and temperate regions* (eds. P.W. Price, T.M. Lewinsohn, G.W. Fernandes and W.W. Benson), pp. 71-89. Wiley, New York.

Lyytinen, A., Alatalo, R.V., Lindström, L. & Mappes, J. (2001) Can ultraviolet cues function as aposematic signals? *Behavioral Ecology*, **12**, 65-70.

Mallet, J. & Gilbert, L.E. Jr. (1995) Why are there so many mimicry rings? Correlations between habitat, behaviour and mimicry in *Heliconius* butterflies. *Biological Journal of the Linnean Society*, **55**, 159-180.

Malmqvist, B. (2000) How does wing length relate to distribution patterns of stoneflies (Plecoptera) and mayflies (Ephemeroptera)? *Biological Conservation*, **93**, 271-276.

Medellín, R.A., Equihua, M. & Amin, M.A. (2000) Bat diversity and abundance as indicators of disturbance in neotropical rainforests. *Conservation Biology*, **14**, 1666-1675.

Merckx, T. & Van Dyck, H. (2002) Interrelations among habitat use, behavior, and flight-related morphology in two cooccurring Satyrine butterflies, *Maniola jurtina* and *Pyronia tithonus*. *Journal of Insect Behavior*, **15**, 541-561.

Merilaita, S. & Kaitala, V. (2002) Community structure and the evolution of aposematic coloration. *Ecology Letters*, **5**, 495-501.

Murcia, C. (1995) Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution*, **10**, 58-62.

Nishida, R. (2002) Sequestration of defensive substances from plants by Lepidoptera. *Annual Review of Entomology*, **47**, 57-92.

Novotny, V. & Basset, Y. (2005) Host specificity of insect herbivores in tropical forests. *Proceedings of the Royal Society, London, Biological Sciences*, **272**, 1083-1090.

Pinheiro, C.E.G. (1996) Palatability and escaping ability in Neotropical butterflies: test with wild kingbirds (*Tyrannus melancholicus*, Tyrannidae). *Biological Journal of the Linnean Society*, **59**, 351-365.

Poulton, E.B. (1890) *The colours of Animals: Their meaning and use especially considered in the case of insects*. Keegan Paul, Trench, Trübner and Co.

Rydell, J. & Lancaster, W.C. (2000) Flight and thermoregulation in moths were shaped by predation from bats. *Oikos*, **88**, 13-18.

Schulze, C.H., Linsenmair, K. E. & Fiedler, K. (2001) Understorey versus canopy: patterns of vertical stratification and diversity among Lepidoptera in a Bornean rain forest. *Plant Ecology*, **153**, 133-152.

Schulze, C.H., Waltert, M., Kessler, P.J.A., Pitopang, R., Shahabuddin, Veddeler, D., Mühlenberg, M., Gradstein, S.R., Leuschner, C., Steffan-Dewenter, I. & Tscharntke, T. (2004) Biodiversity indicator groups of tropical land-use systems: comparing plants, birds, and insects. *Ecological Applications,* **14**, 1321–1333.

Siemann, E., Tilman, D. & Haarstad, J. (1999) Abundance, diversity and body size: patterns from a grassland arthropod community. *Journal of Animal Ecology*, **68**, 824-835.

Simmons, R.B. & Weller, S.J. (2002) What kind of signals do mimetic tiger moths send? A phylogenetic test of wasp mimicry systems (Lepidoptera: Arctiidae: Euchromiini). *Proceedings of the Royal Society of London Series* B, **269**, 983-990.

Süßenbach, D. (2003) *Diversität von Nachtfaltergemeinschaften entlang eines Höhengradienten in Südecuador (Lepidoptera: Pyraloidea, Arctiidae)*. Ph.D. thesis, University of Bayreuth. URL: http://opus.ub.uni-bayreuth.de/volltexte/2003/33/

Talianchich, A., Winston, J.B. & Ghisalberti, E.L. (2003) Palatability and defense in the aposematic diurnal whistling moth, *Hecatesia exultans* Walker (Lepidoptera: Noctuidae: Agaristinae). *Australian Journal of Entomology*, **42**, 276-280.

Tammaru, T. & Haukioja, E. (1996) Capital breeders and income breeders among Lepidoptera – consequences to population dynamics. *Oikos*, **77**, 561-564.

Thomas, C.D., Hill, J.K. & Lewis, O.T. (1998) Evolutionary consequences of habitat fragmentation in a localized butterfly. *Journal of Animal Ecology*, **67**, 485-497.

Toral, E.C., Feinsinger, P. & Crump, M.L. (2002) Frogs and a cloud-forest edge in Ecuador. *Conservation Biology*, **16**, 735-744.

Turner, J.R.G. (1984) Mimicry: The palatability spectrum and its consequences. In: *The Biology of Butterflies* (eds. R.I. Vane-Wright and P.R. Ackery), pp. 141-161. The Royal Entomological Society 41 Queen`s Gate London, Academic Press.

Weller, S.J., Jacobson, N.L. & Conner, W.E. (1999) The evolution of chemical defences and mating systems in tiger moths (Lepidoptera: Arctiidae). *Biological Journal of the Linnean Society*, **68**, 557-578.

West, B. (2003) *Biston betularia* L. (Lep. Geometridae): Continued decline in industrial melanism in north-west Kent. *Entomologist's Record and Journal of Variation*, **115**, 13-16.

5 Diversity and ensemble composition of geometrid moths along a successional gradient in the Ecuadorian Andes

Nadine Hilt[1, *], Gunnar Brehm[1] & Konrad Fiedler[1, 2]

[1]Department of Animal Ecology I, Universitätsstrasse 30, University of Bayreuth, D-95440 Bayreuth, Germany

[2]Department of Population Ecology, Faculty Centre of Ecology, University of Vienna, Althanstrasse 14, A-1090 Vienna, Austria

* Author for correspondence: Tel: + 49 921 552649; Fax: + 49 921 552784; E-mail: n-hilt@gmx.de

Published in Journal of Tropical Ecology, (2006), **22**, in press

5.1 Abstract

Little is known about the change of species-rich tropical insect communities along habitat gradients. Diversity and species richness of geometrid moths were investigated at 15 anthropogenically disturbed sites in a montane area in the Andes of southern Ecuador representing a successional gradient. These plots were compared with six closed-forest understorey sites. We collected a total of 23,720 individuals representing 868 morphospecies. Local diversity increased with forest recovery and decreased with increasing distance to the natural forest. 18.6% of all species were found as unique singletons. The mean proportions of local singletons differed significantly between three succession classes. Forest understorey showed a higher proportion of singletons than early and late successional stages. Ordination of the moth samples showed a clear separation of geometrid ensembles at successional sites vs. the forest understorey sites. Patterns of species turnover were influenced by the degree of habitat openness, and to a lesser extent by elevation. However, faunal differences were not related to geographical distances between the sampling sites. In conclusion, geometrid moth ensembles of regenerating Andean montane forest remain diverse, but change significantly in composition relative to adjacent natural forest, whereas the diversity and composition of the geometrid fauna are far more strongly affected in non-forested habitats and abandoned pastures.

Keywords: habitat disturbance, Geometridae, herbivorous insects, montane rainforest, species composition, species richness

5.2 Introduction

Andean highland ecosystems are among the best represented in protected areas due to the preponderance of highland parks in the eastern Andes (Armenteras *et al.*, 2003). However, less than 4.5-6.4% of the original pre-Columbian extent of Andean and sub-Andean forests are currently protected (Armenteras *et al.*, 2003). Annual deforestation rates continue to be high (0.94%: FAO 1997), especially outside protected areas. This will lead to the loss of many threatened species in the near future (Brooks *et al.*, 2002). Fragmented habitats under human land-use regimes become increasingly important for the conservation of biodiversity. Even though the preservation of large areas of continuous, pristine habitat is crucial for the conservation of many species, human-dominated landscapes cover the majority of land area in many parts of the world (Ricketts *et al.*, 2001). A considerable number of studies have dealt with effects of logging on animal communities (Meijaard *et al.*, 2005). However, less is known about changes of species-rich tropical insect communities along habitat gradients, representing different successional stages of forest recovery and land use after logging. While a substantial body of evidence has been collated for insects in South-East Asian forests (Chey *et al.*, 1997; Holloway, 1998; Willott, 1999; Intachat & Holloway, 2000; Schulze, 2000; Beck *et al.*, 2002; Fiedler & Schulze, 2004), the far more species-rich Neotropical realm has received much less attention in that regard (Ricketts *et al.*, 2001; Brehm & Fiedler, 2005). Hence, it is still difficult to assess how much of the original biodiversity can be maintained in human-dominated tropical landscapes and how the structure and function of communities may change. Since more than half of global diversity in terms of numbers of described species is represented by insects, the way in which these organisms respond to changes in their habitat is an important concern (DeVries *et al.*, 1997; Hamer & Hill, 2000).

The better-known groups of the Lepidoptera have often been advocated as useful indicators of environmental impact (Kitching *et al.*, 2000). More than 90% of the known lepidopteran species are moths, the majority of which are nocturnal (Scoble, 1995; Young, 1997). The Macrolepidoptera are taxonomically relatively well known and usually attractable to light traps. Accordingly, the numbers of species as well as individuals that can be sampled in short periods of time give statistical power in site-to-site comparisons at high spatial and temporal resolution (Kitching *et al.*, 2000; Fiedler & Schulze, 2004). We chose geometrid moths as a model group. With more than 21,000 validly described species globally, of which some 6,400 (30%) occur in the Neotropical region, Geometridae are one of the three most species-rich moth families (Scoble, 1999).

Tropical geometrid moth ensembles (terminology: Fauth *et al.*, 1996) were previously found to reflect ecological differences between habitats (Intachat *et al.*, 1997, 1999) and to show high habitat fidelity (Holloway, 1984; Chey *et al.*, 1997). A number of recent studies dealt with geometrid diversity along altitudinal, habitat and successional gradients in tropical regions (altitudinal gradient: Schulze, 2000; Brehm, 2002; Brehm & Fiedler, 2003; Axmacher *et al.*, 2004a; habitat gradient: Holloway *et al.*, 1992; Chey *et al.*, 1997; Intachat *et al.*, 1997; Willott, 1999; Ricketts *et al.*, 2001; Brehm & Fiedler, 2005; successional gradient: Holloway, 1998; Kitching *et al.*, 2000; Schulze, 2000; Beck *et al.*, 2002; Axmacher *et al.*, 2004b). All these studies indicate that geometrid moths respond sensitively to changes in habitat quality.

We here compared 15 succession sites with six mature-forest understorey sites situated in the montane forest zone of the Ecuadorian Andes to test the following hypotheses:

(1) Disturbed habitats have a significantly lower geometrid diversity than mature forest (Holloway *et al*., 1992; Kitching *et al*., 2000; Beck *et al*., 2002; Brehm & Fiedler, 2005), because of the habitat specificity of geometrid moths (Brehm & Fiedler, 2003);

(2) The proportion of singletons (species represented by only one individual) is higher in early succession stages (chapter 2) and in forest habitats (Willott, 1999; Novotny & Basset, 2000; Ricketts *et al*., 2001; Brehm *et al*., 2003a) compared with intermediate succession stages (chapter 2), because in early succession stages many tourists or dispersers show up and mature tropical forest understorey is generally noted for a high proportion of singletons (Novotny & Basset, 2000);

(3) The dominance of a few species is higher in early succession stages than in mature forest understorey (Axmacher *et al*., 2004a, b; Fiedler & Schulze, 2004). This assumption is based on the idea that after habitat disturbance, the developing pioneer community is dominated by just a few species (Nummelin & Kaitala, 2004).

(4) Between-habitat diversity (β-diversity) reflects the gradient of disturbance. Moth ensembles differ between habitats of different successional age due to their affiliation with plant resources the availability of which changes with progressing succession (Beck *et al*., 2002).

5.3 Methods

Study area, sampling and identification

The study area in southern Ecuador (Reserva Biológica San Francisco, 3°58' S, 79°5' W) is situated within the Eastern Cordillera of the Andes at the northern border of the Podocarpus National Park (Brehm & Fiedler, 2003; Brehm *et al.*, 2005; chapter 3). It is covered with undisturbed to slightly disturbed montane rainforest (Homeier *et al.*, 2002; Paulsch, 2002). At anthropogenically disturbed sites forest has been replaced by pastures, thickets of bracken (mainly *Pteridium arachnoideum* (Kaulf.) Maxon), shrub encroachment, or regenerating forest (Paulsch, 2002; Hartig & Beck, 2003).

Mean annual precipitation reaches around 2,000 mm without a marked dry season, and the average monthly temperature was 15.6°C at an altitude of 1,952 m a.s.l. (Richter, 2003). We selected 15 sites (labelled A to I) representing seven different stages of vegetation succession and including two abandoned pastures (chapter 2). For most of these stages two replicate sites were selected in close proximity (distance to natural forest between 22 and 445 m), but with minimum distances between the sites of 100 m. In addition, moth samples from six sites situated in the understorey of natural forest (labelled 3a to 5b) were analysed (two replicate sites at every 100 m elevation, Brehm & Fiedler, 2003). At all sites, vegetation appeared to be homogeneous around the position of the light tower in a radius of at least 50 m. These 21 sites, situated in a narrow elevational band (1,800-2,000 m), represent a succession gradient of forest recovery. The earliest successional stage was represented by a landslide along a pathway. Landslides are the commonest form of forest disturbance on steep Andean slopes (Ohl & Bussmann, 2004). Other early succession stages included grassy slopes, bracken thickets, and abandoned pastures (all without woody vegetation) and represented some of the most relevant types of habitats due to local land-use practices. Later succession stages were represented by secondary shrubs (about 5-10 y after clearing), secondary forest (about 40 y after clearing) and the transition zone between forest and a clearing; all these sites had extensive cover by woody vegetation. Altitude and geographical co-ordinates of sampling sites were measured using a Garmin GPS III instrument

(Garmin Instruments Inc., Olathe, KS, USA). Ambient temperature during moth sampling was measured every 30 min during each catch unit with an electronic thermometer (TFA, Dostmann, Wertheim, Germany) 1.60 m above ground (on top of the light tower). Temperature data were averaged over all catch nights for each site. Canopy cover was measured using one hemispherical photograph per site taken with a Nikon Coolpix 990 (3.34 megapixels, and an additional hemispheric lens [Nikon Fisheye F8-E8]). From these images, the ‘visible sky’ value as an estimate of habitat openness was calculated with the HemiView program, version 2.1 (Delta-T Devices, Burwell, Cambridge; see Brehm *et al.*, 2003b). Depending on the type of analysis, the progress of succession was either scored on a rank scale (degree of succession) from 1 (young landslide with sparse vegetation) to 7 (mature forest), according to the proportion of woody plants (see Table 1 in chapter 2). Alternatively, sampling sites were grouped into three categories according to their successional stage (early (E) without woody vegetation: N = 10 sites; late (L) with shrubs or young secondary forest: N = 5; understorey of closed-canopy forest (F): N = 6). For analysis of similarities (ANOSIM) the two abandoned pastures sites (P: N = 2) were separated from the earlier succession stages (E: N = 8 sites).

Moths were manually sampled using a portable light ‘tower’ (Fritz Weber, Stuttgart: height 1.60 m, diameter 0.60 m) with weak light sources (Sylvania blacklight-blue, F 15 W/BLB-TB and Phillips TLD 15 W 05). In contrast to automatic light traps, light towers have been demonstrated to catch a wider spectrum of geometrid moth species and a higher number of specimens per unit time (Axmacher & Fiedler, 2004). We considered the use of these low-power light sources sufficient to minimise cross-attraction of moths between sampled habitats (Muirhead-Thomson, 1991; Schulze & Fiedler, 2003). We restricted sampling to the peak time of moth activity during the evening hours between 18h30 and 21h30 local time (closed-canopy forest) and 18h45 and 21h45 (succession habitats without closed canopy). Although ‘late-night species’ as well as strictly diurnal geometrids will have been missed by this approach, this is not expected to influence the comparisons between sites. Specimens were collected during five field periods. Between four and eight nightly catches from each site were pooled and analysed. Catches were restricted to periods without bright moonlight (McGeachie, 1989; Yela & Holyoak, 1997).

Specimens were first sorted to 'parataxonomic units' (*sensu* Krell, 2004) and later taxonomically identified as far as possible using various reference collections (see Acknowledgements). Taxonomy follows Pitkin (2002) and Brehm *et al*. (2005). Voucher specimens of all species are deposited in the State Museum of Natural History (SMNS), Stuttgart, Germany.

Statistical analyses

The choice of appropriate measures of alpha diversity for species-rich tropical moth ensembles was discussed by Brehm *et al*. (2003a). As a measure of local diversity we used Fisher's alpha (calculations with the program *Species diversity and richness*, Version 2.62, developed by P.A. Henderson and R.M.H. Seaby) and Hurlbert's rarefaction method for a standardized number of 350 specimens (URL for software: http://www.zoology.ubc.ca/~krebs, developed by A.J. Kenney and C.J. Krebs). Rarefaction is particularly useful if assemblages are sampled with different intensity or success (Gotelli & Colwell, 2001), and for samples of different size (Hurlbert, 1971; Schulze & Fiedler, 2003).

Insect assemblages in tropical rainforests usually contain large numbers of rare species (singletons). Novotny and Basset (2000) distinguished between 'local singletons', i.e. species found as a single individual in component communities, and 'unique singletons', viz. species found as a single individual in a combined data set. We calculated the proportion of both types of singletons for every sampling site. To compare the proportion of singletons from succession sites vs. mature forest we randomly rarefied the larger cumulative sample (geometrids of all succession habitats, 20,670 individuals) to the level of the smaller sample from natural forest (3,050 individuals). We then compared the proportion of observed singletons in natural forest to the 95% confidence interval for singletons in succession habitats calculated after 10 randomisation runs. Comparisons of the numbers of individuals and species observed per night were performed with ANOVA across the three habitat categories.

Dominance of the commonest species was expressed through the Berger-Parker index (Southwood & Henderson, 2000). We restricted quantitative comparisons of relative abundances to the 10 overall most abundant species (i.e. those recorded with > 235 individuals in total).

We ordinated moth samples by non-metric multidimensional scaling (NMDS: Clarke, 1993) to study species composition of local geometrid ensembles using the full abundance information for all species. To alleviate sampling effects (which are especially prevalent if sampling is not complete, samples contain many rare species, and are of different size and diversity: Brehm & Fiedler, 2004) we used the chord-normalized expected species shared index (Gallagher's CNESS index: Trueblood *et al.*, 1994) as a measure of dissimilarity between samples. The CNESS index can be adjusted by choice of the sample size parameter, *m*. At its minimum of *m* = 1, CNESS emphasises the role of dominant species. At the other extreme, CNESS dissimilarities for maximum *m* values stress the contribution of rare species to faunal differences. We also used an intermediate value (*m* = 170). We calculated CNESS distances using the program COMPAH96 (available from E. Gallagher, University of Massachusetts at Boston, via website, URL: http://alpha.es.umb.edu/faculty/edg/files/edgwebp.htm). Ordinations were performed with an updated version of Statistica 6 (StatSoft Tulsa, UK). The significance of faunal differences between predefined groups of sites was assessed by ANOSIM (Clarke & Warwick, 2001) with 1,000 random permutations. We investigated the association between distance matrices using a rank test based on Spearman coefficients, as implemented in PRIMER v5 (Clarke & Warwick, 2001) with 1,000 random permutations. All other statistical analyses were performed using an updated version of Statistica 6. Where necessary, multiple tests of significance were corrected for a table-wide false discovery rate (FDR) of $P<0.05$ according to the step-up procedure by Benjamini and Hochberg (1995).

Table 1: Numbers of collected species and individuals, sampling nights, two measures of species richness and diversity, the number of singletons, and the habitat category for all 21 study sites. Habitat categories: E = early succession, L = Late succession, F = Forest, P = Abandoned pasture.

Sample site	Altitude (m)	Species number	Number of Individuals	Sample nights	Mean catch per night	Fisher's alpha	Expected species number (rarefied to 350 individuals)	Number of local singletons	Habitat category
A	1913	329	1588	6	265	126.0	134.2	170	E
B1	1872	287	1337	6	223	112.0	140.5	128	E
B2	1925	246	970	6	162	106.2	145.0	109	E
C	1830	277	1529	8	191	98.8	130.6	114	E
D1	1894	194	879	7	126	77.0	112.8	106	E or P
D2	1908	186	746	7	107	79.4	118.5	104	E or P
E1	1832	225	624	7	89	126.2	161.2	121	E
E2	1863	292	1485	6	248	108.7	132.9	135	E
F1	1917	269	928	6	155	127.0	161.0	120	E
F2	1921	361	1553	6	259	147.6	164.6	165	E
G1	1886	414	2079	7	297	155.0	175.0	156	L
G2	1912	376	2016	6	336	136.2	169.7	127	L
H1	1900	334	1629	6	272	127.2	147.5	136	L
H2	1920	366	1444	6	241	158.0	180.1	138	L
I	1973	423	1863	6	311	170.6	186.3	158	L
3a	1800	204	497	4	124	129.3	164.8	119	F
3b	1800	171	384	4	96	118.2	161.3	107	F
4a	1850	181	473	4	118	107.2	149.5	112	F
4b	1875	226	649	4	162	123.1	158.6	118	F
5a	2005	202	618	4	155	104.4	147.5	107	F
5b	2005	190	429	4	107	130.5	167.9	114	F

5.4 Results

Alpha diversity of geometrid moths

We sampled a total of 23,720 individuals representing 868 species during 120 sample nights (Table 1; see for detailed species list Appendix 2, Brehm *et al.*, 2005). Five hundred and sixty-four (65%) of these morphospecies comprising 78.1% of all individuals could be taxonomically identified at species level. 366 species (42.2%) were restricted to the succession sites, 92 (10.6%) to the mature forest understorey and 410 (47.2%) were shared between both types of habitats. The minimum and maximum numbers of collected individuals per site were 384 (site 3b) and 2,079 (site G1), respectively. Numbers of observed species per site ranged from 171 (site 3b) to 423 (site I). The average number of individuals caught per night varied significantly across all three different habitat categories (one-way ANOVA: $F_{2,117} = 12.1$; $P<0.001$; Levene-test for homogeneous variances, $P>0.09$). Nightly catches in later succession stages (mean value ± 1 SD: 291 ± 126 with N = 31; sites G to I) were significantly higher than at earlier succession stages (mean value: 176 ± 146 with N = 65) and forest understorey (mean value: 127 ± 84 with N = 24), respectively. Only the difference between late-successional habitats and the two other habitat classes (early, forest understorey) was significant (Scheffé test $P<0.001$). The mean number of observed species per night (ANOVA: $F_{2,18} = 7.75$, $P<0.005$; Levene-test for homogeneous variances $P>0.05$) was significantly higher in later successional stages (mean ± SD: 62 ± 6) than in earlier ones (43 ± 11) (Scheffé test, $P<0.005$), but the difference in comparison with mature forest understorey (49 ± 5) was not large enough to reach statistical significance (Scheffé test, $P>0.07$).

Values of Fisher's alpha were strongly correlated with rarefied species richness ($r_P = 0.91$, $P<0.001$) and showed therefore the same pattern along the succession gradient (see Table 1). Thus we subsequently restricted our analyses to the rarefied species numbers. Figure 1a shows the rarefied species richness at a standard sample size of 350 individuals. Diversity was significantly higher in the later succession stages than in earlier stages. However, the difference in moth diversity between the later succession stages and the mature forest understorey was not significant. Only the early succession stages had distinctly lower diversity values. Correlations between abiotic factors, e.g. altitude, mean temperature, canopy openness and distance of the sites from the mature forest vs. values of Fisher's alpha and rarefaction were not significant with one exception. Irrespective of the measure used, diversity decreased with increasing distance to the natural forest (distance vs. Fisher's alpha: $r_P = -0.59$, $P<0.005$ and vs. rarefied species numbers: $r_P = -0.65$, $P<0.005$).

A total of 161 species (18.6%) was found as unique singletons, i.e. only with one specimen, and 91 species (10.5%) were doubletons. Rarefaction analysis (i.e. 3,050 individuals, see Methods) was used to compare the proportions of unique singletons between succession and forest sites. The observed proportion of singletons at the forest understorey sites (59.8%) was almost twice as high as at the succession sites (expected proportion of singletons ± SD: 32.2% ± 1.1%). The ratio of singletons at individual sites (local singletons) varied between 33.8% and 62.6% of the species (Table 1). The mean proportions of local singletons (Figure 1b) differed significantly between the three succession classes (ANOVA: $F_{2,18} = 28.2$, $P<0.001$). The highest proportion was found in the forest understorey, followed by the earlier succession stages, while the lowest values were found in succession stages after the onset of recovery of woody vegetation.

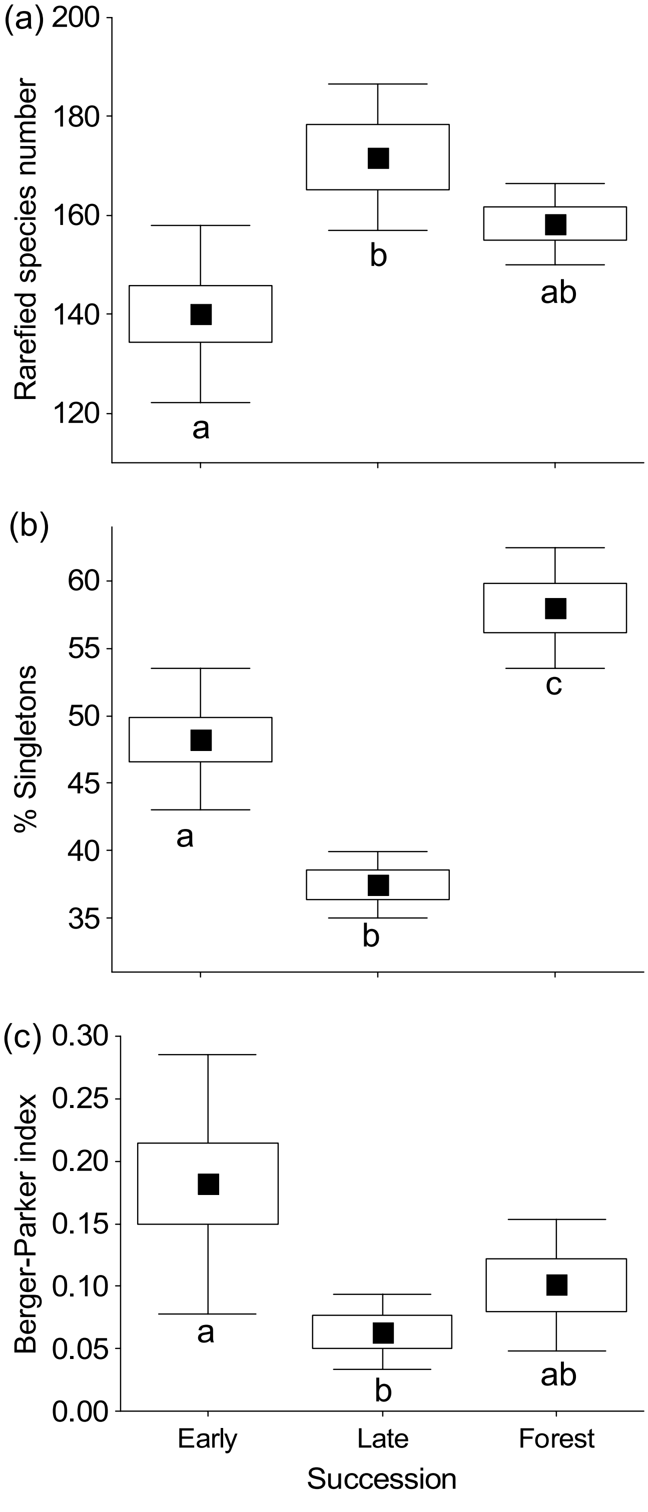


Figure 1: (a) Diversity expressed as rarefied species number (350 individuals; ANOVA: $F_{2,18}$ = 7.82, $P<0.005$; Levene test $P>0.2$), (b) proportion of local singletons (in % of species), and (c) Berger-Parker index for geometrid moths in the three different habitat classes. Boxes labelled with different letters differ significantly at $P<0.05$ (one-way ANOVA followed by Scheffé test). Symbols = means, boxes = ± 1 SE, whiskers = ± 1 SD.

The Berger-Parker index varied between 0.03 (site G1) and 0.32 (sites A and E2). Mean dominance values (Figure 1c) differed among the three habitat categories (Kruskal-Wallis ANOVA: H(2, N=21) = 7.50, $P<0.05$), but the difference was only significant between the early and the late-successional stages (post hoc test, $P<0.05$). The highest values were found in the early stages, followed by the mature forest understorey and the later successional stages. The ten overall commonest species are listed in Table 2. The relative abundance of *Pantherodes conglomerata* decreased significantly along the succession gradient from early stages to mature-forest understorey (Kruskal-Wallis ANOVA: H(2, N=21) = 15.1, $P<0.001$). Some species were equally common in all three habitat categories (*Argyrotome prospectata*, and *Oxydia trychiata,* ranks 3, and 7), whereas some species showed a clear preference for succession sites (*Pantherodes conglomerata*, *Sabulodes thermidora*, *Physocleora* sp., *Perissopteryx* sp. near *nigricomata,* ranks 1, 2, 8, and 9) or forest understorey (*Chloropteryx opalaria, Physocleora pulverata,* ranks 4 and 5). In most cases the relative abundances of these 10 commonest species differed significantly between the habitat categories (Table 2).

Table 2: Relative abundances of the 10 commonest geometrid species. Included are results of Kruskal-Wallis ANOVAs for each species and the mean relative abundance ± SD. *P* values marked with # are not significant after step-up FDR correction of *P*<0.05.

Species name and author	N	Species Rank	H(2, N = 21) statistic	*P* value	Early succession (N=10)	Late succession (N=5)	Forest understorey (N=6)
Pantherodes conglomerata Warren 1894	2597	1	15.1	**0.0005**	17.4 ± 11.0	6.0 ± 2.6	0.4 ± 0.4
Sabulodes thermidora Thierry-Mieg 1894	1006	2	7.9	**0.019**	6.4 ± 4.8	1.5 ± 1.1	3.4 ± 4.2
Argyrotome prospectata Snellen 1874	432	3	3.7	0.159	2.5 ± 2.2	1.0 ± 0.9	1.6 ± 2.3
Chloropteryx opalaria Guenée 1857	334	4	8.5	**0.014**	1.1 ± 0.9	1.3 ± 0.9	2.8 ± 1.3
Physocleora pulverata Warren 1907	327	5	12.7	**0.0018**	0.4 ± 0.3	0.4 ± 0.1	7.9 ± 6.8
Eois paraviolascens Dognin 1900	321	6	6.7	0.036	0.5 ± 0.6	2.8 ± 4.0	0.3 ± 0.3
Oxydia trychiata Guenée 1858	297	7	5.1	0.078	0.8 ± 0.4	1.8 ± 0.8	1.7 ± 1.2
Physocleora sp.	288	8	12.7	**0.002**	1.2 ± 0.9	1.7 ± 0.4	0.1 ± 0.2
Perissopteryx sp. nr. *nigricomata* Warren 1901	249	9	12.8	**0.002**	0.8 ± 0.6	1.8 ± 1.2	0.1 ± 0.1
Perizoma zenobia Thierry-Mieg 1893	242	10	10.9	**0.004**	1.6 ± 1.1	0.2 ± 0.1	1.0 ± 0.8

Species turnover along the succession gradient

For all three different values of the sample size parameter *m* (Figures 2a-c), non-metric two-dimensional scaling of the CNESS index yielded similar ordinations of the moth ensembles. In all three cases the successional sites were significantly separated from the mature forest understorey (ANOSIM with step-up FDR correction; E vs. F: $0.76 < R < 0.82$, $P<0.005$; L vs. F: $0.34 < R < 0.74$, $P<0.05$). Geometrid moth samples from the natural forest understorey formed a distinct group which clearly reflected the altitudinal gradient from the lower sites (3a, 3b) to the higher ones (5a, 5b). A separation between the earlier und later successional sites was only found when the common or moderately abundant species were emphasized, i.e. with $m = 1$ and $m = 170$ (E vs. L: $0.37 < R < 0.40$, $P<0.05$). No difference between these different succession classes could be found, when the rare species were emphasized at $m = 384$ (E vs. L: $R = 0.24$, $P>0.05$). However with increasing *m*, the earlier successional stages were more clearly separated from the two abandoned pasture sites ($m = 170$ and 384; E vs. P: $0.77 < R < 0.90$, $P<0.05$).

Extracted scores of the moth samples along the first NMDS dimension correlated with the following environmental factors (ordered according to strength of the correlation) (Table 3): ‘visible sky’, degree of succession, distance of the sites from the natural forest, and temperature during sampling. Samples were ordered along the second dimension according to the elevation of the sites (correlation between the extracted scores of the second dimension and altitude: $r_P > 0.68$, $P<0.001$). Rank-based matrix correlation tests revealed significant relationships between faunal dissimilarity and the degree of habitat openness (‘visible sky’) as well as elevation and temperature during sampling (Table 4). However, temperature effects were significant only with higher *m* values. Faunal dissimilarity was not at all related to the geographical distance between sampling sites ($P>0.64$). Thus, ‘visible sky’ emerged as the strongest predictor of faunal change, but altitude of sampling sites also significantly influenced faunal similarity.

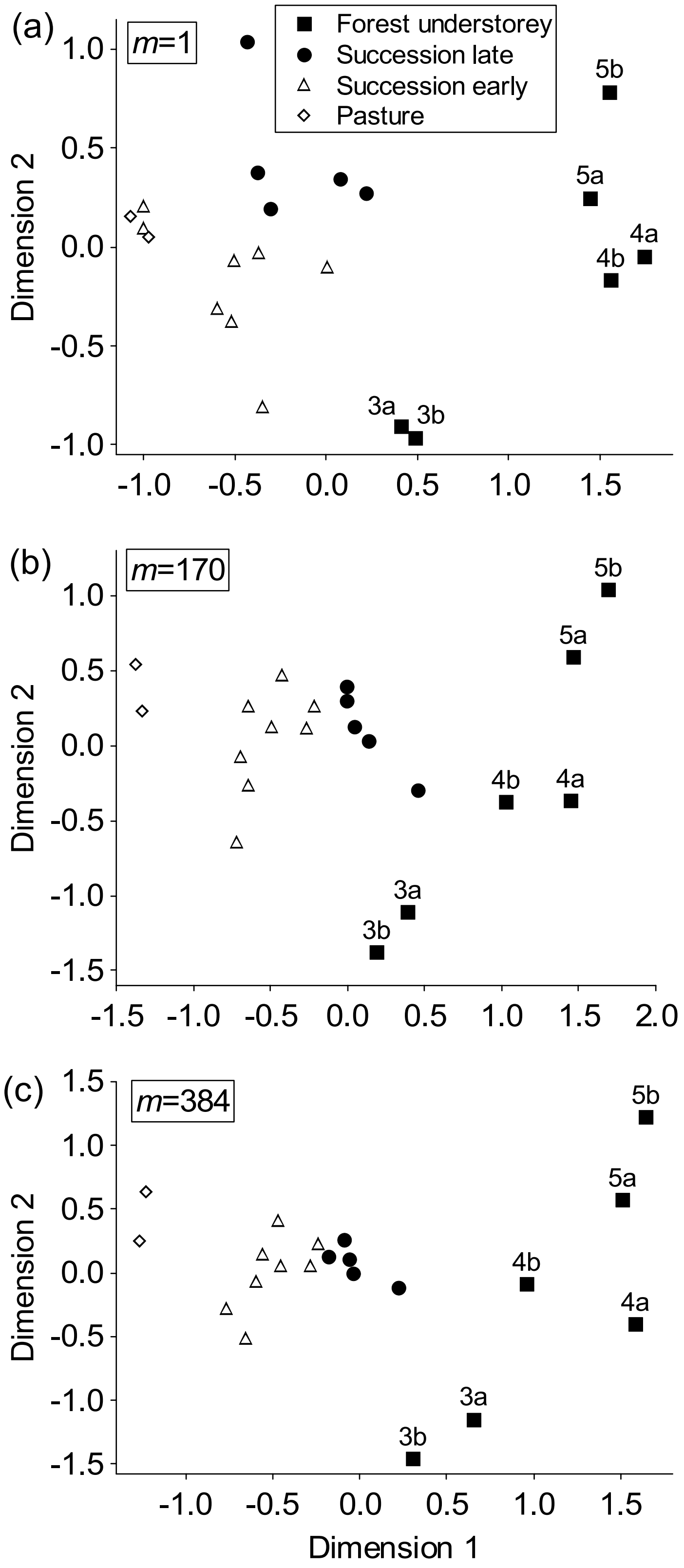


Figure 2: Non-linear two-dimensional scaling plots of moth samples from 21 sites based on CNESS distances with different values of the sample size parameter *m*: (a) *m* = 1, stress 0.10; (b) *m* = 170, stress 0.12, and (c) *m* = 384, stress 0.11.

Table 3: Pearson correlation coefficients between the axis scores of geometrid samples extracted from two-dimensional NMDS ordinations and different environmental factors (altitude, 'visible sky', distance of the sites from forest, and temperature) as well as Spearman rank correlation coefficients for the degree of succession. *m* – Sample size parameter of the CNESS index. All nominally significant results remain so after correction for a FDR of *P*<0.05. n.s.: not significant. * *P*<0.05, ** *P*<0.01, * *P*<0.001**

	Altitude	'Visible sky'	Degree of succession	Distance from forest	Temperature
m = 1					
Axis 1	0.14 n.s.	-0.88***	0.83***	-0.70***	0.50*
Axis 2	0.69***	0.07 n.s.	0.17 n.s.	0.05 n.s.	-0.16 n.s.
m = 170					
Axis 1	0.29 n.s.	-0.89***	0.90***	-0.81***	0.55**
Axis 2	-0.85***	-0.30 n.s.	0.14 n.s.	-0.22 n.s.	0.41 n.s.
m = 384					
Axis 1	-0.23 n.s	0.92***	-0.90***	0.79***	-0.60**
Axis 2	0.85***	0.22 n.s	-0.14 n.s	0.22 n.s	-0.35 n.s.

Table 4: Results of matrix rank correlations (based on Spearman coefficients, 1000 random permutations) between faunal dissimilarity (CNESS distances) and distance matrices for elevation, geographic position, temperature, and 'visible sky'. For environmental variables, Euclidean distances between sites were used. All figures are significant after a step-up FDR correction of *P*<0.05. n.s.: not significant. * *P*<0.05, ** *P*<0.01, * *P*<0.001**

m value	Elevation	Geographic distance	'Visible sky'	Temperature
1	0.26**	-0.05 n.s.	0.73**	0.18 n.s.
170	0.34**	-0.07 n.s.	0.75**	0.20*
384	0.36**	-0.11 n.s.	0.72**	0.21*

5.5 Discussion

High moth diversity in advanced successional stages

With 868 observed geometrid species along a gradient of succession, the study area is very species rich at a small spatial scale (ca. 2 km²). Overall, gamma-diversity across the succession gradient (expressed as Fisher's alpha of all samples combined ± SD) reached a value of 177 ± 2.8. Compared with studies from Africa (188 species, Axmacher *et al*., 2004a), South-East Asia (500 species, Beck *et al*., 2002) and Australia (wet season: 122 species and dry season: 94 species, Kitching *et al*., 2000) at comparably small scales our data underscore the outstanding species richness of Andean montane habitats (Brehm *et al*., 2005).

Contrary to our expectations, the highest geometrid diversity along the succession gradient was found in the later succession stages and not in the mature forest understorey. Thus, geometrid ensembles of advanced succession sites in the Ecuadorian Andes are particularly rich in species and occasionally even slightly surpass those of mature natural forest. High geometrid moth diversity in advanced regenerating forest was also found by Beck *et al*. (2002) along a habitat gradient ranging from cultivated areas to primary rainforest on Borneo. In the montane forest zone on Mt. Kilimanjaro geometrid diversity was likewise not maximal in mature forest, but in disturbed habitats close to intact forest (Axmacher *et al*., 2004b). However, other studies did not find significant differences in moth diversity between disturbed sites and natural forest (SE Asia: Chey *et al*., 1997; Willott, 1999). Apart from minor variations between moth taxa and between regions, all these studies show that moth faunas in tropical secondary forests or in regenerating succession habitats may retain considerable diversity, as long as natural forests as source areas for recolonisation remain in the vicinity (see also Schulze, 2000).

Possible reasons for the lower species richness in the natural forest as compared to later successional stages in Ecuador could be: (1) Sampling effort differed between habitat types (see above). However, rarefaction analyses should have eliminated sampling bias. (2) Sampling was restricted to the understorey at the forest sites, and did not include the canopy layer. For example, Willott (1999) found that moth diversity was 26% lower in understorey samples compared to the understorey and canopy combined. On the contrary, Beck *et al*. (2002) showed that in the Geometridae diversity estimates for combined understorey plus canopy samples did not significantly exceed the scores for understorey ensembles alone (see also Schulze, 2000). A similar pattern was observed in a Costa Rican lowland rainforest (GB, unpublished data), indicating that understorey sampling is likely to be sufficient in areas with steep slopes and small trees (15-20 m in the study area in Ecuador; Homeier, 2004). (3) The effective attraction radius of the light trap may depend on habitat structure, e.g. the density of the vegetation. As a consequence, moths might be attracted from a larger distance in open habitats such as early successional stages. However, the highest numbers of individuals caught per night and the highest local diversities were found in the later successional stages, which have also denser vegetation than the earlier stages.

The reasons for higher numbers of species and individuals in the later successional stages are possibly (1) secondary-forest fauna contains species, which are otherwise more abundant in, or even restricted to, the canopy (Willott, 1999), (2) these habitats contain a mixture species from open habitats such as early successional stages as well as from mature forest. Disturbance creates opportunities for species not found in undisturbed forest, and the habitat mosaic resulting from regeneration after patchy disturbance further increases the number of niches available.

We found no evidence that generally larger numbers of geometrid moth species and individuals would be attracted at open sites than within closed-forest understorey. Mean numbers of observed species per night were only different between the early and later succession stages, but not in comparison with the forest understorey. Brehm and Fiedler (2003) also observed similar average numbers of geometrid individuals during 3-h catch units (which even exceeded 200 individuals per night) at the forest sites. Moreover, as detailed above, a growing number of studies has revealed that diversity of tropical moth ensembles is usually not lower, and sometimes even higher, in habitats under moderate anthropogenic disturbance as compared to closed forest. Collectively, the available pieces of evidence underline that this diversity pattern cannot be disregarded as a sampling artefact of light-trapping. The influence of disturbance on moth diversity also depends on the spatial scale considered (Hill & Hamer, 2004; see also Rahbek, 2005). The extent of such scale dependence needs to be explored in tropical montane forests in the future.

The much lower diversity of geometrid moths in the earlier successional stages can be explained with the preference of many geometrids (especially in the subfamily Ennominae) for woody plants as larval hosts (Scoble, 1999). Furthermore, specialised geometrid species such as the genus *Eois* frequently depend on larval food plants that only occur in mature forests or later stages of succession (Brehm & Fiedler, 2005). Geometrids have also been regarded as a group with limited mobility and relatively high habitat fidelity (Holloway, 1984; Intachat & Holloway, 2000; Thomas, 2002). Although geometrid moths may only rarely disperse across larger distances following disturbance to their natural habitats (Summerville & Crist, 2004), ‘tourist’ species from natural forest are likely to occur in all investigated habitats because of their close proximity to each other (Brehm & Fiedler, 2005). The high proportion of singletons in our samples underscores the fact that such dispersing individuals are common in open habitats (Figure 1b). Thus, species diversity of these early succession habitats may be overestimated.

Rare and abundant species in tropical moth communities

Insect communities in tropical rainforests mostly contain large numbers of rare species. Singletons often comprise more than half of the species total (Novotny & Basset, 2000). In samples from tropical moth ensembles usually *c.* 30-60% of all species occurs as singletons (Willott, 1999; Ricketts *et al*., 2001; Brehm *et al*., 2003a; Schulze & Fiedler, 2003). All these data suggest that these moth samples were drawn from very large species pools. Our results from a successional gradient in the Ecuadorian Andes fit well into this range of observations. As expected, the proportion of unique singletons was much lower (18.6%) than local singletons.

Singletons were far more prevalent in the mature forest than in disturbed habitats. This applied to the comparison of rarefied samples (59.8% vs. 32.2%) as well as when comparing mean local singleton ratios (Figure 1b). This indicates that the contribution of rare species to moth ensembles is reduced as a consequence of habitat disturbance. In our study, the ratio of local singletons was not only high in the mature forest, but also in the earlier succession stages. Many singletons in these open, disturbed habitats must probably be regarded as colonists, which were sampled during dispersal flights from the nearby forest. However, even early successional stages support the existence of geometrid species with caterpillars that feed on ‘pioneer’ plants, e.g. certain members of the genus *Eupithecia* and other species (Brehm & Fiedler, 2005; see also Intachat & Holloway, 2000; Lepš *et al*., 2001).

Dominance in tropical moth assemblages is usually low (Wolda, 1992). The most common species typically attains 5-10% of all individuals in a light-trap sample (Willott, 1999; Schulze, 2000; Brehm, 2002), as opposed to 8-29% in moth ensembles from temperate regions (Germany: undisturbed sites < 8% vs. disturbed sites > 8%; Israel: undisturbed sites c. 17% vs. disturbed sites 25-29%; A. Hausmann, pers. comm.). Dominance in tropical assemblages may increase as a response to habitat disturbance (Fiedler & Schulze, 2004; Nummelin & Kaitala, 2004). For example, Fiedler and Schulze (2004) found that dominance of a few species was more pronounced in Bornean pyraloid ensembles from more heavily disturbed sites. We observed similar changes in ensemble structure in Andean geometrids. The Berger-Parker index was highest in the earlier succession stages (mean ± SD: 18.2 ± 10.4%), but only 10.1 ± 5.3% in mature forest. Interestingly, dominance was lowest in late-successional habitats, and not in natural forest. This indicates that geometrid samples in advanced secondary habitats have a particularly even rank-abundance distribution. The reasons for this may be found in the mosaic nature of these late-successional habitats, where many different species are able to thrive but do not reach full dominance. A few species benefit disproportionately from habitat disturbance, probably because their resources are boosted temporarily.

Nummelin and Kaitala (2004), however, gave a short review of dominance in different data sets (e.g. beetles, butterflies, plants) in logged vs. unlogged forest sites and concluded that dominance indices are not universally suitable indicators of rainforest disturbance.

The most prominent beneficiary among Andean geometrids in our samples was *Pantherodes conglomerata*. Eighteen per cent of all individuals caught in early successional habitats belonged to this single species. At individual sites, *P. conglomerata* made up 5-32% of the geometrid samples. Thus, this species can be regarded as a typical inhabitant of disturbed habitats. Recorded host plants are species of *Boehmeria* (Urticaceae) and *Vernonia* (Asteraceae) (URL: http://www.caterpillars.org). *Boehmeria* sp. is only common in disturbed habitats in the study area (J. Homeier, pers. comm.). Only for a few additional common species are host plant data available: *Physocleora* sp. (Euphorbiaceae: *Alchornea* sp.), *Sabulodes thermidora* (Asteraceae: *Baccharis latifolia*), and *Oxydia trychiata* (Cupressaceae: *Cupressus* sp. and Pinaceae: *Pinus* sp.; Phytolaccaceae: (URL: http://www.nhm.ac.uk/entomology/hostplants/; http://www.caterpillars.org; Brehm, 2003). All these host plants are characteristic of succession habitats (*Baccharis, Alchornea*) or are exotic tree species (*Pinus, Cupressus*). Thus, the commonness of the aforementioned geometrid moths in habitats under anthropogenic influence may well reflect increased resource availability.

Changes in species composition

As discussed above, the proportion of rare species and the contribution of dominant species changed markedly with forest regeneration. Also, taking the entire ensembles into account, there was a distinct change in species composition during succession. However, this was by no means a radical species turnover. Almost half of the species observed were shared between the successional sites and the forest understorey. Ordination analyses revealed a clear segregation of these two habitat categories. However, the more heavily the rare species were weighted (i.e. using intermediate and high values of the sample size parameter *m* for the CNESS distance measure), the more clearly did the ordinations of moth samples mirror the progress of succession. However, the highest resolution was achieved with an intermediate *m* parameter value. This means that neither the most common nor the rarest species have highest indicator potential in the Geometridae. Abundances of some of the commonest species varied erratically which partially obscured differentiation (e.g. between abandoned pastures and early succession habitats). The rare species were for the most part (> 60%) identical in the different succession stages (results not shown), while there was a prominent turnover of these rare geometrids to the forest understorey. Geometrid ensembles in habitats dominated by grassland vegetation (abandoned pastures D1, D2 as well as sites E1, E2) turned out to be different from those at the remaining successional sites. This pattern is largely due to the extreme dominance of *Pantherodes conglomerata* at such sites (see above).

The ordination diagrams yielded two axes that reflected two important environmental gradients. The first NMDS dimension was essentially a disturbance axis and reflected variables such as the degree of openness (‘visible sky’), the degree of habitat disturbance, the distance of the sites to the natural forest and air temperature. Ambient temperature drops more quickly in open habitats (Murcia, 1995; Basset *et al*., 2001; Toral *et al*., 2002). The second axis reflected the altitude of the sites. These ecological interpretations of ordination axes were equally well supported by matrix rank correlation tests and explorations of axis scores extracted by ordination.

Despite the short distances between habitats studied, local ecological processes were strong enough to allow for a differentiation between moth ensembles from mature forest and anthropogenically disturbed sites.

In conclusion, despite the small spatial scale at which this investigation was conducted we found clear patterns of alpha and beta diversity along the succession gradient from early succession stages to the mature forest understorey. Alpha diversity was very high and increased with forest recovery. The analysis of between-habitat diversity revealed clear responses to anthropogenic (disturbance) and natural habitat gradients (altitude) in geometrid moths. This underscores that the usefulness of geometrid moths as sensitive indicators for environmental change. Even though many moths are relatively mobile organisms (Daily, 1996), Ricketts *et al*. (2001) and Summerville and Crist (2004) showed that their diversity often declines strongly in disturbed and secondary habitats, if the connection to source habitats is lost. It is to be expected that similar effects will occur in the moth fauna we have studied here, which is the richest thus far known globally (Brehm *et al*., 2005). Hence, further studies should explore the role of spatial scale (> 1 km from the natural forest) as well as geographical proximity of sites for recolonisation and diversity of disturbed habitats in the Andes.

Acknowledgements

We thank Dirk Süßenbach who provided data from his samples from natural forest. Doreen Fetting, Jörg Hager, Claudia Knake, Georg Petschenka, Claudia Ramenda, Caroline Schulze, Annick Servant, Anna Spengler, Katja Temnow and Anne Walter (all at University of Bayreuth) helped with sampling and processing moths. Giovanni Onore (Pontifícia Universidad Católica del Ecuador, Quito) and Christoph L. Häuser (State Museum of Natural History, Stuttgart) supported the project logistically. Martin R. Honey, Linda M. Pitkin (Natural History Museum, London) and Axel Hausmann (Zoologische Staatssammlung, Munich) provided access to reference collections under their care. Matthias Oesker (Bielefeld) assisted with measuring canopy closure. The Ministerio del Medio Ambiente in Ecuador issued research permits (Nro. 002-PNP-DBAP-RLZCH/MA), and the foundation Nature and Culture International (Loja, Ecuador) allowed access to the study sites and their facilities. The Deutsche Forschungsgemeinschaft financed our work (FOR 402/1-1 TP15, FOR 402/2-1 TP A3).

5.6 References

Armenteras, D., Gast, F. & Villareal, H. (2003) Andean forest fragmentation and the representativeness of protected natural areas in the eastern Andes, Colombia. *Biological Conservation*, **113**, 245-256.

Axmacher, J.C. & Fiedler, K. (2004) Manual versus automatic moth sampling at equal light sources – a comparison of catches from Mt. Kilimanjaro. *Journal of the Lepidopterists' Society*, **58**, 196-202.

Axmacher, J.C., Holtmann, G., Scheuermann, L., Brehm, G., Müller-Hohenstein, K. & Fiedler, K. (2004a) Diversity of geometrid moths (Lepidoptera: Geometridae) along an Afrotropical elevational rainforest transect. *Diversity and Distributions*, **10**, 293-302.

Axmacher, J.C., Tünte, H., Schrumpf, M., Müller-Hohenstein, K., Lyaruu, H.V.M. & Fiedler, K. (2004b) Diverging diversity patterns of vascular plants and geometrid moths during forest regeneration on Mt. Kilimanjaro, Tanzania. *Journal of Biogeography*, **31**, 895-904.

Basset, Y., Charles, E., Hammond, D.S. & Brown, V.K. (2001) Short-term effects of canopy openness on insect herbivores in a rain forest in Guyana. *Journal of Applied Ecology*, **38**, 1045-1058.

Beck, J., Schulze, C.H., Linsenmair, K.E. & Fiedler, K. (2002) From forest to farmland: diversity of geometrid moths along two habitat gradients on Borneo. *Journal of Tropical Ecology*, **18**, 33-51.

Benjamini, Y. & Hochberg, Y. (1995) Controlling the false discovery rate: a pratical and powerful approach to multiple testing. *Journal of the Royal Statistical Society* B, **57**, 289-300.

Brehm, G. (2002) *Diversity of geometrid moths in a montane rainforest in Ecuador*. Ph.D. thesis, University of Bayreuth. URL: http://opus.ub.uni-bayreuth.de/volltexte/2003/20

Brehm, G. (2003) Host-pant records and illustrations of the larvae of 19 geometrid moth species from a montane rainforest in Ecuador (Lepidoptera: Geometridae). *Nachrichten des Entomologischen Vereins Apollo, N.F.*, **24**, 29-34.

Brehm, G. & Fiedler, K. (2003) Faunal composition of geometrid moths changes with altitude in an Andean montane rain forest. *Journal of Biogeography*, **30**, 431-440.

Brehm, G. & Fiedler, K. (2004) Ordinating tropical moth ensembles from an elevational gradient: a comparison of common methods. *Journal of Tropical Ecology*, **20**, 165-172.

Brehm, G. & Fiedler, K. (2005) Diversity and community structure of geometrid moths of disturbed habitat in a montane area in the Ecuadorian Andes. *Journal of Research on the Lepidoptera*, **38**, 1-14.

Brehm, G., Süßenbach, D. & Fiedler, K. (2003a) Unique elevational diversity patterns of geometrid moths in an Andean montane rainforest. *Ecography*, **26**, 456-466.

Brehm, G., Homeier, J. & Fiedler, K. (2003b) Beta diversity of geometrid moths (Lepidoptera: Geometridae) in an Andean montane rainforest. *Diversity and Distributions*, **9**, 351-366.

Brehm, G., Pitkin, L.M., Hilt, N. & Fiedler, K. (2005) Montane Andean rain forests are a global diversity hotspot of geometrid moths. *Journal of Biogeography*, **32**, 1621-1627.

Brooks, T.M., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A.B., Rylands, A.B., Konstant, W.R., Flick, P., Pilgrim, J., Oldfield, S., Magin, G. & Hilton-Taylor, C. (2002) Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology*, **16**, 909-923.

Chey, V.K., Holloway, J.D. & Speight, M.R. (1997) Diversity of moths in forest plantations and natural forests in Sabah. *Bulletin of Entomological Research*, **87**, 371-385.

Clarke, K.R. (1993) Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, **18**, 117-143.

Clarke, K.R. & Warwick, R.M. (2001) *Change in marine communities: an approach to statistical analysis and interpretation*. (2nd edition). Primer-E, Plymouth. 172 pp.

Daily, G.C. (1996) Nocturnality and species survival. *Proceedings of the National Academy of Sciences of the United States of America*, **93**, 11709-11712.

DeVries, P.J., Murray, D. & Lande, R. (1997) Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. *Biological Journal of the Linnean Society*, **62**, 343-364.

FAO 1997. *State of the world's forests 1997*, FAO, Rome. 200 pp.

Fauth, J.E., Bernardo, J., Camara, M., Resetarits, W.J., Van Buskirk, J. & McCollum, S.A. (1996) Simplifying the jargon of community ecology: a conceptual approach. *The American Naturalist*, **147**, 282-286.

Fiedler, K. & Schulze, C.H. (2004) Forest modification affects diversity (but not dynamics) of speciose tropical pyraloid moth communities. *Biotropica*, **36**, 615-627.

Gotelli, N.J. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**, 379-391.

Hamer, K.C. & Hill, J.K. (2000) Scale-dependent effects of habitat disturbance on species richness in tropical forests. *Conservation Biology*, **14**, 1435-1440.

Hartig, K. & Beck, E. (2003) The bracken fern (*Pteridium arachnoideum* (Kaulf.) Maxon) dilemma in the Andes of Southern Ecuador. *Ecotropica*, **9**, 3-13.

Hill, J.K. & Hamer, K.C. (2004) Determining impacts of habitat modification on diversity of tropical forest fauna: the importance of spatial scale. *Journal of Applied Ecology*, **41**, 744-754.

Holloway, J.D. (1984) The larger moths of Gunung Mulu National Park; a preliminary assessment of their distribution, ecology and potential as environmental indicators. *Sarawak Museum Journal*, **30**, 149-190.

Holloway, J.D. (1998) The impact of traditional and modern cultivation practices, including forestry, on lepidopteran diversity in Malaysia and Indonesia. In: *Dynamics of tropical ecosystems* (eds. D.M. Newbery, H.H.T. Prins and N.D. Brown), pp. 567-597. Blackwell, Oxford.

Holloway, J.D., Kirk-Spriggs, A.H. & Chey, V.K. (1992) The response of some rain forest insect groups to logging and conversion to plantation. *Philosophical Transactions of the Royal Society* B, **335**, 425-436.

Homeier, J. (2004) Baumdiversität, Waldstruktur und Wachstumsdynamik zweier tropischer Bergregenwälder in Ecuador und Costa Rica. *Dissertationes Botanicae*, **391**, 1-207.

Homeier, J., Dalitz, H. & Breckle, S.-W. (2002) Waldstruktur und Baumartendiversität im montanen Regenwald der Estación Científica San Francisco in Südecuador. *Berichte der Reinhold-Tüxen-Gesellschaft*, **14**, 109-118.

Hurlbert, S.H. (1971) The nonconcept of species diversity: a critique and alternative parameters. *Ecology*, **52**, 577-586.

Intachat, J. & Holloway, J.D. (2000) Is there stratification in diversity or preferred flight height of geometroid moths in Malaysian lowland tropical forest? *Biodiversity and Conservation*, **9**, 1417-1439.

Intachat, J., Holloway, J.D. & Speight, M.R. (1997) The effect of different forest management practices on geometroid moth populations and their diversity in Peninsular Malaysia. *Journal of Tropical Forest Science*, **9**, 411-430.

Intachat, J., Holloway, J.D. & Speight, M.R. (1999) The impact of logging on geometroid moth populations and their diversity in lowland forests of Peninsular Malaysia. *Journal of Tropical Forest Science*, **11**, 61-78.

Kitching, R.L., Orr, A.G., Thalib, L., Mitchell, H., Hopkins, M.S. & Graham, A.W. (2000) Moth assemblages as indicators of environmental quality in remnants of upland Australian rain forest. *Journal of Applied Ecology*, **37**, 284-297.

Krell, F.-T. (2004) Parataxonomy vs. taxonomy in biodiversity studies – pitfalls and applicability of 'morphospecies' sorting. *Biodiversity and Conservation*, **13**, 795-812.

Lepš, J., Novotny, V. & Basset, Y. (2001) Habitat and successional status of plants in relation to the communities of their leaf-chewing herbivores in Papua New Guinea. *Journal of Ecology*, **89**, 186-199.

McGeachie, W.J. (1989) The effects of moonlight illuminance, temperature and wind speed on light-trap catches of moths. *Bulletin of Entomological Research*, **79**, 185-192.

Meijaard, E., Sheil, D., Nasi, R., Augeri, D., Rosenbaum, B., Iskandar, D., Setyawati, T., Lammertink, M., Rachmatika, I., Wong, A., Soehartono, T., Stanley, S. & O'Brien, T. (2005) *Life after logging: reconciling wildlife conservation and production forestry in Indonesian Borneo*. Center for International Forestry Research, Bogor, Indonesia. 345 pp.

Muirhead-Thomson, R.C. (1991) *Trap responses of flying insects*. Academic Press, London. 287 pp.

Murcia, C. (1995) Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution*, **10**, 58-62.

Novotny, V. & Basset, Y. (2000) Rare species in communities of tropical insect herbivores: pondering the mystery of singletons. *Oikos*, **89**, 564-572.

Nummelin, M. & Kaitala, S. (2004) Do species dominance indices indicate rain forest disturbance by logging? *Biotropica*, **36**, 628-632.

Ohl, C. & Bussmann, R. (2004) Recolonisation of natural landslides in tropical mountain forests of Southern Ecuador. *Feddes Repertorium*, **115**, 248-264.

Paulsch, A. (2002) *Development and application of a classification system for undisturbed and disturbed tropical montane forest based on vegetation structure*. Ph.D. thesis, University of Bayreuth. URL: http://opus.ub.uni-bayreuth.de/volltexte/2002/1/

Pitkin, L.M. (2002) Neotropical ennomine moths: a review of the genera (Lepidoptera: Geometridae). *Zoological Journal of the Linnean Society*, **134**, 121-401.

Rahbek, C. (2005) The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters*, **8**, 224-239.

Richter, M. (2003) Using epiphytes and soil temperatures for eco-climatic interpretations in southern Ecuador. *Erdkunde*, **57**, 161-181.

Ricketts, T.H., Daily, G.C., Ehrlich, P.R. & Fay, J.P. (2001) Countryside biogeography of moths in a fragmented landscape: biodiversity in native and agricultural habitats. *Conservation Biology*, **15**, 378-388.

Schulze, C.H. (2000) *Auswirkungen anthropogener Störungen auf die Diversität von Herbivoren – Analysen von Nachtfalterzönosen entlang von Habitatgradienten in Ost-Malaysia*. Ph.D. thesis, University of Bayreuth.

Schulze, C.H. & Fiedler, K. (2003) Vertical and temporal diversity of a species-rich moth taxon in Borneo. In: *Arthropods of tropical forests: spatio-temporal dynamics and resource use in the canopy* (eds. Y. Basset, V. Novotny, S. Miller and R.L. Kitching), pp. 69-85. Cambridge University Press, Cambridge.

Scoble, M.J. (1995) *The Lepidoptera: form, function, and diversity*. Oxford University Press, Oxford. 404 pp.

Scoble, M.J. (ed.) (1999) *Geometrid moths of the world – a catalogue (Lepidoptera: Geometridae).* CSIRO Publishing, Collingwood. 999 pp.

Southwood, T.R.E. & Henderson, P.A. (2000) *Ecological methods*. (Third edition). Blackwell, Oxford. 592 pp.

Summerville, K.S. & Crist, T.O. (2004) Contrasting effects of habitat quantity and quality on moth communities in fragmented landscapes. *Ecography*, **27**, 3-12.

Thomas, A.W. (2002) *Moth diversity in a northeastern North American, red spruce forest, II. The effect of silvicultural practices on geometrid diversity (Lepidoptera: Geometridae)*. Canadian Forest Service, Atlantic Forestry Service, Fredericton. 25 pp.

Toral, E.C., Feinsinger, P. & Crump, M.L. (2002) Frogs and a cloud-forest edge in Ecuador. *Conservation Biology*, **16**, 735-744.

Trueblood, D.D., Gallagher, E.D. & Gould, D.M. (1994) Three stages of seasonal succession on the Savin Hill Cove mudflat, Boston Harbor. *Limnology and Oceanography*, **39**, 1440-1454.

Willott, S.J. (1999) The effects of selective logging on the distribution of moths in a Bornean rainforest. *Philosophical Transactions of the Royal Society of London* B, **354**, 1783-1790.

Wolda, H. (1992) Trends in abundance of tropical forest insects. *Oecologia*, 89, 47-52.

Yela, J.L. & Holyoak, M. (1997) Effects of moonlight and meteorological factors on light and bait trap catches of noctuid moths (Lepidoptera: Noctuidae). *Environmental Entomology*, **26**, 1283-1290.

Young, M. (1997) *The natural history of moths*. Poyser, London. 271 pp.

6 Temporal dynamics of rich moth ensembles in the montane forest zone in southern Ecuador

Nadine Hilt[1]*, Gunnar Brehm[2] & Konrad Fiedler[3]

[1] Department of Animal Ecology I, Universitätsstrasse 30, University of Bayreuth, 95440 Bayreuth, Germany

[2] Institut für Spezielle Zoologie und Evolutionsbiologie mit Phyletischem Museum, Erbertstrasse 1, 07743 Jena, Germany

[3] Department of Population Ecology, Faculty Centre of Ecology, University of Vienna, Althanstrasse 14, 1090 Vienna, Austria

* Author for correspondence: E-mail: n-hilt@gmx.de

submitted: Biotropica, revision: 27.01.2006

6.1 Abstract

We studied temporal dynamics of highly diverse moth ensembles (Lepidoptera: Arctiidae and Geometridae) in early and late succession stages of forest recovery in the montane zone of southern Ecuador. Moths were sampled using weak light sources (2 x 15 W tubes per trap) during three sampling periods (March-April 2002, wet season; October-November 2002, and August-October 2003, both ‘dry’ seasons). In the family Arctiidae, moth abundance hardly varied between sampling periods. Estimates of local diversity were lower in the year 2002 (wet and dry season) than in the dry season 2003, and ensemble composition was more strongly affected by sampling period rather than habitat differences. Geometridae ensembles revealed stronger temporal patterns. Geometrid abundance increased about two-fold from the wet to the dry season, and temporal effects on species composition were far more pronounced that in arctiids. These differences might hint to variation in the dependence of geometrid vs. arctiid larvae on ephemeral plant resources. Despite these significant temporal dynamics, in both families only a few of the more common species analyzed individually showed strong temporal changes in abundance. Almost all common species occurred as adults during all sampling periods. Therefore, even though temporal dynamics of moth ensembles are not negligible, both moth families are suitable ‘indicators’ of community diversity and change along the succession gradient. However, samples must be large enough, and preferably should be collated over various times of the year and in parallel, to allow for valid statements about moth diversity and species compositions in relation to habitat differences. This undermines the validity of the concept of ‘rapid biodiversity inventories’ for speciose tropical insect communities.

Keywords: Arctiidae, Geometridae, temporal dynamics, successional gradient

6.2 Introduction

More than half of all described species are insects (Groombridge, 1992). They are thus of central importance for understanding patterns and processes of biological diversification (e.g. DeVries *et al.*, 1997). Moths of families such as the Arctiidae and Geometridae offer great potential to unravel mechanisms underlying patterns of tropical insect diversity. They are easily sampled and have a relatively well advanced taxonomy (Brehm *et al.*, 2005). As a consequence, arctiid and geometrid moths have frequently served as model targets in tropical insect ecology (e.g. Holloway, 1987; Intachat & Holloway, 2000; Axmacher *et al.*, 2004; Brehm *et al.*, 2005).

Patterns in temporal variation of insect population abundances or community composition, and their underlying processes, are of major interest to ecologists. It has commonly been observed that insect abundance changes both in long-term (e.g. years) as well as in short-term cycles (e.g. weeks) (for reviews see Wolda, 1978; Cook & Graham, 1996). While data on population size fluctuations and concomitant changes at community level are available for many temperate-zone ecosystems, much less is still known about dynamics of Lepidoptera of the humid or seasonal tropics (Wolda, 1978; Ehrlich, 1984; DeVries *et al.*, 1997; Schulze & Fiedler, 2003). Climatic singularities such as strong ENSO-associated drought periods dramatically affect tropical butterfly populations and assemblages (Cleary, 2003; Hill *et al.*, 2003). But even in perhumid rainforests of South East Asia, where a true dry season does not occur regularly, pronounced fluctuations in the abundance of individual species or entire guilds are frequent, although consistent temporal trends are not always apparent (Schulze & Fiedler, 2003; Fiedler & Schulze, 2004). Despite pronounced temporal fluctuations in total catch size (i.e. variation in the number of observed species and individuals), diversity of South East Asian Pyraloidea (Schulze & Fiedler, 2003) and Geometridae (Intachat & Holloway, 2000) showed no clear cyclic trends (see also Barlow & Woiwod, 1990).

In more seasonal tropical climates, fluctuations in abundance and species richness have been documented in a number of insect groups (Wolda, 1978; Smythe, 1982; Wolda & Wong, 1988). For example, DeVries *et al.* (1997) observed that both species richness and abundance of nymphalid butterflies in a lowland forest in Ecuador are depressed during the dry season and increase at the beginning of the rainy season. This seasonal pattern recurs in many other insect groups (such as Coleoptera, Hymenoptera, Homoptera, Lepidoptera, Orthoptera: e.g. Janzen, 1984; Wolda & Wong, 1988; Brown, 1991; Wolda, 1992; Pinheiro *et al.*, 2002). However, the magnitude of intra- and interannual variation in species richness and abundance of tropical insects remains poorly known. Moreover, temporal dynamics of faunas might vary between more natural and anthropogenically altered habitats (but see Fiedler & Schulze, 2004), or between taxonomic groups. These considerations also have practical consequences, e.g. for conservation-oriented assessment of local faunas or for the purpose of ‘bioindication’. If temporal dynamics lead to strong variation in diversity or species composition, the exact timing of sampling will be essential to warrant comparability and representativeness of samples in monitoring programs. Only if species diversity and composition of faunas remain largely stable over time, short-time sampling programs performed at different times will yield data that allow for further comparisons. This has frequently been assumed, but rarely tested, for those humid tropical habitats that are perceived as largely ‘aseasonal’ (Schulze & Fiedler, 2003; Fiedler & Schulze, 2004).

We here analyse the temporal variation in diversity and species composition of species-rich ensembles of mobile herbivorous insects along a succession gradient in southern Ecuador. We chose two different moth families as model groups, namely the Arctiidae and the Geometridae. Species of both taxa are abundant and taxonomically well documented, and they can easily be sampled at artificial light sources. Yet, the two families differ prominently in important life-history traits such as body size distributions, host-plant relationships, or the incidence of aposematism, mimicry and sequestration of toxic plant compounds (chapter 4, Kitching & Rawlins, 1999; Minet & Scoble, 1999). We specifically address the following questions:

- How variable are the communities over time (three sampling periods distributed over 18 months, two periods in the drier and one in the very humid part of the year) with regard to overall abundance and local diversity?
- Do the abundances of dominant species vary over time, and does this temporal variability differ between two different classes of succession habitats (early vs. late stages of forest recovery)?
- How variable is species composition over time (temporal β-diversity)?
- Do temporal dynamics of community composition differ along the succession gradient?

6.3 Methods

Study area

Moths were collected within the Eastern Cordillera of the Andes at the northern border of the Podocarpus National Park in southern Ecuador (3°58´ S, 79°5´ W) (chapter 2, Brehm *et al.*, 2005). There are 10–11 humid months per year (Richter, 2003) with a mean annual precipitation of c. 2,000 mm and a mean annual air temperature of 15.5° C at 1,950 m above sea level. The rainfall maximum occurs between April and September (the wettest months are April, May and June). A pronounced dry season is typically lacking in the eastern Andean slopes at altitudes between 1,000 and 3,600 m a.s.l. (Fleischbein *et al.*, 2005). The drier season, locally called 'veranillo', is caused by the Low Level Jet stream, which reaches the eastern Andean slopes between October and March (Bendix & Lauer, 1992). The mean monthly temperature and precipitation for the years 2002 and 2003 are shown in Fig. 1 (data see Richter, 2003).

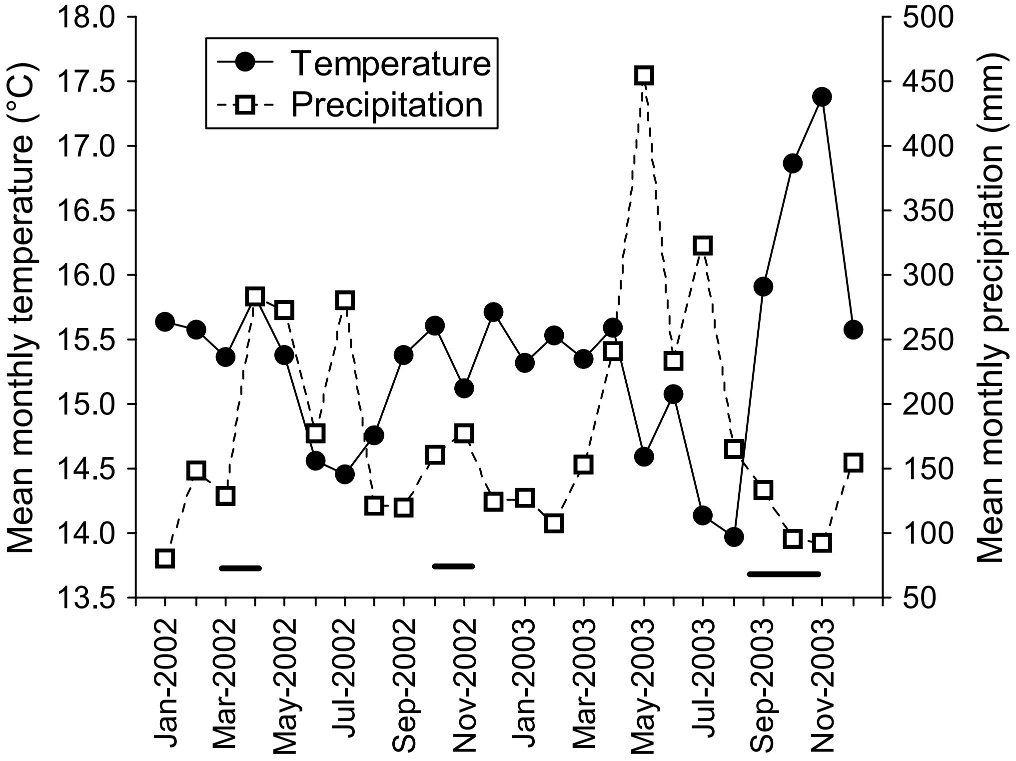


Figure 1: Temperature and precipitation data for the study area (1,960 m a.s.l.) in the years 2002 and 2003 (data from Richter, 2003 and updated; R. Rollenbeck, pers. comm.). Horizontal lines indicate the three sampling periods in these two years.

The potential natural vegetation is evergreen montane rainforests (Homeier, 2004), but the forest has often anthropogenically been replaced by pastures, thickets of bracken (Hartig & Beck, 2003), shrub encroachment, or regenerating forest (Paulsch, 2002). We selected 15 sites representing different stages of vegetation succession (see chapter 2 for details about the vegetation at the sites and the distances between them). These sites (altitudinal range between 1,800–2,005 m a.s.l.) depict a gradient of forest recovery after a landslide as well as some of the most relevant types of disturbed habitats as a result of human land use practices. The sampling sites were grouped into two categories according to their successional stage (early [**E**] without woody vegetation: N=10 sites, or N=8 if the two pastures sites are excluded; late [**L**] with substantial coverage by woody shrubs or secondary forest aged ca. 40 years: N=5).

Sampling and identification

Moths were sampled manually by attraction to weak light sources (2 x 15 W tubes; Sylvania blacklight-blue, F 15 W/BLB-TB and Philips FLD 15 W 05; in a white gauze cylinder, F. Weber, Stuttgart; height 1.6 m; diameter 0.6 m). Low-power light sources are sufficient to minimize cross-attraction of moths between sampled habitats (Schulze & Fiedler, 2003; Beck & Linsenmair, 2006). The effective 'radius of attraction' for moths has been estimated to be only between 10 and 30 m (Muirhead-Thomson, 1991; Beck & Linsenmair, 2006). We restricted sampling to the peak time of moth activity during the evening hours between 18:45 and 21:45. Moths were collected during three periods in the years 2002 (wet season: March to April [**P1**], dry season: October to November [**P2**]) and 2003 (dry season: August to October [**P3**]). These three periods showed the climatic characters typical for the region (Fig. 1). Rainfall was very high in P1, distinctly lower in veranillo P2, and even lower in veranillo P3. Temperature was unusually high in the very dry veranillo P3 and otherwise rather constant. At each site and within each period, 2-4 nightly catches were pooled to provide the data basis for the subsequent analyses. Catches were restricted to phases between four days after full moon until six days before full moon, because the moon phase has an important impact on the efficiency of light traps (McGeachie, 1989; Yela & Holyoak, 1997).

Specimens were sorted to morphospecies and later taxonomically identified as far as possible using published literature and reference collections (see Acknowledgements; species lists can be found in Brehm *et al.*, 2005; Appendix 1 for Arctiidae and Appendix 2 for Geometridae).

Quantitative analysis

We calculated Fisher’s alpha as a measure of local diversity using a program developed by Henderson & Seaby (1998). Numbers of arctiid and geometrid individuals and diversity estimates were compared between pooled samples of each of the three sampling periods. Fisher’s alpha values were statistically compared using Solow’s (1993) test with 10,000 random permutations, implemented in Henderson and Seaby’s program. Additionally, numbers of species and individuals, and values of Fisher’s alpha for every site in the three different periods were compared using a repeated measurements ANOVA approach. The extent of temporal abundance variation of individual species was tested in the commonest species only, i.e. species where the total catch (summed over all sites and seasons) was N>100 for Arctiidae (20 species) and N>150 for Geometridae (17 species). For rarer species sampling effects are expected to be so pronounced that they undermine credibility of detailed species-level analyses. In these common species, numbers of moths were converted to relative abundances (setting the total catch per each site and sampling period as 1), since light-trap data do not provide sound measures of absolute abundance, but yield useful data of relative abundances for those species that are attracted to light (Fiedler & Schulze, 2004). Relative abundances were then analyzed by two-way ANOVA with habitat type and collecting period as effects. Where necessary to homogenize variances, data were log- or square-root transformed. If these transformations failed to homogenize variances, a rank transformation (Conover & Iman, 1981) was applied.

To alleviate sampling effects in comparisons of the species composition of rich, but incompletely sampled moth ensembles we used the chord-normalized expected species shared index (Gallagher’s CNESS index: Trueblood *et al.*, 1994) as a measure of dissimilarity between samples. This index is widely independent of sample size and diversity, and does allow for the inclusion of rare species. We calculated CNESS distances using the program COMPAH96 (available from E. Gallagher, University of Massachusetts, Boston, URL: http://alpha.es.umb.edu/faculty/edg/files/edgwebp.htm). CNESS distance values between individual samples depend on a sample size parameter m, which can range from $m = 1$ to the largest common sample size $m = m_{\max}$. At low m values the CNESS distance is more strongly affected by common species, whereas with increasing m values the rare species receive successively larger emphasis. We graphically present ordinations only for $m = 1$, whereas for ANOSIM calculations we selected three to four different m values for each taxon: $m = 1$, m = intermediate and m = maximum. This approach allows to assess how robust, or sensitive, analyses of β-diversity are with respect to the commonness or rarity of species, and thus to concomitant sampling effects.

Species composition of local moth ensembles was visualized using non-metric multidimensional scaling (NMDS: Clarke, 1993; Brehm & Fiedler, 2004). Ordinations were performed with Statistica 6.1 (StatSoft, 2004). The significance of faunal differences between predefined groups of sites was assessed by ANOSIM (Clarke & Warwick, 2001) with 1,000 random permutations. The R statistics of ANOSIM was used as a measure of effect size. Exclusion of all rare species of Arctiidae (i.e. those represented with overall 15 or fewer individuals) from our analyses yielded the same results as with all species included (data not shown). Hence, we used all species in our ensemble-wide comparisons irrespective of their commonness or rarity. Where necessary, multiple tests of significance were corrected for a table-wide false discovery rate (FDR) of $P<0.05$ according to the step-up procedure by Benjamini & Hochberg (1995).

6.4 Results

Temporal variation in overall moth abundance and diversity

The temporal pattern in the mean number of moths caught per night differed between the two families. Arctiid abundance (Fig. 2a) did not significantly differ between seasons, and was only slightly and non-significantly higher in late succession habitats (two-way ANOVA with repeated measurements: habitat: $F_{1,24} = 1.75$, $P>0.19$; season: $F_{2,48} = 0.21$, $P>0.80$; interaction term: $F_{2,48} = 0.09$,

$P>0.91$; Levene test all $P>0.1$). On the contrary, mean numbers of geometrid individuals caught per night (Fig. 2b) almost doubled from the wet season to the veranillo and were also, but less strongly so, influenced by the habitat (two-way ANOVA with repeated measurements: habitat: $F_{1,24} = 6.00$, $P<0.05$; season: $F_{2,48} = 9.04$, $P<0.001$; interaction term: $F_{2,48} = 0.10$, $P>0.90$, Levene test all $P>0.1$).

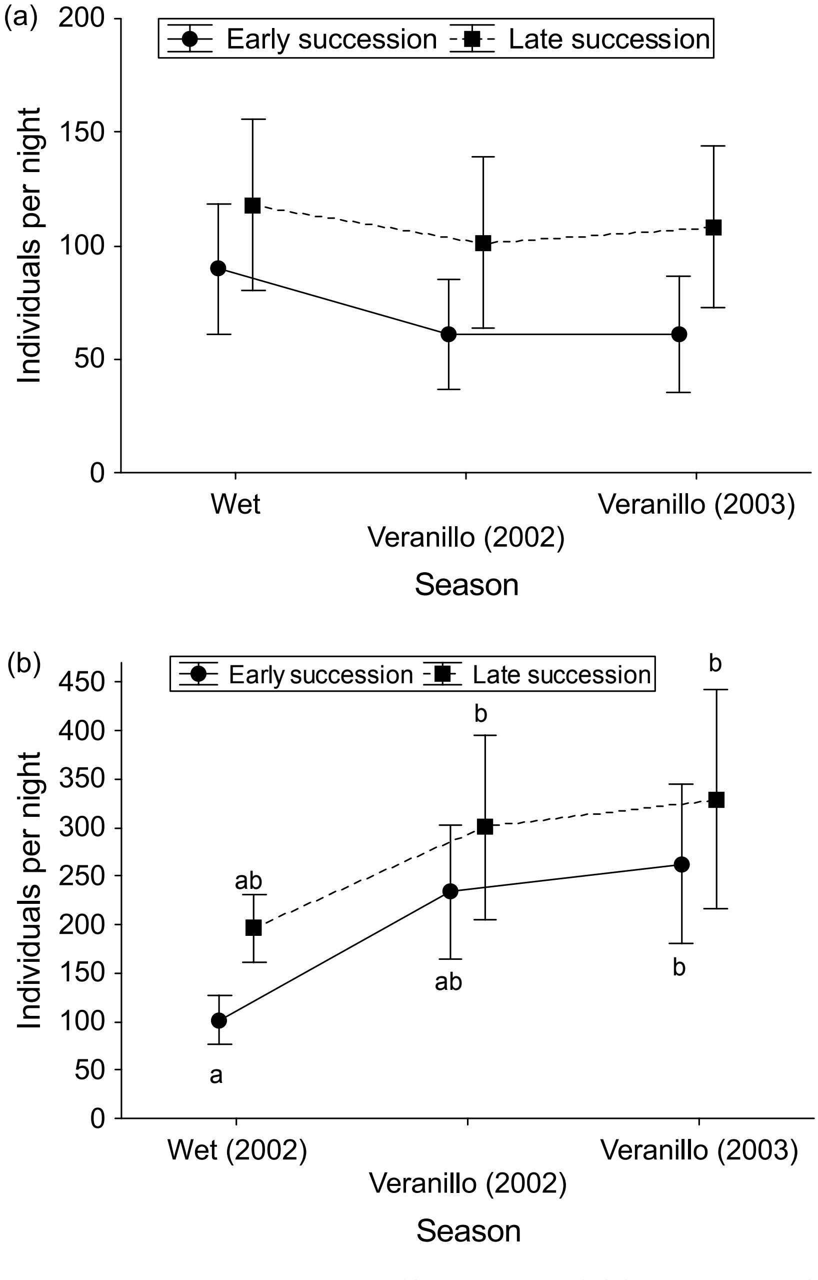


Figure 2: Mean numbers ± 95% intervals of (a) arctiid and (b) geometrid individuals attracted per night in the two different succession habitat classes and the three sampling periods. Wet season: March-April 2002; veranillo (drier season): October-November 2002, and August-October 2003. Symbols accompanied by different letter codes are significantly different (Scheffé post-hoc test, *P*<0.05, following two-way repeated measures ANOVA). See text for statistical results.

In the Geometridae, diversity estimates (Fisher's alpha) were significantly lower for the dry season P2 than for the two other seasons. This result was only obtained when combining all samples from each sampling period (Table 1), but was far less so distinct comparing individual sites (Table 2). There was a clear habitat effect and a weaker temporal effect (two-way ANOVA with repeated measurements: habitat: $F_{1,11} = 18.06$, $P<0.005$; season: $F_{2,22} = 3.85$, $P<0.05$; interaction term: $F_{2,22} = 0.02$, $P>0.98$). In the Arctiidae, diversity was also lowest in period P2. This temporal difference was significant when comparing means of individual sites (two-way ANOVA with repeated measurements: habitat: $F_{1,11} = 4.56$, $P<0.06$; season: $F_{2,22} = 13.57$, $P<0.001$; interaction term: $F_{2,22} = 0.72$, $P>0.49$), but was only weakly expressed when analysing cumulated samples (Tables 1 and 2). The habitat effect (early vs. late succession) on local species diversity was only a weak trend ($P<0.06$).

Table 1: Numbers of arctiid and geometrid individuals (N), observed species (S), and estimates of Fisher's alpha with 95% confidence intervals. Catches at the 15 sites were pooled for each of the three sampling periods (P1 to P3) over all sites and sampling nights. Different superscript letters indicate significant results of Solow tests (pairwise comparisons within families) at *P*<0.05.

	Sampling period	Individuals (N)	Species (S)	Fisher's Alpha	Number of sites and sampling nights
Arctiidae	Mar – Apr 2002 (P1)	2693	191	47.0^{ab} ± 3.5	13 sites / 27 sampling nights
	Oct - Nov 2002 (P2)	2257	168	42.0^{b} ± 3.3	15 sites / 34 sampling nights
	Aug - Oct 2003 (P3)	2767	204	50.9^{a} ± 3.9	15 sites / 33 sampling nights
Geometridae	Mar – Apr 2002 (P1)	3629	519	165.7^{a} ± 26.4	13 sites / 27 sampling nights
	Oct - Nov 2002 (P2)	7772	586	147.2^{b} ± 11.6	15 sites / 33 sampling nights
	Aug - Oct 2003 (P3)	9269	653	160.4^{a} ± 11.9	15 sites / 35 sampling nights

Table 2: Arctiid and geometrid individuals (N), and values of Fisher's alpha (Alpha) for 13 succession sites (excluding abandoned pasture sites D1 and D2, which were only sampled in periods P2 and P3) across the three sampling periods (P1-P3). Statistics: results of ANOVA with repeated measurements.

	Site	Habitat	P1 N	P2 N	P3 N	P1 Alpha	P2 Alpha	P3 Alpha
Arctiidae	A	Early	269	142	235	36.1	21.0	41.8
	B1	Early	228	294	120	38.1	27.7	37.8
	B2	Early	110	130	134	28.4	32.1	61.2
	C	Early	71	25	108	17.1	28.8	29.0
	E1	Early	81	38	282	17.2	13.4	34.9
	E2	Early	209	153	199	32.3	40.1	48.4
	F1	Early	108	106	137	33.1	28.2	45.2
	F2	Early	428	158	244	31.8	28.0	35.3
	G1	Late	313	289	280	39.2	30.1	36.6
	G2	Late	225	260	236	32.3	35.3	47.7
	H1	Late	120	78	95	37.8	37.1	47.1
	H2	Late	202	119	237	44.3	33.8	39.6
	I	Late	329	254	346	41.6	37.6	56.6
Mean ± 1 SD			207.2 ± 108.3	157.4 ± 90.9	204.1 ± 78.7	33.0 ± 8.3	30.2 ± 7.2	43.2 ± 9.1
Statistics				$F_{2,22}$ = 2.03, P>0.15			**$F_{2,22}$ = 13.57, P<0.01**	
Geometridae	A	Early	229	503	856	112.7	74.0	88.8
	B1	Early	168	314	488	82.9	87.4	83.8
	B2	Early	321	504	728	78.9	69.8	84.8
	C	Early	274	727	336	50.2	60.4	91.9
	E1	Early	173	416	682	86.0	81.5	98.2
	E2	Early	385	813	841	96.8	71.0	87.9
	F1	Early	346	607	676	96.2	90.8	114.9
	F2	Early	362	775	832	101.9	121.4	114.0
	G1	Late	346	741	520	140.7	116.4	137.9
	G2	Late	472	147	345	111.1	126.8	127.9
	H1	Late	224	313	1019	106.4	92.4	95.1
	H2	Late	132	587	292	123.6	130.7	142.3
	I	Late	197	505	241	150.5	135.9	158.2
Mean ± 1 SD			279.2 ± 101.5	534.8 ± 201.6	604.3 ± 251.5	102.9 ± 26.5	96.8 ± 26.1	109.7 ± 24.9
Statistics				**$F_{2,22}$ = 9.16, P<0.005**			**$F_{2,22}$ = 3.85, P<0.05**	

Contribution of individual species to temporal ensemble dynamics

Arctiidae and Geometridae showed a strikingly similar pattern of the distribution of species across three sampling periods (Table 3). In both families, 52% of the species, which represented approximately 92% of all sampled moth individuals, were observed in all three sampling periods (P1-P3). 21-23% of the species occurred in two periods, and 24.9% of geometrid species and 26.8% of arctiid species were sampled in only one period, respectively. However, these latter species accounted for but a small fraction (1.4 to 1.9%) of the total catch.

Table 3: Distribution of arctiid and geometrid species and their relative proportions (in %, in parentheses) among three sampling periods (P1 to P3) for the 15 succession sites.

	Arctiidae		Geometridae	
	Number of species (total N = 250)	Represented number of individuals (total N = 7717)	Number of species (total N = 775)	Represented number of individuals (total N = 20670)
All periods	130 (52.0)	7240 (93.8)	402 (51.9)	19126 (92.6)
Two periods	53 (21.2)	329 (4.3)	180 (23.2)	1246 (6.0)
One period only	67 (26.8)	148 (1.9)	193 (24.9)	298 (1.4)
P1 only	25 (10.0)	53 (0.7)	44 (5.7)	63 (0.3)
P2 only	13 (5.2)	15 (0.2)	60 (7.7)	86 (0.4)
P3 only	29 (11.6)	80 (1.0)	89 (11.5)	149 (0.7)

Relative proportions of the commonest species were tested to assess whether certain species show preferred flight periods. Overall, 23 out of 37 common moth species (9 out of 17 Geometridae, 14 of 20 Arctiidae) showed no significant temporal abundance fluctuations (Tables 4 and 5). A few species in both families showed different relative abundances along the succession gradient independent of collecting period or season. The arctiids *Agkonia pega, Areva albogrisea* and *Metalobosia holophaea* as well as the geometrids *Eois paraviolascens, Microxydia ruficomma, Perizoma emmelesiata, Perizoma zenobia* and *Sabulodes thermidora* differed in their relative abundance between early and later succession stages. Very few species showed pronounced temporal abundance fluctuations irrespective of the habitat. *Agylla nivea, Agylla seperata, Cosmosoma meridense* (all Arctiidae) and *Chloropteryx opalaria*, *Lomographa tributaria, Physocleora* sp. (all Geometridae) were numerous in the wet season, whereas *Epectaptera* sp. and *Pantherodes conglomerata* occurred frequently in the veranillo, but were rare in the wet season. Others exhibited a significant habitat × season interaction with regard to their relative abundance (e.g. Arctiidae: *Napata* sp.; Geometridae: *Lissochlora latuta*). For example, the arctiid *Macroptila laniata* was common in early succession sites and in the wet season, whereas the geometrids *Oxydia trychiata* and *Perissopteryx nigricomata* were often found in the later succession stages and in the veranillo. In *Oxydia trychiata* and *Perissopteryx nigricomata*, habitat had a stronger effect on relative abundances, whereas season had a stronger effect in *Pantherodes colubraria* and *Macroptila laniata*.

Table 4: Results of two-way analyses of variance (ANOVA) on relative abundances of 20 common arctiid moth species with total catch N>100 for the 15 sites, according to habitat categories (early vs. late succession) and sampling period (March-April 2002, October-November 2002, August-October 2003). Species were sorted in descending order according to their total absolute abundance. Bold figures indicate significant differences at the *P*<0.05 level which persist after FDR correction. * *P*<0.05, ** *P*<0.01 * *P*<0.005, **** *P*<0.001, n.s.: not significant.**

Species name	***F*(Habitat)** (df = 1;37)	***F*(Period)** (df = 2;37)	***F*(Interaction)** (df = 2;37)
Macroptila laniata	**6.97***	**12.0******	n.s.
Cosmosoma sp.15	n.s.	n.s.	n.s.
Agylla zucarina	n.s.	n.s.	n.s.
Agylla hampsoni	n.s.	n.s.	n.s.
Metalobosia holophaea	**7.48****	n.s.	n.s.
Holophaea endoleuca	n.s.	n.s.	n.s.
Agylla sp.14	n.s.	n.s.	n.s.
Agylla flavitincta	n.s.	n.s.	n.s.
Agylla seperata	n.s.	**5.87****	n.s.
Cosmosoma meridense	n.s.	**3.70***	n.s.
Areva albogrisea	**13.52******	n.s.	n.s.
Agylla sp.19	4.30*	n.s.	n.s.
Agkonia pega	**8.89****	n.s.	n.s.
Napata sp.3	n.s.	**3.61***	**3.60***
Eucereon zizana	n.s.	n.s.	n.s.
Agylla nitridalis	n.s.	n.s.	n.s.
Ischnocampa mamona	n.s.	n.s.	n.s.
Agylla nivea	n.s.	**5.61****	n.s.
Epectaptera sp.1	n.s.	**4.14***	n.s.
Agylla sp.25	n.s.	n.s.	n.s.

Table 5: Results of two-way analysis of variance (ANOVA) on relative abundances of 17 common geometrid moth species with total catch N>150 for the 15 sites, according to habitat categories (early vs. late succession) and sampling period (March-April 2002, October-November 2002, August-October 2003). Species were sorted in descending order according to their absolute total abundance. Bold figures indicate significant effects at the *P*<0.05 level which persist after FDR correction. * *P*<0.05, ** *P*<0.01 * *P*<0.005, **** *P*<0.001, n.s.: not significant.**

Species name	***F*(Habitat)** (df = 1;37)	***F*(Period)** (df = 2;37)	***F*(Interaction)** (df = 2;37)
Pantherodes conglomerata	n.s.	**14.97********	n.s.
Sabulodes thermidora	**22.75********	n.s.	n.s.
Argyrotome prospectata	4.61*	n.s.	n.s.
Eois paraviolascens	**11.00******	n.s.	n.s.
Physocleora sp.	n.s.	**8.62********	n.s.
Chloropteryx opalaria	n.s.	**8.82******	n.s.
Oxydia trychiata	**15.89********	**9.19********	n.s.
Perissopteryx nigricomata	**26.78********	**10.70********	n.s.
Perizoma zenobia	**52.39********	n.s.	n.s.
Lomographa tributaria	n.s.	**8.42********	n.s.
Nemoria nigrisquama	n.s.	n.s.	n.s.
Eois chrysocraspedata	n.s.	n.s.	n.s.
Microxydia ruficomma	**6.10***	n.s.	n.s.
Pantherodes colubraria	**6.62***	**11.97********	n.s.
Lissochlora latuta	**17.82********	n.s.	**5.30****
Perizoma emmelesiata	**13.10********	n.s.	n.s.
Melinodes saeta	n.s.	n.s.	n.s.

Temporal dynamics of ensemble composition

Two-dimensional ordinations based on CNESS values with m = 1 (i.e. emphasizing dominant species: Fig. 3a) and concomitant ANOSIM calculations for the 15 succession sites revealed a distinct segregation of arctiid faunas between early and late succession stages, and a slightly weaker segregation according to the three sampling periods (Table 6). When emphasizing the moderately abundant (m = 10) or the rare species ($m_{\max}$ = 25), the effect of sampling period remained unaffected, whereas habitat effects became diluted and non-significant (Table 6). The geometrid fauna showed a similar picture as the arctiid ensembles (Fig. 3b). For m = 1, there also occurred a distinct segregation between early and late succession stages, as well as between the three sampling periods (Table 6).

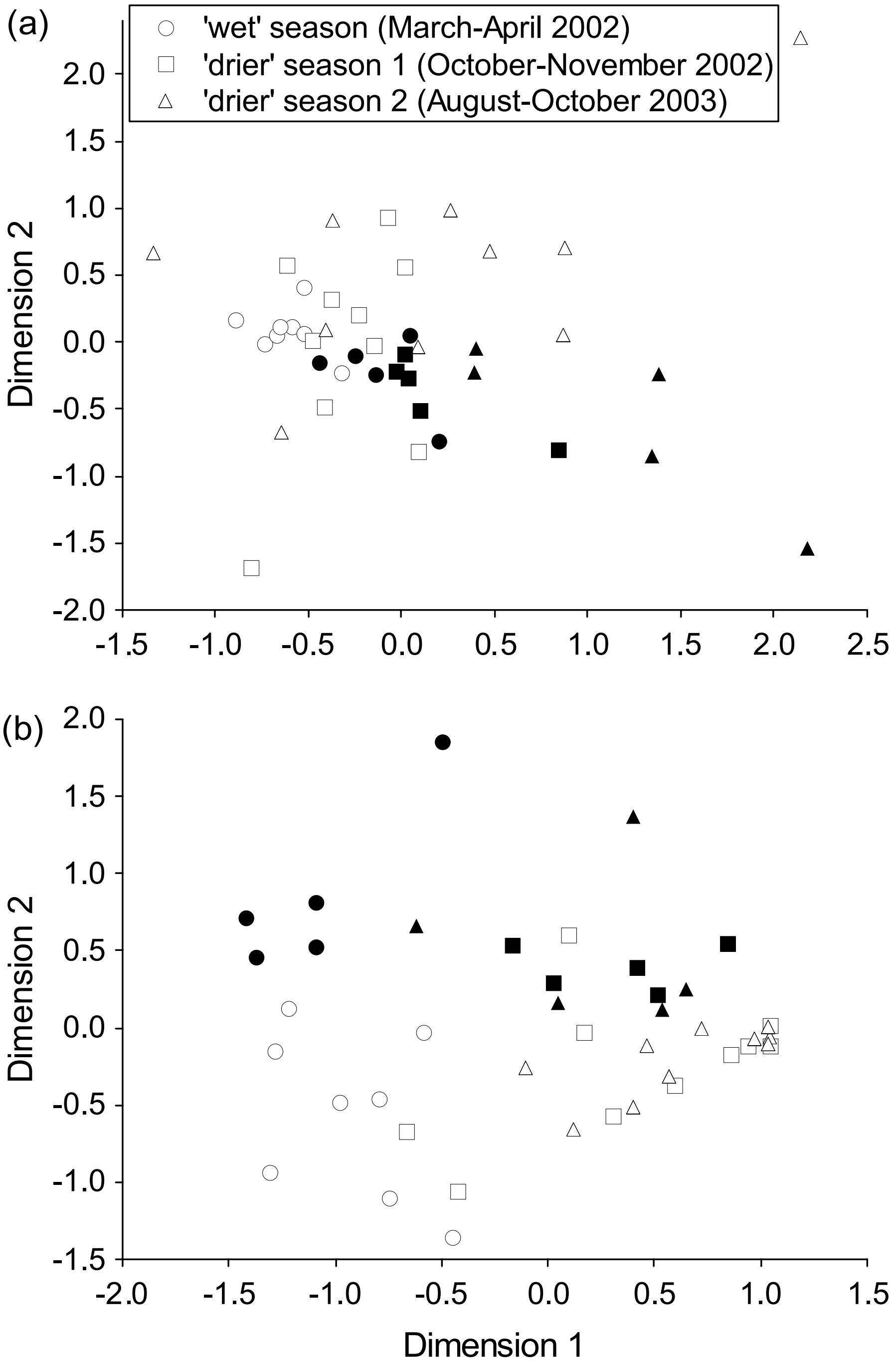


Figure 3: Nonlinear two-dimensional scaling plots for the arctiid samples (a; stress: 0.185) and geometrid samples (b; stress: 0.147) of the 15 succession sites, segregated according to the three sampling periods and two habitat types. Ordinations are based on CNESS distance values with *m* = 1. Empty symbols (O□Δ): early succession stages; filled symbols: later succession stages (●■▲).

Significant pairwise differences only emerged between the wet season (P1) and the two drier seasons (P2 and P3), respectively, but not between the drier seasons of successive years. With increasing *m* values, samples taken in these two drier seasons became significantly segregated from each other. For all *m* values, the influence of collecting period was slightly stronger than the habitat effect. Moreover, in all tests except for the comparison between the periods P1 and P2 at *m* = 1, Geometridae faunas showed far stronger spatial and temporal differentiation than Arctiidae ensembles, as evidenced by the much higher *R* values.

Table 6: Influence of habitat and sampling period on β-diversity of arctiid and geometrid samples at 15 succession sites. Given are ANOSIM results for two-way crossed analyses (Global *R* and *p*), as well as pairwise comparisons among the three sampling periods. Results are reported for CNESS faunal distances at different levels of the sample size parameter *m*. P1: March to April 2002; P2: October to November 2002; P3: August to October 2003. Figures in italics indicate no significant effects at the *P*<0.05 level after FDR correction.

	Arctiidae			Geometridae		
	m	R	*P*	*m*	R	*P*
Habitat	1	0.27	0.003	1	0.31	0.001
Season		0.19	0.002		0.41	0.001
P1 vs. P2		*0.14*	*0.02*		0.60	0.001
P1 vs. P3		0.33	0.002		0.78	0.001
P2 vs. P3		0.16	0.002		0.01	0.36
Habitat	10	*0.16*	*0.043*	50	0.42	0.001
Season		0.19	0.001		0.45	0.001
P1 vs. P2		*0.11*	*0.036*		0.55	0.001
P1 vs. P3		0.32	0.001		0.61	0.001
P2 vs. P3		0.16	0.002		0.27	0.001
Habitat	25	0.06	0.22	100	0.32	0.001
Season		0.17	0.001		0.40	0.001
P1 vs. P2		0.08	0.094		0.48	0.001
P1 vs. P3		0.30	0.001		0.52	0.001
P2 vs. P3		0.15	0.002		0.28	0.001
Habitat				132	0.26	0.002
Season					0.37	0.001
P1 vs. P2					0.43	0.001
P1 vs. P3					0.48	0.001
P2 vs. P3					0.26	0.001

6.5 Discussion

Temporal dynamics of moth abundance and diversity

Seasonality of tropical insect populations and communities has almost universally been detected wherever well defined wet and dry seasons alternate regularly (e.g. Wolda, 1978, 1980, 1992; DeVries *et al.*, 1997, 1999; Novotny & Basset, 1998; Kitching *et al.*, 2000). Even in perhumid tropical ecosystems with weakly pronounced climatic seasonality, a great variety of temporal patterns in the abundance of light-trapped insects was found (e.g. Kato *et al.*, 1995). However, in perhumid regions of SE Asia all moth ensembles studied thus far revealed little evidence for cyclic seasonal dynamics (e.g. Barlow & Woiwod, 1990; Orr & Häuser, 1996; Intachat & Holloway, 2000; Schulze & Fiedler, 2003), even though leaf flushing, flowering or fruit set of many plants that serve as larval host plants display seasonal peaks (Sakai *et al.*, 1999; Wich & van Schaik, 2000; Hamann, 2004). It must, however, be stressed that our survey of Ecuadorian moths did not allow for detecting seasonal phenomena in a strict sense. Our data cover only three sampling periods distributed over 18 months. We have sampled only two veranillos and lack a replicate wet season for the succession habitats covered in the present study. However, sampling in two more years (1999 and 2000) in natural forest in the same area revealed many parallels to the 2002 and 2003 data. For example, Geometridae abundances were generally higher in the veranillos of these two years than in the wet period, while Arctiidae showed less pronounced fluctuations (Brehm, 2002; Süßenbach, 2003). Therefore, even though further monitoring will be required to better understand temporal changes in these diverse moth faunas we feel that our data are sufficiently robust to warrant interpretation.

In our study area in the Eastern Andes of southern Ecuador, the montane rainforests receive substantial rainfall throughout the year. However, a period occurs between September and January when precipitation rates drop to 75 to 150 mm per month, while excessive rainfall occurs between April and July (Fig. 1; Richter, 2003). These climatic cycles are also reflected by patterns in plant phenology in the southern Ecuadorian Andean forest. For example, Homeier (2004) discriminated two groups of trees regarding to their main flowering phase. Most tree species such as *Heliocarpus americanus* and *Clethra revoluta* had their main flowering phase in the wettest months (March to June), whereas other species (*Tabebuia chrysantha, Purdiaea nutans*) flowered in the drier period (August to December). However, the proportion of flowering and fruiting tree individuals shows strong annual variation. Dziedzioch (2001) investigated the phenology of ornithophilous plant species in the same study area. She showed that most species flowered during March and September, peaking in the wettest month (April). Hence, at least for herbivores that rely on young foliage or reproductive plant organs the availability of resources varies strongly over time.

Most previous studies conducted in seasonal tropical areas showed an increase in insect abundance in the wet season, suggesting that a seasonal correlation with rainfall is typical of tropical insect communities (overview in Janzen, 1973; DeVries & Walla, 2001; Intachat *et al.*, 2001; Pinheiro *et al.*, 2002). The onset of rainfall triggers budbreak and flowering in many plants and thus makes available resources for lepidopteran larvae (fresh plant biomass) as well as adults (flower nectar). Accordingly, the more severe the dry season is, the stronger the association between rainfall and moth ensembles is to be expected. Only few studies found decreasing insect abundance in the wet season (e.g. Boinski & Scott, 1988). This can be expected if strong rainfall negatively affects flight performance or insect behaviour. As a consequence, differences in the tightness of the link between insect dynamics and temporal patterns in climate should be attributable to variation between regions and with regard to the direct and indirect constraints imposed by climate onto different taxonomic groups.

In our extensive data set, geometrid moths showed a clear increase in abundance for all habitat categories from the wet season to the drier one. However, mean local geometrid diversity was equal across the two seasons (wet (P1) vs. veranillo (P2/3); mean Fisher's alpha: 102.9 vs. 103.2). Thus, higher Geometridae abundance in the dry seasons did not translate into higher diversities of resulting samples. In contrast, abundance of arctiid moths did not vary significantly across three sampling periods. Arctiid diversity showed some minor seasonal differences: the two successive dry seasons differed in their diversity when cumulated samples were compared, and also on a site-to-site basis. Together with the much higher faunal differentiation as revealed by ANOSIM this indicates that Andean geometrid moths respond more sensitively than arctiid moths to variation in weather and its effects on vegetation, but also on forest disturbance. In line with this hypothesis, mainly geometrid abundance and to a lesser extent diversity was lower in the samples from veranillo P2, which was characterized by distinctly lower temperatures and higher precipitation, than the veranillo P3 of the subsequent year (Fig. 1).

More than 50% of the moth species, which represented >90% of all individuals, were caught in all three periods. This pattern was strikingly similar between the two studied moth families. Moreover, among the common moth species, few showed clear abundance peaks at certain times of the year. For example, the geometrid species *Pantherodes colubraria* and *P. conglomerata* had strong abundance peaks during the veranillos, whereas *Physocleora* sp. and *Chloropteryx opalaria* as well as the arctiid *Macroptila laniata* occurred in highest numbers in the wet season. Yet all of them do occur as adults also during other months of the year. Along an elevational gradient in natural forest in the same region in southern Ecuador, Süßenbach (2003) found that only a few abundant arctiid and pyraloid moth species showed strong temporal abundance variation. These abundant species were largely responsible for the differences he observed between wet season and veranillo ensembles, but most of them were also found in both seasons.

Our observations that most moth species are on the wing during the whole year confirm observations made by Hebert (1980) in humid tropical forests in Papua New Guinea. Stork and Brendell (1990) observed similar patterns for beetles in Sulawesi, and Novotny and Basset (1998) for adult stages of sap-sucking hemipterans in New Guinea. More prominent seasonal abundance fluctuations were, in contrast, reported from regions in South and Central America with a pronounced dry season (Brazil: Pinheiro *et al.*, 2002; Costa Rica: Janzen, 1973; Boinski & Fowler, 1989; Eastern Ecuador: DeVries *et al.*, 1997; DeVries & Walla, 2001; Panama: Wolda, 1992).

Temporal dynamics on the ensemble level

Multivariate analyses on ensemble level (NMDS ordinations, ANOSIM) revealed that arctiid and geometrid samples all changed over time with regard to species composition. As with the abundance, these temporal effects were far more pronounced in the Geometridae. Temporal effects were consistently larger than habitat effects in this family and did hardly vary depending on how strongly, or weakly, the rare or abundant species were weighted (using different levels of the sample size parameter *m* in the CNESS index). In contrast, temporal effects were overall smaller (as indicated by lower *R* values in ANOSIM comparisons) in the family Arctiidae. Pyraloid moth ensembles in natural forest also showed higher temporal variation as compared to the Arctiidae (Süßenbach, 2003). The higher temporal dynamics of Andean geometrid and pyraloid moths relative to the Arctiidae may be linked to the dependence of many geometrid or pyraloid caterpillars on young foliage, inflorescences, or fruits. For example, the larvae of large geometrid clades such as the Eupitheciini and Geometrinae predominantly feed on inflorescences and seeds (McGuffin, 1958; Holloway, 1997; Brehm, 2003); sources which change temporally in our study area (Homeier, 2004, see above). In contrast, larvae of Arctiidae are not known as specialist flower feeders, and may be less affected by the phenology of the surrounding vegetation. However, available host plant data are currently too scarce for a more thorough evaluation of the factors underlying pronounced abundance fluctuations, and their variation across moth taxa. Moreover, long-term studies would be urgently needed to assess which of the temporal patterns documented here are really related to cyclic, ‘seasonal’ patterns in climate and plant phenology.

Temporal dynamics and the estimation of community parameters

Our observations show that highly speciose Andean moth ensembles (Arctiidae and Geometridae) have a substantial β-diversity both with regard to sampling time and habitat. In remnants of upland rainforest in Australia, Kitching *et al.* (2000) also found a segregation of moth assemblages according to season (wet vs. dry) and forest type. DeVries *et al.* (1997) reported a high β-diversity of fruit-feeding butterflies in a lowland Ecuadorian rain forest in vertical, horizontal, and temporal dimensions. Such findings may have imminent consequences for topics in applied ecology, such as assessing and monitoring insect faunas for conservation purposes. If diversity or species composition change profoundly with time (e.g. between seasons), then only sampling and monitoring programs performed during exactly the same time periods will yield meaningful data for comparisons between habitats or for assessing management effects.

In Borneo, Schulze and Fiedler (2003) as well as Fiedler and Schulze (2004) observed that α-diversity and dynamics of speciose pyraloid moth assemblages largely reflected habitat differences, even though species composition did change over time. During a three year-study on SE Asian hawkmoths, species richness and species composition were also strongly indicative of habitat differences between sites, and hardly differed between seasons and years (Beck, 2005; Beck & Linsenmair, 2006). Under such circumstances, samples taken at almost any time will yield reliable information about species richness and composition, provided that the samples are large enough and thus representative and amenable to statistical analysis. In our samples, the Arctiidae comprise such a case. Here, diversity and species composition turned out to be only marginally affected by temporal patterns, especially if rare species (whose records are particularly susceptible to sampling effects) are not weighted too high. Geometridae, in contrast, revealed higher temporal variation, and therefore sufficient care must be taken when comparisons are made across samples which were collated at different times. However, arctiid as well as geometrid moth ensembles in southern Ecuador well mirrored anthropogenic habitat disturbance and forest recovery (Brehm & Fiedler, 2005; chapters 2, and 5), thus corroborating the potential of tropical moth ensembles to be used as environmental indicators (Kitching *et al.*, 2000; Holloway & Intachat, 2003; Summerville *et al.*, 2004).

In conclusion, samples from species rich tropical moth communities can reliably be used for statements about the diversity and species composition, for example along environmental gradients. However, it should always be explicitly assessed how variable community patterns are over time. Preferably, even in humid tropical regions without a real dry season, sampling should be spread as evenly as resources permit over the annual cycle. Quantitative measures of community patterns (i.e. α- and β-diversity) remained largely unaffected and still mirrored habitat differences in both moth families tested here irrespective of the sampling period. Moreover, as evidenced by diverse moth ensembles in our study area, the highest insect abundances and diversities are not universally found in the more humid parts of the year.

Acknowledgments

We thank Rütger Rollenbeck for a synopsis of climate data for the study period. Giovanni Onore (Pontifícia Universidad Católica del Ecuador, Quito) and Christoph L. Häuser (Staatliches Museum für Naturkunde, Stuttgart) supported the project logistically. Christoph L. Häuser, Martin R. Honey and Linda M. Pitkin (Natural History Museum, London) and Axel Hausmann (Zoologische Staatssammlung, Munich) provided access to reference collections under their care. Suzanne Rab-Green (American Museum of Natural History, New York) and Benoît Vincent (Paris) kindly identified some species. Special thanks go to John Slogett for helpful comments on this manuscript. The Ministerio del Medio Ambiente in Ecuador issued research permits (Nro. 002-PNP-DBAP-RLZCH/MA), and the foundation Nature and Culture International (Loja, Ecuador) allowed access to the study sites and their facilities. The Deutsche Forschungsgemeinschaft financed our work (FOR 402/1-1 TP15, FOR 402/2-1 A3).

6.6 References

Axmacher, J.C., Holtmann, G., Scheuermann, L., Brehm, G., Müller-Hohenstein, K. & Fiedler, K. (2004) Diversity of geometrid moths (Lepidoptera: Geometridae) along an Afrotropical elevational rainforest transect. *Diversity and Distribution*, **10**, 293-302.

Barlow, H.S. & Woiwod, I.P. (1990) Seasonality and diversity of Macrolepidoptera in two lowland sites in the Dumonga-Bone National Park, Sulawesi Utara. In: *Insects and the rain-forests of South East Asia (Wallacea)*, (eds. J. Knight and J.D. Holloway), pp. 167-172. London: The Royal Entomological Society.

Beck, J. (2005) *The macroecology of Southeast-Asian hawkmoths (Lepidoptera: Sphingidae).* Ph.D. thesis, University of Würzburg. URL: http://opus.bibliothek.uni-wuerzburg.de/opus/volltexte/2005/1300/

Beck, J. & Linsenmair, K.E. (2006) Feasibility of light-trapping in community research on moths: Attraction radius of light, completeness of samples, nightly flight times and seasonality of Southeast-Asian hawkmoths (Lepidoptera: Sphingidae). *Journal of Research on the Lepidoptera*, **39**, in press.

Bendix, J. & Lauer, W. (1992) Die Niederschlagsjahreszeiten in Ecuador und ihre klimadynamische Interpretation. *Erdkunde*, **46**, 118-134.

Benjamini, Y. & Hochberg, Y. (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society B* **57**, 289-300.

Boinski, S. & Fowler, N.L. (1989) Seasonal patterns in a tropical lowland forest. *Biotropica*, **21**, 223-233.

Boinski, S. & Scott, P.E. (1988) Association of birds with monkeys in Costa Rica. *Biotropica*, **20**, 136-143.

Brehm, G. (2002) Diversity of geometrid moths in a montane rainforest in Ecuador. Ph.D. thesis, University of Bayreuth. URL: http://opus.ub.uni-bayreuth.de/volltexte/2003/20.

Brehm, G. (2003) Host-plant records and illustration of the larvae of 19 geometrid moth species from a montane rainforest in Ecuador. *Nachrichten des Entomologischen Vereins Apollo, Frankfurt, N.F.* 24: 29-34.

Brehm, G. & Fiedler, K. (2004) Ordinating tropical moth ensembles from an elevational gradient: a comparison of common methods. *Journal of Tropical Ecology*, **20**, 165-172.

Brehm, G. & Fiedler, K. (2005) Diversity and community structure of geometrid moths of disturbed habitat in a montane area in the Ecuadorian Andes. *Journal of Research on the Lepidoptera*, **38**, 1-14.

Brehm, G., Pitkin, L.M., Hilt, N., Fiedler, K. (2005) Tropical Andean rain forests are a global diversity hotspot of geometrid moths**.** *Journal of Biogeography*, **32**, 1621-1627.

Brown, K.S. Jr. (1991) Conservation of neotropical environments: Insects as indicators. In: *The conservation of insects and their habitats* (eds. N.M. Collins and J.A. Thomas), pp. 449-504. London: Academic Press.

Clarke, K.R. (1993) Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, **18**, 117-143.

Clarke, K.R. & Warwick, R.M. (2001) *Change in marine communities: an approach to statistical analysis and interpretation*. Primer-E, Plymouth.

Cleary, D.F.R. (2003) An examination of scale of assessment, logging and ENSO-induced fires on butterfly diversity in Borneo. *Oecologia*, **135**, 313-321.

Conover, W.J. & Iman, R.L. (1981) Rank transformations as a bridge between parametric and nonparametric statistics. *The American Statistician*, **35**, 124-129.

Cook, L.M. & Graham, C.S. (1996) Evenness and species number in some moth populations. *Biological Journal of the Linnean Society*, **58**, 75-84.

DeVries, P.J., Murray, D. & Lande, R. (1997) Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. *Biological Journal of the Linnean Society*, **62**, 343-364.

DeVries, P.J., Walla, T.R. & Greeney, H. (1999) Species diversity in spatial and temporal dimensions of fruit-feeding butterflies from two Ecuadorian rainforests. *Biological Journal of the Linnean Society*, **68**, 333-353.

DeVries, P.J. & Walla, T.R. (2001) Species diversity and community structure in neotropical fruit-feeding butterflies. *Biological Journal of the Linnean Society*, **74**, 1-15.

Dziedzioch, C. (2001) *Artenzusammensetzung und Ressourcenangebot kolibribesuchter Pflanzen im Bergregenwald Südecuadors*. Ph.D. thesis, University of Ulm. URL: http://vts.uni-ulm.de/doc.asp?id=610

Ehrlich, P.R. (1984) The structure and dynamics of butterfly populations. In: *The biology of butterflies* (eds. R.I. Vane-Wright and P.R. Ackery), pp. 25-58. Symposium of the Royal Entomological Society of London, Number 11, Academic Press.

Fiedler, K. & Schulze, C.H. (2004) Forest modification affects diversity (but not dynamics) of speciose tropical pyraloid moth communities. *Biotropica*, **36**, 615-627.

Fleischbein, K., Wilcke, W., Goller, R., Boy, J., Valarezo, C., Zech, W. & Knoblich, K. (2005) Rainfall interception in a lower montane forest in Ecuador: effects of canopy properties. *Hydrological Processes*, **19**, 1355-1371.

Groombridge, B. (ed.) (1992) *Global Biodiversity. Status of the Earth's Living Resources*. London: Chapman and Hall.

Hamann, A. (2004) Flowering and fruiting phenology of a Philippine submontane rain forest: climatic factors as proximate and ultimate causes. *Journal of Ecology*, **92**, 24-31.

Hartig, K. & Beck, E. (2003) The bracken fern (*Pteridium arachnoideum* (Kaulf.) Maxon) dilemma in the Andes of Southern Ecuador. *Ecotropica*, **9**, 3-13.

Hebert, P.D.N. (1980) Moth communities in montane Papua New Guinea. *Journal of Animal Ecology*, **49**, 593-602.

Henderson, P.A. & Seaby, R.M.H. (1998) *Species diversity and richness*. Version 2.62. Pennington: Pisces Conservation Ltd.

Hill, J.K., Hamer, K.C., Dawood, M.M., Tangah, J. & Chey, V.K. (2003) Rainfall but not selective logging affect changes in abundance of a tropical forest butterfly in Sabah, Borneo. *Journal of Tropical Ecology*, **19**, 35-42.

Holloway, J.D. (1987) Macrolepidoptera diversity in the Indo-Australian tropics: geographic, biotopic and taxonomic variations. *Biological Journal of the Linnean Society*, **30**, 325-341.

Holloway, J.D. (1997) The moths of Borneo: family Geometridae, subfamilies Sterrhinae and Larentiinae. *Malayan Nature Journal*, **51**, 1-242.

Holloway, J.D. & Intachat, J. (2003) Aspects of the diversity of Geometridae (Lepidoptera) in Pasoh Forest Reserve. In*: Pasoh: ecology of a lowland rain forest in Southeast Asia* (eds. T. Okuda, N. Manokaran, Y. Matsumoto, K. Niiyama, S.C. Thomas and P.S. Ashton), pp. 293-313. Springer, Tokyo.

Homeier, J. (2004) Baumdiversität, Waldstruktur und Wachstumsdynamik zweier tropischer Bergregenwälder in Ecuador und Costa Rica. *Dissertationes Botanicae*, **391**, 1-207.

Intachat, J. & Holloway, J.D. (2000) Is there stratification in diversity or preferred flight height of geometrid moths in Malaysian lowland tropical forest? *Biodiversity and Conservation*, **9**, 1417-1439.

Intachat, J., Holloway, J.D. & Staines, H. (2001) Effects of weather and phenology on the abundance and diversity of geometroid moths in a natural Malaysian tropical rain forest. *Journal of Tropical Ecology*, **17**, 411-429.

Janzen, D.H. (1973) Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. *Ecology*, **54**, 687-708.

Janzen, D.H. (1984) Two ways of being a tropical big moth: Santa Rosa saturniids and sphingids. *Oxford Surveys in Evolutionary Biology*, **1**, 85-140.

Kato, M., Inoue, T., Hamid, A.A., Nagamitsu, T., Merdek, M.B., Nona, A.R., Itino, T., Yamane, S. & Yumoto, T. (1995) Seasonality and vertical structure of light-attracted insect communities in a dipterocarp forest in Sarawak. *Researches on Population Ecology*, **37**, 59-79.

Kitching, I.J. & Rawlins, J.E. (1999) The Noctuoidea. In: *Handbook of Zoology. Lepidoptera, Moths and Butterflies, vol. 1* (ed. N.P. Kristensen), pp. 355-401. Berlin, New York, Walter de Gruyter.

Kitching, R.L., Orr, A.G., Thalib, L., Mitchell, H., Hopkins, M.S. & Graham, A.W. (2000) Moth assemblages as indicators of environmental quality in remnants of upland Australian rain forest. *Journal of Applied Ecology*, **37**, 284-297.

McGeachie, W.J. (1989) The effects of moonlight illuminance, temperature and wind speed on light-trap catches of moths. *Bulletin of Entomological Research*, **79**, 185-192.

McGuffin, W.C. (1958) Larvae of the Nearctic Larentiinae (Lepidoptera: Geometridae). *The Canadian Entomologist* **90**, Supplement 8: 1-104.

Minet, J. & Scoble, M.J. (1999) The drepanoid/geometroid assemblage. In: *Handbook of Zoology. Lepidoptera, Moths and Butterflies, vol. 1* (ed. N.P. Kristensen), pp. 301-320. Berlin, New York, Walter de Gruyter.

Muirhead-Thomson, R.C. (1991) *Trap responses of flying insects*. Academic Press, London.

Novotny, V. & Basset, Y. (1998) Seasonality of sap-sucking insects (Auchenorrhyncha, Hemiptera) feeding on *Ficus* (Moraceae) in a lowland rain forest in New Guinea. *Oecologia*, **115**, 514-522.

Orr, A.G. & Häuser, C.L. (1996) Temporal and spatial patterns of butterfly diversity in a lowland tropical rainforest. In: *Tropical Rainforest Research – Current Issues* (eds. D.S. Edwards, W.E. Booth and S.C. Choy), pp. 125-138. Dordrecht: Kluwer Academic Publishers.

Paulsch, A. (2002) *Development and application of a classification system for undisturbed and disturbed tropical montane forest based on vegetation structure*. Ph.D. thesis, University of Bayreuth. URL: http://opus.ub.uni-bayreuth.de/volltexte/2002/1

Pinheiro, F., Diniz, I.R., Coelho, D. & Bandeira, M.P.S. (2002) Seasonal pattern of insect abundance in the Brazilian cerrado. *Austral Ecology*, **27**, 132-136.

Richter, M. (2003) Using epiphytes and soil temperatures for eco-climatic interpretations in southern Ecuador. *Erdkunde*, **57**, 161-181.

Sakai, S., Momose, K., Yumoto, T., Nagamitsu, T., Nagamasu, H., Hamid, A.A. & Nakashizuka, T. (1999) Plant reproductive phenology over four years including an episode of general flowering in a lowland dipterocarp forest, Sarawak, Malaysia. *American Journal of Botany*, **86**, 1414-1436.

Schulze, C.H. & Fiedler, K. (2003) Vertical and temporal diversity of a species-rich moth taxon in Borneo. In: *Arthropods of tropical forests: spatio-temporal dynamics and resource use in the canopy* (eds. Y. Basset, V. Novotny, S. Miller and R.L. Kitching), pp. 69-85. Cambridge University Press, Cambridge.

Smythe, N. (1982) The seasonal abundance of night-flying insects in a neotropical forest. In: *The ecology of a tropical forest* (eds. E.G. Leigh, A.S. Rand and D.M. Windsor), pp. 309-318. Washington, DC: Smithsonian Institution Press.

Solow, A.R. 1993. A simple test for change in community structure. *Journal of Animal Ecology*, **62**, 191-193.

Stork, N.E. & Brendell, M.J.D. (1990) Variation in the insect fauna of Sulawesi trees with season, altitude and forest type. In: *Insects in the rain forest of South East Asia (Wallacea)* (eds. W.J. Knight and J.D. Holloway), pp. 173-190. London: The Royal Entomological Society of London.

Süßenbach, D. (2003) *Diversität von Nachtfaltergemeinschaften entlang eines Höhengradienten in Südecuador (Lepidoptera: Pyraloidea, Arctiidae)*. Ph.D. thesis, University of Bayreuth. URL: http://opus.ub.uni-bayreuth.de/volltexte/2003/33

Summerville, K.S., Ritter, L.M. & Crist, T.O. (2004) Forest moth taxa as indicators of lepidopteran richness and habitat disturbance: a preliminary assessment. *Biological Conservation*, **116**, 9-18.

Trueblood, D.D., Gallagher, E.D. & Gould, D.M. (1994) Three stages of seasonal succession on the Savin Hill Cove mudflat, Boston Harbor. *Limnology and Oceanography*, **39**, 1440-1454.

Wich, S.A. & van Schaik, C.P. (2000) The impact of El Nino on mast fruiting in Sumatra and elsewhere in Malesia. *Journal of Tropical Ecology*, **16**, 563-577.

Wolda, H. (1978) Fluctuations in abundance of tropical insects. *American Naturalist*, **112**, 1017-1045.

Wolda, H. (1980) Seasonality of tropical insects. I. Leafhoppers (Homoptera) in Las Cumbres, Panama. *Journal of Animal Ecology*, **49**, 277-290.

Wolda, H. (1992) Trends in abundance of tropical forest insects. *Oecologia*, **89**, 47-52.

Wolda, H. & Wong, M. (1988) Tropical insect diversity and seasonality. Sweep samples versus light-traps. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, series C*, **91**, 203-216.

Yela, J.L. & Holyoak, M. (1997) Effects of moonlight and meteorological factors on light and bait trap catches of noctuid moths (Lepidoptera: Noctuidae). *Environmental Entomology*, **26**, 1283-1290.

7 Synopsis

Diversity patterns and species composition of arctiid and geometrid moth assemblages

The threats which tropical rainforests are facing have long been recognised (e.g. Laurance, 1998, Brooks *et al*., 2002; Armenteras *et al*., 2003). An increasing number of studies addressed insect communities of natural tropical forests in different parts of the world (Africa: deJong & Congdon, 1993; Axmacher *et al*., 2004; South East Asia: Holloway, 1984; Intachat & Holloway, 2000; South America: Braun, 2002; Brehm, 2002; Süßenbach, 2003; Brehm *et al*., 2005). However, due to continuous pressures that lead to habitat conversion (Bawa & Seidler, 1998), habitats such as secondary forests and forest remnants are becoming increasingly more important for the conservation of tropical biodiversity (Ricketts *et al*., 2001). Thus, responses of insects to anthropogenic disturbance of tropical forests are of current conservation concern (for a recent review with regard to Lepidoptera see Hamer & Hill, 2000; see also Schulze, 2000; Hamer *et al*., 2003). The dramatic responses of some insect groups to severe forms of forest disturbance such as clear felling and conversion to grassland have been relatively well documented (Holloway *et al*., 1992; Daily & Ehrlich, 1995). However, responses to less severe forms of disturbance are poorly understood (Hamer & Hill, 2000), because of inconsistent results: some studies have shown a reduction in diversity following even minor habitat disturbance (e.g. Daily & Ehrlich, 1995; Hill *et al*., 1995), whereas others have concluded that disturbance even results in an increase of insect diversity (e.g. Hamer *et al*., 1997; Spitzer *et al*., 1997; Beck *et al*., 2002; Schulze & Fiedler, 2003; Fiedler & Schulze, 2004).

In view of that controversy, I investigated diversity and species composition of two different moth families (Lepidoptera: Arctiidae, Geometridae) along a Neotropical montane succession gradient which ranged from a barely vegetated landslide to the mature forest understorey. Due to their different life histories and morphologies (reviews: Kitching & Rawlins, 1999; Minet & Scoble, 1999), different responses of these insect families to forest disturbance and recovery were expected.

Results from lowland habitats in other tropical regions suggest that Arctiidae may benefit from anthropogenic disturbance (e.g. Kitching *et al.*, 2000; Schulze, 2000). Similar results were found in this study (**chapters 2 and 3**). Diversity was highest in the later succession stages and decreased with forest recovery. The intermediate disturbance hypothesis (Connell, 1978) might provide an explanatory framework for the pattern observed in Ecuador. This hypothesis implies that species diversity is highest in communities experiencing intermediate levels of disturbance. Thus, early as well as very late stages of forest recovery should exhibit lower diversity.

Overall, the highest diversity was found at the edge of the mature forest. However, Didham (1997) pointed out that an increase in insect abundance and diversity at forest edges is almost certainly a result of invasion of generalist species from disturbed habitats outside the forest fragment (Kotze & Samways, 2001), also termed the mass effect (Shmida & Wilson, 1985). Kotze and Samways (2001) observed no significant increase in numbers of carabid and ant individuals or species at very sharp Afromontane forest edges, i.e. no biological edge effect (for a review see Murcia, 1995). Carabid abundance and species richness decreased from forest to grassland, while ant species richness increased. However, their results are in sharp contrast to many other studies performed at anthropogenic, mainly clear-cut forest edges. Some invertebrates such as ants, arachnids, beetles in general, carabid beetles in particular, and social wasps prefer habitat edges rather than habitat interiors (Kotze & Samways, 2001). In this study there were also some species (e.g. *Hypercompe nemophila* (Herrich-Schäffer 1853), *Holophaea endoleuca* (Dognin 1909), *Cosmosoma meridense* (Rothschild 1911), *Elysius melanoplaga* (Hampson 1901)), which had their highest individual numbers in the studied forest edge and migrated from the disturbed areas to the forest edge. In contrast to the good flight capacity and therefore potentially high dispersal ability of many arctiid moths (e.g. Kitching & Rawlins, 1999; Solis & Pogue, 1999), geometrid moths tend to be weaker fliers and exhibit a relatively high habitat fidelity (Holloway, 1984; Chey *et al.*, 1997; Thomas, 2002). Therefore they may respond more sensitively to changes in habitat quality (e.g. Willott, 1999; Kitching *et al.*, 2000; Beck *et al.*, 2002) such as forest destruction. Local diversity of geometrid moths indeed increased with forest recovery and decreased with increasing distance to natural forest (**chapter 5**). Similar results were found along habitat in Africa (e.g. Axmacher *et al.*, 2004), in South East Asia (e.g. Chey *et al.*, 1997; Kitching *et al.*, 2000; Beck *et al.*, 2002) and in the Neotropical region (e.g. Brehm & Fiedler, 2005). Hence, with regard to local ensemble diversity Geometridae indeed reflected changes in habitat quality more closely than Arctiidae moths.

These differential responses of moth ensemble diversity to habitat succession strongly undermined the potential to use one taxon to predict diversity patterns in the other. Rather strong correlations between the alpha diversity of local ensembles only occurred within families (e.g. family vs. subordinated subfamilies or tribes; see Table 1). In contrast, no significant relationships in alpha diversity were found between families, or between taxa that belong to different families. Even within the family Arctiidae, diversity patterns were only concordant between Phaegopterini and Ctenuchini. These discrepancies in the alpha diversity patterns between the two families are rooted in their different life-histories, flight capability, host plant preferences, etc.

Overall, results from other studies indicate that the effects of forest disturbance on species diversity are heavily scale dependent (Hamer & Hill, 2000; Hill & Hamer, 2004; Rahbek, 2005). At small spatial scales, as in the present study, habitat disturbance indeed frequently increases diversity, whereas at larger scales there is higher diversity in undisturbed forests (Hamer & Hill, 2000).

Table 1: Concordance between local diversity of moth ensembles across different taxonomic levels. Given are Pearson's correlation coefficients between Fisher's alpha diversity of Arctiidae, Geometridae and various subordinated taxa. A: Arctiidae, G: Geometridae. All values were significant at a table-wide FDR of *P*<0.05.

	Arctiidae total	Ennominae (G)	Larentiinae (G)	Phaegopterini (A)	Ctenuchini (A)	Lithosiinae (A)
Geometridae total	0.18, n.s.	0.94***	0.73***	-0.24, n.s.	-0.14, n.s.	0.12, n.s.
Arctiidae total		0.1, n.s.	-0.01, n.s.	0.63**	0.65**	0.74***
Ennominae (G)			0.55*	-0.27, n.s.	-0.19, n.s.	-0.002, n.s.
Larentiinae (G)				-0.26, n.s.	-0.25, n.s.	0.02, n.s.
Phaegopterini (A)					0.68***	0.15, n.s.
Ctenuchini (A)						0.21, n.s.

* *P*<0.01, ** *P*<0.005, *** *P*<0.001, n.s. not significant (*P*>0.05)

Insect communities in tropical rain forests usually contain large numbers of rare species (Novotny & Basset, 2000; Basset *et al.*, 2004). These are species, which are found as a single individual (singleton) in a combined data set. The proportion of rare species in sweep net collections, where sampling effort was restricted in time, amounted to 60% for Chalcidoidea in Sulawesi (Noyes, 1989), and to 65% for all arthropod taxa in Costa Rica (Janzen & Schoener, 1968). In these cases the excessively high number of 'rare' species may be strongly influenced by the sampling effort (Basset & Kitching, 1991). In support of that latter view, in a relatively extensive light-trapping study extending over a year in Malaysia, Barlow and Woiwod (1989) found a far lower proportion of rare species of Macrolepidoptera (37.7%). Similar values were reported by Basset and Kitching (1991) from an Australian rainforest tree for arboreal arthropods (35.7%) and by Willott (1999) in a selectively logged rainforest in Borneo for moths (37%). In this present study, where a very extensive sampling was performed, the proportions of unique singletons were 21.3% for arctiid and 18.6% for geometrid moths. This indicates that very substantial samples (in the range of many thousands of individuals per taxon) need to be assembled from speciose tropical insect ensembles to achieve meaningful estimates of the commonness, or rarity, of species. In contrast to this rather low fraction of global singletons, the mean proportions of local singletons (i.e. species that were observed only once per site) was substantially higher and differed significantly between the three succession stages. For both families the fraction of local singletons was highest in the mature forest understorey (> 50%) (**chapters 2, 3** and **5**). This observation well fits the expectation that mature tropical forests provide more niches and support more species that are 'rare' during most of the time. In this respect, the two target families Arctiidae and Geometridae did not differ from another.

High dominance of a few species is often viewed as an effect of anthropogenic habitat disturbance (e.g. Beck *et al.*, 2002), but recent studies have called this generalization into question (Nummerlin & Kaitala, 2004). In the present study dominance values were generally high (mean proportion of the commonest species of total catch, averaged over all 21 sites; Arctiidae: 14.7 ± 6.2% and Geometridae: 13.1 ± 9.2%) (**chapters 2, 3** and **5**) compared to other tropical moth assemblages (e.g. geometrid moths in the same study area: median: 6.7%; Brehm, 2002; Brehm & Fiedler, 2005). The two commonest moth species were *Macroptila laniata* (Dognin 1899) in the Arctiidae and *Pantherodes conglomerata* (Warren 1894) in the Geometridae. Contrary to expectation, the highest dominance values of arctiid individual species were found in the mature forest sites (**chapters 2** and **3**), whereas the highest dominance values for geometrid moths were observed in the early succession stages, followed by the mature forest understorey and the later succession stages (**chapter 5**). The commonest geometrid moth (*P. conglomerata*) showed a significant decrease of relative abundance along the succession gradient with forest recovery. One reason for this decrease could be that its host-plants (*Boehmeria* and *Vernonia* species) were common in the more open succession sites (J. Homeier, pers. comm.). Within the arctiid tribe Ctenuchini the same two species (*Cosmosoma* sp15 and *Holophaea endoleuca* (Dognin 1909)) were dominant in all succession habitats, and also in natural forest sites, whereas in the tribe Phaegopterini the dominant species changed along the succession gradient. In the early succession stages the most dominant species was *Leucanopsis nayapana* (Schaus 1941), but in the later succession stages as well as in the mature forest understorey this role was taken over by the two species *Ischnocampa sordida* (Felder 1874) and *I. mamona* (Dognin 1892). The larval host plants of none of these common arctiids are known thus far, but one might predict that, as in the case of the geometrid *P. conglomerata*, resource availability plays a major role in regulating local abundance also in these moths.

Basset and Kitching (1991) found in a fogging sample from an Australian rainforest tree a similar dominance value of 12%, which contrasts sharply with higher values reported from arthropod communities in several tree species both from Britain and South Africa (average 33% and 26%, respectively; Southwood *et al.*, 1982). Spitzer *et al.* (1997) found a high degree of dominance of a single butterfly species, which accounted for about half of all individuals in closed forest. Whilst moths in Costa Rica showed high dominance values in the understorey in contrast to the canopy (0.32 vs. 0.12; Brehm, 2005). Nummelin and Kaitala (2004) gave a short review of dominance patterns in different data sets relating to beetles, butterflies, and plants in logged vs. unlogged forest sites and concluded that dominance indices such as the Berger-Parker index are not always suitable indicators of rainforest disturbance. My own results corroborate this view, with arctiid moths exhibiting unexpectedly high dominance in natural forest. The reasons for that remain inexplicable in the absence of valid data on resource requirements of even the most dominant species.

Some field studies have suggested that if only species richness is measured, the effect of habitat loss on forest lepidopteran communities may appear rather innocuous (Summerville, 2004; Beck, 2005), because small patches of forest habitat are capable of supporting nearly as many butterfly and moth species as larger patches in both, temperate (Summerville & Crist, 2003) and tropical ecosystems (Ricketts *et al.*, 2001). Although patterns of alpha diversity were different between the families (decrease of arctiid diversity and increase of geometrid diversity with forest recovery, poor correlations between taxa, see Table 1 above), the patterns of beta diversity were strikingly similar between arctiids and geometrids (see Table 2). Faunal differentiation was highly concordant for all used *m* values (1 to 152) of the CNESS distance coefficient between the two moth families. At high *m* values, i.e. when emphasizing the contribution of rare species, these relationships even tended to become more pronounced. Similarly, patterns of faunal change were very parallel between subordinated taxa within the family Arctiidae, despite their diverging life-habits (**chapter 3**). These findings show that, while alpha diversity patterns of moths were highly idiosyncratic across taxa, the mode of community change along the succession gradient was much more concordant. In line with that conclusion, there was a distinct separation of arctiid and geometrid ensembles at succession sites from those in mature forest understorey (**chapters 2** and **5**), which even translated to the level of arctiid subfamilies and tribes (**chapter 3**). However, the patterns of faunal change were not completely identical between the moth taxa. For example, emphasizing the common species, only Phaegopterini and Lithosiinae showed a clear distinction between the ensembles from succession habitats and forest, respectively. The Ctenuchini, on the contrary, showed only a clear separation between the succession sites and the forest sites when the rare species were accentuated. This suggests that only a few species of Ctenuchini are abundant and behave as relative habitat generalists in the study area (e.g. *Cosmosoma* sp19, *C. meridense* (Rothschild 1911), *Holophaea endoleuca*, *Eucereon zizana* (Dognin 1897)), whereas most wasp moths occur at generally low abundances and appear to be forest specialists. Again, life-history data on these species are needed to test this hypothesis which now could be generated from community-wide multivariate analyses.

Table 2: Concordance of faunal distances between moth families. Given are matrix rank correlations, *r* (based in Spearman coefficients, 1000 random permutations) between faunal dissimilarity (CNESS distances) of the two moth families (Arctiidae, Geometridae), and for different *m* values. All *r* values are highly significant at *P*<0.001.

		Arctiidae															
***m* value**		**1**	**5**	**10**	**12**	**20**	**30**	**40**	**50**	**60**	**70**	**76**	**80**	**90**	**100**	**125**	**152**
Geometridae	**1**	0.576	0.649	0.686	0.691	0.696	0.696	0.698	0.696	0.694	0.693	0.69	0.688	0.681	0.675	0.656	0.638
	5	0.612	0.683	0.718	0.722	0.726	0.725	0.726	0.723	0.721	0.719	0.716	0.713	0.706	0.7	0.681	0.662
	10	0.643	0.717	0.753	0.756	0.76	0.759	0.759	0.757	0.754	0.752	0.748	0.746	0.738	0.732	0.712	0.694
	12	0.653	0.727	0.762	0.765	0.769	0.768	0.768	0.765	0.762	0.759	0.756	0.753	0.746	0.74	0.72	0.701
	20	0.678	0.757	0.796	0.799	0.803	0.802	0.801	0.797	0.793	0.79	0.786	0.783	0.776	0.769	0.749	0.729
	30	0.686	0.773	0.816	0.82	0.827	0.827	0.825	0.821	0.816	0.813	0.809	0.806	0.798	0.791	0.771	0.752
	40	0.692	0.785	0.833	0.839	0.848	0.848	0.846	0.841	0.836	0.832	0.828	0.826	0.818	0.811	0.791	0.772
	50	0.692	0.789	0.841	0.848	0.859	0.861	0.859	0.855	0.85	0.846	0.842	0.84	0.832	0.825	0.805	0.787
	60	0.691	0.79	0.845	0.852	0.865	0.868	0.866	0.862	0.857	0.853	0.849	0.847	0.839	0.832	0.813	0.795
	70	0.685	0.788	0.847	0.856	0.871	0.875	0.874	0.87	0.865	0.862	0.858	0.856	0.848	0.841	0.823	0.805
	76	0.683	0.788	0.848	0.857	0.873	0.877	0.876	0.873	0.868	0.864	0.861	0.858	0.851	0.844	0.825	0.807
	80	0.68	0.786	0.847	0.857	0.875	0.879	0.879	0.875	0.871	0.867	0.863	0.861	0.854	0.847	0.829	0.811
	90	0.676	0.784	0.848	0.858	0.878	0.883	0.884	0.881	0.877	0.873	0.87	0.868	0.86	0.854	0.836	0.818
	100	0.672	0.782	0.848	0.86	0.88	0.887	0.888	0.885	0.882	0.878	0.875	0.873	0.866	0.86	0.843	0.825
	125	0.665	0.778	0.848	0.861	0.885	0.894	0.896	0.894	0.891	0.889	0.886	0.884	0.878	0.872	0.856	0.839
	152	0.659	0.774	0.848	0.861	0.888	0.898	0.902	0.901	0.899	0.897	0.894	0.893	0.887	0.881	0.866	0.851

A clear discrimination among lepidopteran assemblages based on forest types was also found in remnants of upland Australian rainforests (moths: Kitching *et al.*, 2000), in natural and selectively logged forests of northern Borneo (butterflies: Hamer *et al.*, 2003), as well as along two habitat gradients on Borneo (geometrids: Beck *et al.*, 2002; Pyraloidea: Fiedler & Schulze, 2004), and in a comparative analyses between anthropogenically disturbed habitats vs. intact montane rainforest in Ecuador (geometrids: Brehm & Fiedler, 2005).

Patterns of beta diversity were best predicted by the degree of habitat openness, and to a lesser extent by elevation. Geometrid moths responded more sensitively than arctiid moths regarding to habitat openness (Fig. 1). Statistical differentiation between samples (measured as the *R* statistics of ANOSIM) was always higher for the Geometridae, irrespective of the emphasis on rare or abundant species. In both families the best resolution was achieved at low to medium *m* values. In addition, the decay of community differentiation at higher *m* values was far less pronounced in the geometrids. One reason for that observation could be that in the far bigger dataset of geometrid moths sampling effects with rare species were less problematic.

Faunal differences were not related to geographical distances between the sampling sites. Thus, even on the small spatial scale of my study the community differences observed can be related to local ecological effects and are not just a side effect of dispersal from source areas (such as the neighbouring natural forest).

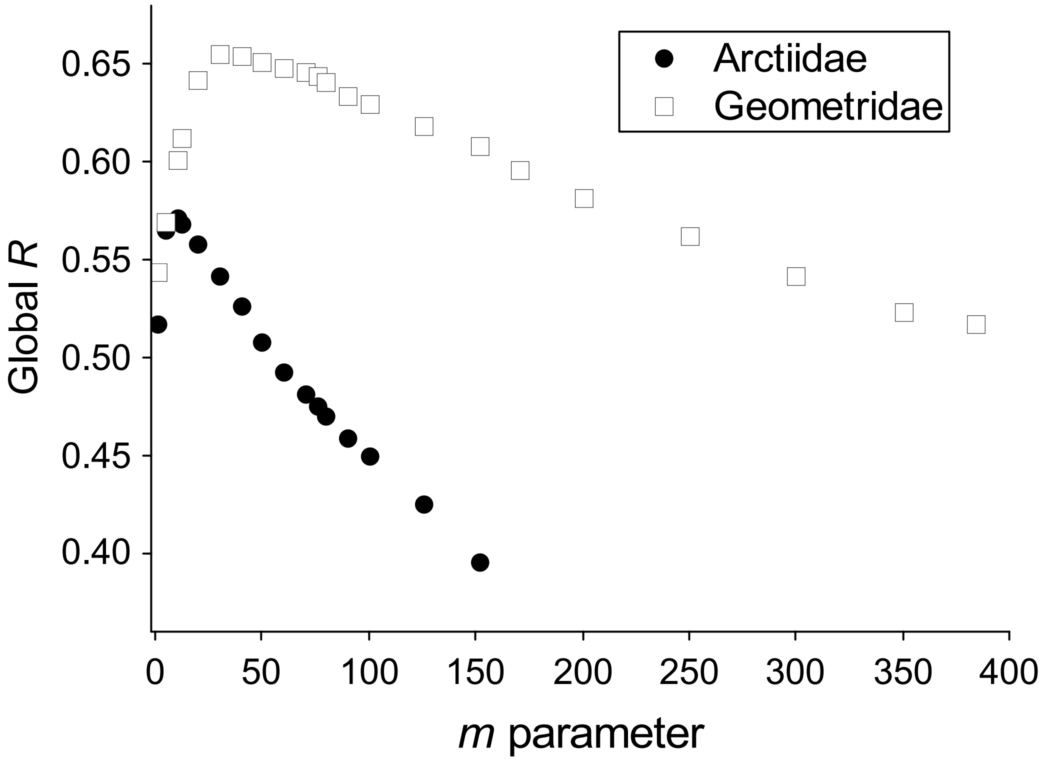


Figure 1: Discriminatory power of Analyses of Similarities (expressed as values of the global *R* statistics, one-way ANOSIM, 1000 permutations) as a function of the sample size parameter *m* (of CNESS indexes as a measure of faunal distances) for the two studied moth families. Basis for the analyses were the moth samples from 21 sites in and around the Reserva Biológica San Francisco, separated into four habitat categories (natural forest understorey, late succession habitats with woody vegetation, early succession habitats without woody vegetation, abandoned pastures). Highest resolution is obtained at *m* = 10 for the Arctiidae and *m* = 30 for the Geometridae.

Recapitulating, tropical arctiid as well as geometrid ensembles were previously found to reflect ecological differences between habitats, but with a clearer picture for geometrid moths (see also Intachat *et al.*, 1997, 1999), although both families showed different and partially opposite local diversity patterns along the succession gradient. The same observation was made in the same Ecuadorian study area along an elevational gradient through natural forest. Three moth families (Arctiidae, Geometridae and Pyraloidea), and all their larger subordinated taxa, revealed idiosyncratic patterns of alpha diversity, but highly concordant patterns of beta diversity (K. Fiedler, G. Brehm & D. Süßenbach, pers. comm.; see also Brehm *et al.*, 2003; Süßenbach, 2003). Thus, taxon-specific patterns in diversity and gross taxonomic composition contrasted sharply with concordant patterns of species turnover along the tropical elevational gradient. My data on faunal turnover along the succession gradient fully corroborate these results: while patterns of species richness were taxon-specific, species turnover was almost identical between Arctiidae and Geometridae despite their prominent morphological and ecological differentiation.

Body size and external appearance of arctiid moths

Body size is one of the most significant features of organisms (e.g. Chown & Klok, 2003; Komonen *et al.*, 2004), and body size distributions are often used to characterize and compare communities in response to the influence of abiotic and biotic factors (e.g. Lawton, 1991; Schulze *et al.*, 2001). Therefore, body size and proboscis development were analysed in arctiid moths along the succession gradient (**chapter 4**). There was pronounced taxon-specific variation in traits such as forewing length, body length, and wing load. However, analyses on species level revealed no differences in body-size related traits along the succession gradient. On the individual level, there was a decrease in forewing and body length as well as wing surface area with forest recovery. The size distributions of all species and total individual numbers showed a unimodal distribution similar to a log-normal distribution, with one exception: the body length of the individuals showed a bimodal distribution. Morse *et al.* (1988) also found that the body length distribution for beetles in Bornean rainforests approximately conformed to a log-normal distribution. Similar results were obtained by other authors (e.g. Hemminsen, 1934; Schoener & Janzen, 1968). Ricketts *et al.* (2001) found for five moth families (namely Notodontidae, Arctiidae, Crambidae, Geometridae and Noctuidae) a decline in mean wing length with the distance from forest. At the small spatial scale of my study, such effects were not discernible.

Basset and Kitching (1991) found for an Australian rainforest tree that most collected arthropod species were small. This observation is similar to other studies, which emphasized that most arthropods sampled from tropical vegetation are small (e.g. Janzen & Schroeder, 1968; Erwin & Scott, 1980). For rainforest arboreal arthropods, several selection pressures may lead to a reduction of body size (see Basset & Kitching, 1991). One reason could be that small body size may actually increase dispersal abilities (Gaston & Lawton, 1988), and this factor certainly represents an important selective advantage in dynamic rainforest environments (Morse *et al.*, 1988). However, in my study I did not find any differences in body length or forewing length for arctiid species related to succession, but the species found in the forest understorey had a broader frequency distribution of forewing length and body length. Also, there were some variations to that pattern at subordinated level. Larger Phaegopterini occurred more frequently in succession sites, whereas larger Ctenuchini and Lithosiinae were mainly found in mature forest understorey. Ctenuchini showed a broader frequency distribution in the later succession stages vs. the earlier ones and the forest sites. The functional significance of these subtle variations remains obscure. Generally, it was surprising to see that ecological differences (here: between succession habitats) explained so little variation in morphological characters, whereas most variation occurred between phylogenetic lineages.

For moths, a functional proboscis is important for the uptake of food resources such as nectar, sap from rotting fruits, or pyrrolizidine alkaloids (PAs). Yet, reduction of the proboscis up to the degree that no food at all can be gained during the adult stage is not uncommon among the Lepidoptera (Hebert, 1983; Hunter, 1991; Tammaru & Haukioja, 1996). However, the non-feeders form a clear minority among temperate-zone Macrolepidoptera, e.g. they make up about 15% of the species in northern Europe (Tammaru & Haukioja, 1996). In the Old World tropics (and in temperate-zone regions: e.g. Hunter, 1991) many species of the subfamily Arctiinae have a rudimentary to non-functional proboscis (Schulze *et al.*, 2001). In the Ecuadorian samples, there was a significant difference with regard to proboscis length along the succession gradient. Arctiids with reduced proboscis were twice as common at the succession sites compared to the mature forest understorey. This suggests that non-feeding arctiids are at an advantage in colonizing disturbed habitats. However, 91.6% of the species had a functional proboscis, whereas only 5.2% had a rudimentary proboscis and 3.2% had no apparent proboscis at all. Thus, capital breeders are a small minority among Neotropical arctiids, in contrast to their Old World relatives. There were some differences in proboscis length between taxa. All Ctenuchini studied had a functional proboscis, and in the Phaegopterini and Lithosiinae reductions of the proboscis were rare. In contrast, all Arctiini and half of the sampled Pericopini species had no functional or only a rudimentary proboscis. Schulze *et al.* (2001) found differences in the abundance of representatives of nectar-feeding vs. non-feeding arctiid species between understorey and canopy of a Bornean rainforest. Nectar-feeders clearly dominated in the canopy (> 90% of all tiger moth species), whereas in the understorey the occurrence of nectar-feeders and non-feeders was almost balanced. In Ecuador, nectar-feeding and pharmacophagy are obviously far more important for adult arctiid moths, but somewhat less so in open disturbed habitats.

Lepidopteran wings show colour patterns that often have functions in defence and predator avoidance (aposematism, mimicry, mimetic camouflage). Aposematism (Poulton, 1890) is an anti-predator defence combining a warning signal, most often black in combination with yellow, orange, or red (Cott, 1957) or other bright coloration, with unpalatability or toxicity (e.g. Merilaita & Kaitala, 2002). The origin and evolution of allelochemical sequestration in tiger moths (Arctiidae) is a complex interplay of larval and adult strategies and phylogenetic history (Weller *et al.*, 1999). Such host-plant derived defense is usually associated with aposematism and/or mimicry among arctiids.

In this study 287 arctiid species were scored according to their external appearance as either cryptic (49.5% of species / 64.2% of individuals) or aposematic (50.5% of species / 35.8% of individuals) (**chapter 4**). Overall, the relative incidence of aposematism in arctiid moths did not change along the succession gradient; however, such patterns became apparent at lower systematic levels. Aposematic species among Phaegopterini and Lithosiinae were more prevalent at succession sites, whereas Ctenuchini showed the reverse picture. These data do not suggest that predation pressure by visually hunting enemies of arctiids would differ consistently between forest and succession habitats, but selection pressures may well differ for certain moth species depending on their specific life cycles and habits. Clearly, more specific knowledge on the life-histories of individual arctiid species, and on their relevant predators, will be required to gain more insight into possible effects of habitat disturbance on the functionality and complexity of aposematism and mimicry rings (e.g. Brown, 1984; Beccaloni, 1997a, b; DeVries *et al.*, 1999).

Temporal dynamics among arctiid and geometrid moths

It has commonly been observed that insect abundance changes both, in long-term (e.g. years) as well as in short-term cycles (e.g. weeks; for reviews see Wolda, 1978). Seasonal fluctuations in abundance and species richness have been documented in a number of Neotropical insect groups (Wolda, 1978; Smythe, 1982; Wolda & Wong, 1988). However, much less is still known about dynamics of Lepidoptera of the humid or seasonal tropics (e.g. Ehrlich, 1984; DeVries *et al.*, 1997; DeVries & Walla, 2001).

Therefore, I also analysed the temporal variation in diversity and species composition of species-rich ensembles of mobile herbivorous insects along a succession gradient (**chapter 6**). Despite prominent fluctuations of moth abundance, local moth diversity was relatively constant over time for arctiids, whereas geometrid moths fluctuated more clearly in individual numbers, species numbers, and local diversity over the three sampling periods. One possible reason for these fluctuations could be that single dominant species such as *Pantherodes conglomerata* often show strong abundance fluctuations, which will in turn influence diversity measures such as Fisher's alpha (see Fiedler & Schulze, 2004). However, only a few of the common species showed strong temporal changes in abundance in both families, and more than 50% of the species, which accounted for >90% of all sampled individuals, were found in all three sampling periods. Similar results were found by Süßenbach (2003) for pyraloid and arctiid moths in the same study area in the mature forest understorey. Thus, none of the common moth species covered by the present study (see also Brehm, 2002 and Süßenbach, 2003) can be termed as seasonal in a strict sense.

Even in perhumid rainforests of South East Asia, where a true dry season does not occur regularly, pronounced fluctuations in the abundance of individual species or entire guilds are frequent, although consistent temporal trends are not always apparent (e.g. Schulze & Fiedler, 2003; Fiedler & Schulze, 2004; also Barlow & Woiwod, 1989, 1990; Intachat & Holloway, 2000). My results are consistent with these studies, even though the study region in southern Ecuador does show a clear climatic seasonality (a short drier period between October and February termed veranillo). This climatic cyclicity is also reflected in consistent seasonal patterns of plant phenology (e.g. Homeier, 2004). Apparently, many of the more common moths are not that strongly dependent on plant phenology that they would be forced to undergo some way of dormancy to avoid periods of resource scarcity – a phenomenon that is commonly seen for example among moths in Costa Rican dry forests (Janzen, 1987). Nevertheless, the pronounced abundance fluctuations of certain common species (e.g. Arctiidae: *Agylla nitridalis* (Maassen 1890), *A. seperata* (Schaus 1894), *Napata* sp.; Geometridae: *Lomographa tributaria* (Walker 1862), *Pantherodes conglomerata*) suggest that resources for these species (e.g. young foliage or inflorescences of host plants) are not equally available all year round. In this respect it is noteworthy that geometrid ensembles showed greater temporal differentiation than arctiids. This might indicate that geometrid larvae are generally more dependent on ephemeral resources (young foliage, inflorescences) than arctiids. This hypothesis is in line with the (scarce) knowledge about larval host plants and merits further testing.

Multivariate analyses of moth samples revealed a significant separation of the arctiid and geometrid ensembles according to the sampling period as well as the different habitat categories. Segregation between samples was usually more strongly affected by sampling period than by habitat. Furthermore, the effect of the sampling period increased with increasing time period between the single sampling periods. Therefore, comparisons between sites should be based on samples that have been taken in the closest possible sequence (Fiedler & Schulze, 2004). My data show that, despite all consistent patterns to be seen in moth ensembles from the montane zone in Ecuador, these insect assemblages are highly dynamic over time. However, if moth samples are large enough and preferably collated over various times of the year, it is nevertheless possible to achieve valid statements about moth diversity and species compositions in relation to habitat differences.

Concluding remarks

Tropical montane rainforests are less well known than lowland rainforests, although evidence is accumulating that diversity and endemism of some taxa might be as high or even higher in the mountainous ranges of the tropics (Brehm, 2002; Brehm *et al.*, 2005). Although in this study local diversity for both families turned out to be high in the later succession stages, it appears to be very important to protect the remaining mature forests as source areas for the moths. Even though many moths are relatively mobile organisms (Daily, 1996), Ricketts *et al.* (2001) as well as Summerville and Crist (2004) showed that their diversity often strongly declines in disturbed and secondary habitats, if the connection to source habitats such as rainforest patches is lost. I found a strong impoverishment of arctiid and geometrid ensembles on abandoned pastures only 400 m away from intact forest, and a drop-out of rare forest species at even smaller spatial scales. However, further studies are needed to investigate the influence and the role of spatial scale (Hamer & Hill, 2000) on the moth ensembles and their species diversity. Moreover, alternatives in landuse and conservation practices such as management of secondary forests and restoration of degraded lands must be sought for (Bawa & Seidler, 1998).

In recent years, many authors have proposed that the diversity of entire species-rich groups can be estimated by sampling a subset of the fauna that is easily collected and readily identifiable (e.g. Summerville *et al.*, 2004; Schulze *et al.*, 2004). In my extensive moth data sets, however, correlations between diversity measures of subordinated arctiid taxa, or between the entire arctiid family and subordinated taxa, were rather low (**chapter 3**, Table 1 above). Overall, these results leave little scope for the use of small manageable subsets of Neotropical arctiid moths as diversity indicators for this large, prominent moth family in Andean habitats (Brehm & Fiedler, 2003). Similar results were found by Lawton *et al.* (1998), who examined species richness in several animal groups (birds, butterflies, beetles, ants, termites, nematodes) sampled along a disturbance gradient in Cameroon. They suggested that assessments of habitat change based on familiar groups such as birds or butterflies may often be misleading because of low pair-wise correlations between groups and weak trends with disturbance. This lack of congruence should further caution against the assumption that detailed studies of one or a few groups of organisms can serve as indicators for other such groups (Kessler *et al.*, 2001).

However, my data do allow the identification of individual ‘indicator’ species among the more common arctiid and accordingly geometrid species (N > 50) for the three different succession stages (**chapters 2, 3** and **5**). The species *Agylla argentifera* (Walker 1866), *Ischnocampa tristis* (Schaus 1889), *Eucereon perstriatum* (Hampson 1909) (all three Arctiidae), *Pantherodes conglomerata* and *Perissopteryx* sp near *nigricomata* (Warren 1901) (both Geometridae) showed a clear preference for succession sites, whereas *Mesothen roseifemur* (Draudt 1915), *Correbia lycoides* (Walker 1854) (both Arctiidae), *Physocleora pulverata* (Warren 1907) and *Chloropteryx opalaria* (Guenée 1857) (both Geometridae) were exclusively recorded in near-natural forest.

Overall, in the framework of rapid biodiversity assessment, Arctiidae and Geometridae across this succession gradient in southern Ecuador did not make up excellent target organisms as indicators for other groups such as butterflies, beetles, etc. but they may well serve as sensitive indicators for environmental changes, as evidenced by their clear and concordant patterns in species turnover along environmental gradients.

The most prominent deficit is that life-cycles and host-plant associations of tropical nocturnal Lepidoptera remain unknown in most cases (e.g. Brehm, 2003; Dyer *et al*., 2005; Janzen & Hallwachs, 2005). My study approach on the level of extremely rich and diverse communities was successful in analysing patterns and generating hypotheses that can explain such patterns. However, these hypotheses now need to be tested by data on the role of individual moth species in their habitats. For that purpose, many more rearing data are needed in order to reveal insights into general patterns of host-plant relationships of tropical herbivorous moths. Only with an increasing understanding of the functional relationships between moths and their environment will it be possible to unravel the processes that generate the complex, and often unexpected, diversity patterns as presented in this study. However, since the accumulation of such data will need much more time and effort, while the habitat degradation continues at an alarming rate, the study of community-wide patterns will remain an indispensable tool for habitat assessments in the near future. The present study is, hopefully, one further step along this way.

References

Armenteras, D., Gast, F. & Villareal, H. (2003) Andean forest fragmentation and the representativeness of protected natural areas in the eastern Andes, Colombia. *Biological Conservation*, **113**, 245-256.

Axmacher, J.C., Holtmann, G., Scheuermann, L., Brehm, G., Müller-Hohenstein, K. & Fiedler, K. (2004) Diversity of geometrid moths (Lepidoptera: Geometridae) along an Afrotropical elevational rainforest transect. *Diversity and Distributions*, **10**, 293-302.

Barlow, H.S. & Woiwod, I.P. (1989) Moth diversity of a tropical forest in Peninsular Malaysia. *Journal of Tropical Ecology*, **5**, 37-50.

Barlow, H.S. & Woiwod, I.P. (1990) Seasonality and diversity of Macrolepidoptera in two lowland sites in the Dumoga-Bone National Park, Sulawesi Utara. In: *Insects and the Rain Forests of South East Asia (Wallacea)* (eds. W.J. Knight and J.D. Holloway), pp. 167-172. London: The Royal Entomological Society of London.

Basset, Y. & Kitching, R.L. (1991) Species number, species abundance and body length of arboreal arthropods associated with an Australian rainforest tree. *Ecological Entomology*, **16**, 391-402.

Basset, Y., Mavoungou, J.F., Mikissa, J.B., Missa, O., Miller, S.E., Kitching, R.L. & Alonso, A. (2004) Discriminatory power of different arthropod data sets for the biological monitoring of arthropod data sets for the biological monitoring of anthropogenic disturbance in tropical forests. *Biodiversity and Conservation*, **13**, 709-732.

Bawa, K.S. & Seidler, R. (1998) Natural forest management and conservation of biodiversity in tropical forests. *Conservation Biology*, **12**, 46-55.

Beccaloni, G.W. (1997a) Vertical stratification of ithomiine butterfly (Nymphalidae: Ithomiinae) mimicry complexes: the relationship between adult flight height and larval host-plant height. *Biological Journal of the Linnean Society*, **62**, 313-341.

Beccaloni, G.W. (1997b) Ecology, behaviour and natural history of ithomiine butterflies (Lepidoptera: Nymphalidae) and their mimics in Ecuador. *Tropical Lepidoptera*, **8**, 103-124.

Beck, J. (2005) *The macroecology of Southeast-Asian hawkmoths (Lepidoptera: Sphingidae).* Ph.D. thesis, University of Würzburg. URL: http://opus.bibliothek.uni-wuerzburg.de/opus/volltexte/2005/1300/

Beck, J., Schulze, C.H., Linsenmair, K.E. & Fiedler, K. (2002) From forest to farmland: diversity of geometrid moths along two habitat gradients on Borneo. *Journal of Tropical Ecology*, **18**, 33-51.

Braun, H. (2002) *Die Laubheuschrecken (Orthoptera, Tettigoniidae) eines Bergregenwaldes in Süd-Ecuador – faunistische, bioakustische und ökologische Untersuchungen*. Ph.D. thesis, University of Erlangen-Nürnberg.

Brehm, G. (2002) *Diversity of geometrid moths in a montane rainforest in Ecuador*. Ph.D. thesis, University of Bayreuth. URL: http://opus.ub.uni-bayreuth.de/volltexte/2003/20/

Brehm, G. (2003) Host-plant records and illustrations of the larvae of 19 geometrid moth species from a montane rainforest in Ecuador (Lepidoptera: Geometridae). *Nachrichten des Entomologischen Vereins Apollo*, **24**, 29-34.

Brehm, G. (2005) Contrasting patterns of vertical stratification in two moth families in a Costa Rican lowland rain forest. *Basic and Applied Ecology*, in press.

Brehm, G. & Fiedler, K. (2003) Faunal composition of geometrid moths changes with altitude in an Andean montane rain forest. *Journal of Biogeography*, **30**, 431-440.

Brehm, G. & Fiedler, K. (2005) Diversity and community structure of geometrid moths of disturbed habitat in a montane area in the Ecuadorian Andes. *Journal of Research on the Lepidoptera*, **38**, 1-14.

Brehm, G., Pitkin, L.M., Hilt, N. & Fiedler, K.(2005) Montane Andean rain forests are a global diversity hotspot of geometrid moths. *Journal of Biogeography*, **32**, 1621-1627.

Brehm, G., Süßenbach, D. & Fiedler, K. (2003) Unique elevational diversity patterns of geometrid moths in an Andean montane rainforest. *Ecography*, **26**, 456-466.

Brooks, T.M., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A.B., Rylands, A.B., Konstant, W.R., Flick, P., Pilgrim, J., Oldfield, S., Magin, G. & Hilton-Taylor, C. (2002) Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology*, **16**, 909-923.

Brown, K.S. Jr. (1984) Chemical ecology of dehydropyrrolizidine alkaloids in adult ithomiinae (Lepidoptera: Nymphalidae). *Revista Brasileira de Biologia*, **44**, 435-460.

Chey, V.K., Holloway, J.D. & Speight, M.R. (1997) Diversity of moths in forest plantations and natural forests in Sabah. *Bulletin of Entomological Research*, **87**, 371-385.

Chown, S.L. & Klok, C.J, (2003) Altitudinal body size clines: latitudinal effects associated with changing seasonality. *Ecography*, **26**, 445-455.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science*, **199**, 1302-1310.

Cott, H.B. (1957) *Adaptive Coloration in Animals*. Methuen LTD, London.

deJong, R. & Congdon, T.C.E. (1993) The montane butterflies of the eastern Afrotropics. In: *Biogeography and ecology of the rain forests of Eastern Africa* (eds. J.C. Lovett and S.K. Wasser), pp. 133-172. Cambridge University Press, Cambridge.

Daily, G.C. (1996) Nocturnality and species survival. *Proceedings of the National Academy of Sciences of the United States of America*, **93**, 11709-11712.

Daily, G.C. & Ehrlich, P.R. (1995) Preservation of biodiversity in small rainforest patches: rapid evaluations using butterfly trapping. *Biodiversity and Conservation*, **4**, 35-55.

DeVries, P.J., Murray, D. & Lande, R. (1997) Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. *Biological Journal of the Linnean Society*, **62**, 343-364.

DeVries, P.J., Lande, R. & Murray, D. (1999) Associations of co-mimetic ithomiine butterflies on small spatial and temporal scales in a neotropical rainforest. *Biological Journal of the Linnean Society*, **67**, 73-85.

DeVries, P.J. & Walla, T.R. (2001) Species diversity and community structure in neotropical fruit-feeding butterflies. *Biological Journal of the Linnean Society*, **74**, 1-15.

Didham, R.K. (1997) An overview of invertebrate responses to forest fragmentation. In: *Forests and Insects* (eds. A.D. Watt, N.E. Stork and M.D. Hunter), pp. 303-320. Chapman & Hall, London.

Dyer, L.E, Gentry, G.L., Greeney, H., Walla, T. (2005) *Caterpillars and parasitoids of an Ecuadorian cloud forest.* URL: http://www.caterpillars.org. accessed March 2005.

Ehrlich, P.R. (1984) The structure and dynamics of butterfly populations. In: *The biology of butterflies* (eds. R.I. Vane-Wright and P.R. Ackery), pp. 25-58. Symposium of the Royal Entomological Society of London, Number 11, Academic Press.

Erwin, T.L. & Scott, J.C. (1980) Seasonal and size patterns, trophic structure and richness of Coleoptera in the tropical arboreal ecosystem: the fauna of the tree *Luehea seemannii* Triaha and Planch in the Canal Zone of Panama. *Coleopterists' Bulletin*, **34**, 305-322.

Fiedler, K. & Schulze, C.H. (2004) Forest modification affects diversity (but not dynamics) of speciose tropical pyraloid moth communities. *Biotropica*, **36**, 615-627.

Gaston, K.J. & Lawton, J.H. (1988) Patterns in body size, population dynamics, and regional distribution of bracken herbivores. *The American Naturalist*, **132**, 662-680.

Hamer. K.C. & Hill, J.K. (2000) Scale-dependent effects of habitat disturbance on species richness in tropical forests. *Conservation Biology*, **14**, 1435-1440.

Hamer, K.C., Hill. J.K., Benedick, S., Mustaffa, N., Sherratt, T.N., Maryati, M. & Chey, V.K. (2003) Ecology of butterflies in natural and selectively logged forests of northern Borneo: the importance of habitat heterogeneity. *Journal of Applied Ecology*, **40**, 150-162.

Hamer, K.C., Hill, J.K., Lace, L.A. & Langan, A.M. (1997) Ecological and biogeographical effects of forest disturbance on tropical butterflies of Sumba, Indonesia. *Journal of Biogeography*, **24**, 67-75.

Hebert, P.D.N. (1983) Egg dispersal patterns and adult feeding behaviour in the Lepidoptera. *Canadian Entomologist*, **115**, 1477-1481.

Hemmingsen, A.M. (1934) A statistical analysis of the differences in body size of related species. *Videnskabelige Meddelelser Dansk Naturhistorisk Forening Kobenhavn*, **98**, 125-160.

Hill, J.K. & Hamer, K.C. (2004) Determining impacts of habitat modification on diversity of tropical forest fauna: the importance of spatial scale. *Journal of Applied Ecology*, **41**, 744-754.

Hill, J.K., Hamer, K.C., Lace, L.A. & Banham, W.M.T. (1995) Effects of selective logging on tropical forest butterflies on Buru, Indonesia. *Journal of Applied Ecology*, **32**, 754-760.

Holloway, J.D. (1984) The larger moths of Gunung Mulu National Park; a preliminary assessment of their distribution, ecology and potential as environmental indicators. *Sarawak Museum Journal*, **30**, 149-190.

Holloway, J.D., Kirk-Spriggs, A.H. & Chey, V.K. (1992) The response of some rain forest insect groups to logging and conversion to plantation. *Philosophical Transactions of the Royal Society* B, **335**, 425-436.

Hunter, A.F. (1991) Traits that distinguish outbreaking and nonoutbreaking Macrolepidoptera feeding on northern hardwood trees. *Oikos*, **60**, 275-282.

Intachat, J. & Holloway, J.D. (2000) Is there stratification in diversity or preferred flight height of geometroid moths in Malaysian lowland tropical forest? *Biodiversity and Conservation*, **9**, 1417-1439.

Intachat, J., Holloway, J.D. & Speight, M.R. (1997) The effect of different forest management practices on geometroid moth populations and their diversity in Peninsular Malaysia. *Journal of Tropical Forest Science*, **9**, 411-430.

Intachat, J., Holloway, J.D. & Speight, M.R. (1999) The impact of logging on geometroid moth populations and their diversity in lowland forests of Peninsular Malaysia. *Journal of Tropical Forest Science*, **11**, 61-78.

Janzen, D.H. (1987) How moths pass the dry season in a Costa Rican dry forest. *Insect Science and its Application*, **8**, 489-500.

Janzen, D. H. and Hallwachs, W. (2005) *Dynamic database for an inventory of the macrocaterpillar fauna, and its food plants and parasitoids, of the Area de Conservacion Guanacaste (ACG), northwestern Costa Rica*. URL: http://janzen.sas.upenn.edu.

Janzen, D.H. & Schoener, T.W. (1968) Differences in insect abundance and diversity between wetter and drier sites during a tropical dry season. *Ecology*, **49**, 96-110.

Kessler, M., Herzog, S.K., Fjeldså, J. & Bach, K. (2001) Species richness and endemism of plant and bird communities along two gradients of elevation, humidity and land use in the Bolivian Andes. *Diversity and Distributions*, **7**, 61-77.

Kitching, I.J. & Rawlins, J.E. (1999) The Noctuoidea. In: *Handbook of Zoology. Lepidoptera, Moths and Butterflies*, vol. 1 (ed. N.P. Kristensen), pp. 355-401. Berlin, New York, Walter de Gruyter.

Kitching, R.L., Orr, A.G., Thalib, L., Mitchell, H., Hopkins, M.S. & Graham, A.W. (2000) Moth assemblages as indicators of environmental quality in remnants of upland Australian rain forest. *Journal of Applied Ecology*, **37**, 284-297.

Komonen, A., Grapputo, A., Kaitala, V., Kotiaho, J.S. & Päivinen, J. (2004) The role of niche breadth, resource availability and range position on the life history of butterflies. *Oikos*, **105**, 41-54.

Kotze, D.J. & Samways, M.J. (2001) No general edge effects for invertebrates at Afromontane forest/grassland ecotones. *Biodiversity and Conservation*, **10**, 443-466.

Laurance, W.F. (1998) A crisis in the making: responses of Amazonian forests to land use and climate change. *Trends in Ecology and Evolution*, **13**, 411-415.

Lawton, J.H. (1991) Species richness, population abundances, and body size in insect communities: tropical versus temperate comparisons. In: *Plant-animal Interactions: Evolutionary ecology in tropical and temperate regions* (eds. P.W. Price, T.M. Lewinsohn, G.W. Fernandes and W.W. Benson), pp. 71-89. Wiley, New York.

Lawton, J.H., Bignell, D.E., Bolton, B., Bloemers, G.F., Eggleton, P., Hammond, P.M., Hodda, M., Holt, R.D., Larsen, T.B., Mawdsley, N.A., Stork, N.E., Srivastava, D.S. and Watt, A.D. (1998) Biodiversity inventories, indicator taxa and the effects of habitat modification in tropical forest. *Nature*, **391**, 72-76.

Merilaita, S. & Kaitala, V. (2002) Community structure and the evolution of aposematic coloration. *Ecology Letters*, **5**, 495-501.

Morse, D.R., Stork, N.E. & Lawton, J.H. (1988) Species number, species abundance and body length relationships of arboreal beetles in Bornean lowland rain forest trees. *Ecological Entomology*, **13**, 25-37.

Murcia, C. (1995) Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution*, **10**, 58-62.

Novotny, V. & Basset, Y. (2000) Rare species in communities of tropical insect herbivores: pondering the mystery of singletons. *Oikos*, **89**, 564-572.

Noyes, J.S. (1989) The diversity of Hymenoptera in the tropics with special reference to Parasitica in Sulawesi. *Ecological Entomology*, **14**, 197-207.

Nummelin, M. & Kaitala, S. (2004) Do species dominance indices indicate rain forest disturbance by logging? *Biotropica*, **36**, 628-632.

Poulton, E.B. (1890) *The colours of Animals: Their meaning and use especially considered in the case of insects*. Keegan Paul, Trench, Trübner and Co.

Rahbek, C. (2005) The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters*, **8**, 224-239.

Ricketts, T.H., Daily, G.C., Ehrlich, P.R. & Fay, J.P. (2001) Countryside biogeography of moths in a fragmented landscape: biodiversity in native and agricultural habitats. *Conservation Biology*, **15**, 378-388.

Schoener, T.W. & Janzen, D.H. (1968) Notes on environmental determinants of tropical versus temperate insect size pattern. *American Naturalist*, **102**, 207-224.

Schulze, C.H. (2000) *Auswirkungen anthropogener Störungen auf die Diversität von Herbivoren – Analysen von Nachtfalterzönosen entlang von Habitatgradienten in Ost-Malaysia*. Ph.D. thesis, University of Bayreuth.

Schulze, C.H. & Fiedler, K. (2003) Vertical and temporal diversity of a species-rich moth taxon in Borneo. In: *Arthropods of tropical forests: spatio-temporal dynamics and resource use in the canopy* (eds. Y. Basset, V. Novotny, S. Miller and R.L. Kitching), pp. 69-85. Cambridge University Press.

Schulze, C.H., Linsenmair, K.E. & Fiedler, K. (2001) Understorey versus canopy: patterns of vertical stratification and diversity among Lepidoptera in a Bornean rain forest. *Plant Ecology*, **153**, 133-152.

Schulze, C.H., Waltert, M., Kessler, P.J.A., Pitopang, R., Shahabuddin, I., Veddeler, D., Mühlenberg, M., Gradstein, S.R., Leuschner, C., Steffan-Dewenter, I. & Tscharntke, T. (2004) Biodiversity indicator groups of tropical land-use systems: comparing plants, birds, and insects. *Ecological Applications*, **14**, 1321-1333.

Shmida, A. & Wilson, W. (1985) Biological determinants of species diversity. *Journal of Biogeography*, **12**, 1-20.

Smythe, N. (1982) The seasonal abundance of night-flying insects in a neotropical forest. In: *The ecology of a tropical forest* (eds. E.G. Leigh. Jr, A.S. Rand and D.M. Windsor), pp. 309-318. Washington, DC: Smithsonian Institution Press.

Solis, M.A. & Pogue, M.G. (1999) Lepidopteran biodiversity: Patterns and estimators. *American Entomologist*, **45**, 206-212.

Southwood, T.R.E., Moran, V.C. & Kennedy, C.E.J. (1982) The richness, abundance and biomass of the arthropod communities on trees. *Journal of Animal Ecology*, **51**, 635-649.

Spitzer, K., Jaroš, J., Havelka, J. & Lepš, J. (1997) Effect of small-scale disturbance on butterfly communities of an Indochinese montane rainforest. *Biological Conservation*, **80**, 9-15.

Süßenbach, D. (2003) *Diversität von Nachtfaltergemeinschaften entlang eines Höhengradienten in Südecuador (Lepidoptera: Pyraloidea, Arctiidae)*. Ph.D. thesis, University of Bayreuth. URL: http://opus.ub.uni-bayreuth.de/volltexte/2003/33/

Summerville, K.S. (2004) Functional groups and species replacement: testing for the effects of habitat loss on moth communities. *Journal of the Lepidopterists' Society*, **58**, 114-117.

Summerville, K.S. & Crist, T.O. (2003) Determinants of lepidopteran community composition and species diversity in eastern deciduous forests: roles of season, eco-region and patch size. *Oikos*, **100**, 134-148.

Summerville, K.S. & Crist, T.O. (2004) Contrasting effects of habitat quantity and quality on moth communities in fragmented landscapes. *Ecography*, **27**, 3-12.

Summerville, K.S., Ritter, L.M. & Crist, T.O. (2004) Forest taxa as indicators of lepidopteran richness and habitat disturbance: a preliminary assessment. *Biological Conservation*, **116**, 9-18.

Tammaru, T. & Haukioja, E. (1996) Capital breeders and income breeders among Lepidoptera – consequences to population dynamics. *Oikos*, **77**, 561-564.

Thomas, A.W. (2002) *Moth diversity in a northeastern North American, red spruce forest, II. The effect of silvicultural practices on geometrid diversity (Lepidoptera: Geometridae)*. Canadian Forest Service, Atlantic Forestry Service, Fredericton.

Weller, S.J., Jacobson, N.L. & Conner, W.E. (1999) The evolution of chemical defences and mating systems in tiger moths (Lepidoptera: Arctiidae). *Biological Journal of the Linnean Society*, **68**, 557-578.

Willott, S.J. (1999) The effects of selective logging on the distribution of moths in a Bornean rainforest. *Philosophical Transactions of the Royal Society of London* B, **354**, 1783-1790.

Wolda, H. (1978) Fluctuations in abundance of tropical insects. *American Naturalist*, **112**, 1017-1045.

Wolda, H. & Wong, M. (1988) Tropical insect diversity and seasonality. Sweep samples versus light-traps. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, series C*, **91**, 203-216.

8 Summary

The diversity of two very species-rich families of arctiid and geometrid moths was investigated in a montane area in the Andes in southern Ecuador (Reserva Biológica San Francisco, 3°58´ S, 79°5´ W) along a succession gradient ranging from a barely vegetated landslide area to mature forest understorey between 1,800 and 2,005 m above sea level. This study was part of a larger interdisciplinary project on diversity and functioning of a tropical mountain rainforest ecosystem.

Moths were collected during three field periods in the years 2002 (March to April, October to November) and 2003 (August to October) at the 15 succession sites. Moths were manually sampled by attraction to weak light sources (2 x 15 W tubes: black light and super-actinic light) in a white gauze cylinder from 18:45 to 21:45 h. Data from this study (15 succession sites) were compared with data from six natural forest understorey sites sampled in the years 1999 and 2000 in the same region.

A total of 9,211 arctiid moths representing 287 species, of which 135 belong to the tribe Phaegopterini, followed by Ctenuchini/Euchromiini (82), Lithosiinae (54), Pericopini (9), and Arctiini (7), as well as 23,720 geometrid moths representing 868 species were recorded at 21 sites. Large proportions of the samples (Arctiidae: 70.4% of species, 76.1% of individuals; Geometridae: 65% of species, 78.1% of individuals) were identified to species level.

The study deals with patterns of alpha- and beta-diversity, ensemble structure, wing colouration and various other morphological traits of arctiid moths along the succession gradient. In addition, temporal dynamics of moth ensembles as well as the role of environmental factors such as temperature or habitat openness as predictors of faunal change at small spatial scales were investigated.

General patterns in moth samples

Local ensembles representing these two ecologically very different moth families (Arctiidae, Geometridae) were both characterized by a few very common species, whereas the vast majority of species was rare. The proportion of unique singletons accounted for 21.3% in the Arctiidae and 18.6% in the Geometridae. Both families also showed a strikingly uniform picture with regard to the proportion of individuals belonging to the most dominant species. The mean proportion of the commonest species averaged over all 21 sites was 14.7% of total catch in the Arctiidae, and 13.1% in the Geometridae.

Almost half of the observed species were shared between the succession sites and the mature forest understorey (141 arctiid species (49%) and 410 geometrid species (47%)). 109 arctiid (38%) and 366 geometrid (42%) species were restricted to the succession sites, while 37 arctiid (13%) and 92 geometrid (11%) species were only found in natural forest understorey.

Faunal composition of Arctiidae

Proportions of higher arctiid taxa changed distinctly along the succession gradient. Ctenuchini (wasp moths) contributed more strongly to ensembles in mature natural forest, whereas Lithosiinae (lichen moths) numerically decreased with forest recovery. Phaegopterini were approximately equally distributed across the succession gradient. These observations can be linked to life-history characters of the moth groups. Many Ctenuchini larvae are suspected to be host-plant specialists, and adult moths are often pharmacophagous on PA plants. On the contrary, Lithosiinae larvae are suspected to feed, at least in part, on lichens, which grow abundantly in early succession stages of tropical montane habitats. Species of the large tribe Phaegopterini are more frequently polyphagous as larva, and the adult moths of many species are robust good flyers with considerable dispersal potential.

Alpha-diversity of Arctiidae and Geometridae

The alpha-diversity (intra-habitat or local diversity) of arctiid and geometrid moths as a whole, as well as of the tribes Phaegopterini, Ctenuchini and Lithosiinae, was measured using Fisher’s alpha and rarefied species numbers. Patterns of local diversity differed between these two families. Local diversity was high and ranged between 21.7 and 53.6 (Fisher’s alpha) for arctiid moths, and 77.0-170.6 (Fisher’s alpha) for Geometridae. Arctiidae showed a decrease with forest recovery and a pronounced maximum of diversity in later succession stages, whereas geometrid diversity increased with forest recovery and was more similar between late succession sites and forest understorey. The three larger subordinated arctiid taxa contributed differentially to this remarkable richness: Phaegopterini were always the most diverse clade, followed by Ctenuchini and Lithosiinae. The observed patterns well fit to the perception that tropical geometrids are more bound to woody vegetation, whereas a number of arctiids are more common in succession habitats.

Beta-diversity of moths along the succession gradient

Similarities of ensembles of all arctiid and geometrid moths and of the subordinated taxa Phaegopterini, Ctenuchini and Lithosiinae were assessed using the CNESS (chord-normalized expected species shared) index with different values of the sample size parameter *m*. Moth samples were ordinated with non-metric two-dimensional scaling (NMDS), and faunal groupings according to habitat classes explored using Analysis of Similarities (ANOSIM).

The two moth taxa showed strikingly similar patterns of beta-diversity, although they differed in their alpha-diversity patterns. Ordinations of the moth samples revealed a clear separation, for arctiid as well as geometrid ensembles, from succession sites vs. the natural forest understorey. Abandoned pastures held an impoverished, distinct fauna. Faunal segregation was more pronounced when emphasizing the contribution of rare species. Within the Arctiidae, these patterns of faunal turnover persisted also on lower systematic levels (tribes Phaegopterini, Lithosiinae). Ordination axes primarily reflected the degree of habitat disturbance (e.g. openness of vegetation, degree of succession and distance of the sites to mature forest) and to a lesser extent altitude. However, faunal differences were not at all related to geographical distances between the sampling sites. This striking parallelism of species turnover across moth taxa was also confirmed using matrix rank correlations.

Body size, proboscis length and external appearance of Arctiidae

Different body size characters such as forewing length, body length, wing surface area, or wing load were analysed. There was strong taxon specific variation in all these traits, whereas analyses on the species level revealed no clear differences in morphological traits along the succession gradient. If moth individuals were considered as unit of analysis, there was a decrease in forewing and body length as well as wing surface area with increasing forest recovery. Pooled species and individual numbers largely revealed unimodal distribution patterns, similar to a log-normal distribution, of their size parameters. Only the body length of the moths showed a bimodal distribution. Larger Phaegopterini were more common at the disturbed succession sites, whereas larger Ctenuchini and Lithosiinae were mainly found in mature forest understorey. Body size distribution of Ctenuchini was broader in the later succession stages vs. the earlier ones and the forest sites.

Species with reduced proboscis were overall rare (8.4% of total species, 5.3% of total individuals), but were twice as common at succession sites compared to the mature forest understorey. There were also some differences of the proboscis development between taxa.

Arctiid species were equally divided into cryptic vs. aposematic species. Generally, the relative occurrence of aposematism in arctiid moths did not change with forest recovery; but such patterns emerged at lower systematic levels. Aposematic species among Phaegopterini and Lithosiinae were more common at succession sites, whilst Ctenuchini showed the reverse picture, namely an increase of aposematism with forest recovery.

Temporal dynamics of moth ensembles

Despite conspicuous variations of moth abundance, local arctiid moth diversity was relatively constant over time, whereas geometrid moths showed more pronounced fluctuations in individual numbers, species numbers as well as local diversity over the three sampling periods. Overall, only a few of the common arctiid and accordingly geometrid species showed strong temporal changes in abundance, and more than 50% of the species (which collectively represented >90% of all sampled individuals) were found in all three sampling periods. Multivariate analyses of moth samples showed a segregation of the arctiid and geometrid ensembles according to the sampling period (wet season vs. drier *veranillo*) as well as between the different habitat categories relative to succession. The dissimilarity of samples increased with increasing time period between the sampling periods. In Geometridae temporal dynamics of faunas was far stronger than in Arctiidae and partly exceeded the differentiation according to habitat. In the Arctiidae, this was not the case. This might indicate that arctiids depend less on seasonally variable resource availability than geometrids do.

Local diversity of both moth families were high, even in disturbed sites. Thus, moths showed a good dispersal potential for recolonisation of anthropogenic disturbed sites in proximity to the mature forest and at the small spatial scale of the present study. However, with increasing distance to the natural forest moth diversity decreased. Despite the differences in the local diversity between the families, there was an unexpected similarity in their pattern of beta-diversity. Therefore, beta-diversity emerged as a better indicator for the impact of forest disturbance than alpha-diversity, the latter being largely taxon-specific. The divergence of diversity patterns across the moth taxa studied here also shows that none of them can be reasonably used *prima facie* as ‘biodiversity indicator group’ for another, or even for other organisms. However, due to their sensitivity on the community level all moth taxa tested here emerged as good indicators for environmental changes such as forest disturbance, even at very small spatial scales. In this respect, sensitivity of Geometridae was higher than in Arctiidae.

9 Zusammenfassung

Entlang eines Sukzessions- bzw. Störungsgradienten wurde die Diversität der zwei sehr artenreichen Nachtfalterfamilien Arctiidae (Bärenspinner) und Geometridae (Spanner) in einem montanen Gebiet in den Anden Südecuadors (Reserva Biológica San Francisco, 3°58´ S, 79°5´ W) untersucht. Der Gradient begann bei frühen Sukzessionsstadien (Bergrutsch, Weidebrachen, Farnflächen) und erstreckte sich über Gebüsch- und ca. 40jährige Sekundärwaldflächen bis hin zum Naturwald innerhalb eines engen Höhenbandes von 1800 bis 2005 m ü. NN. Die vorliegende Studie war in die Arbeit einer interdisziplinären Forschergruppe integriert, die die Diversität sowie funktionale Zusammenhänge in einem tropischen Bergregenwald-Ökosystem untersucht.

Die Tiere wurden auf 15 Sukzessionsflächen während dreier Feldaufenthalte in den Jahren 2002 (März bis April, Oktober bis November) und 2003 (August bis Oktober) gesammelt. Die Nachtfalter wurden mittels Lichtfang erfasst und manuell abgesammelt. Der Lichtfang wurde mit einem Leuchtturm, ausgestattet mit je einer 15 W Schwarz- bzw. Mischlichtlampe, jeweils für 3 Stunden pro Nacht von 18:45 bis 21:45 Uhr betrieben. Diese schwachen Lichtquellen erlauben eine Beurteilung der Fauna mit hoher räumlicher Auflösung. Die eigenen Daten von den 15 Sukzessionsflächen wurden mit Fangergebnissen von sechs benachbarten Naturwaldstandorten in derselben Höhenlage, die im Rahmen vorangegangener Arbeiten erhoben worden waren, verglichen.

Insgesamt wurden 9211 Individuen der Arctiidae, verteilt auf 287 Arten, nachgewiesen. Davon gehörten 135 Arten der Tribus Phaegopterini, 82 den Ctenuchini, 54 den Lithosiinae, 9 den Pericopini und 7 den Arctiini an. Zudem wurden 23720 Individuen der Geometridae mit insgesamt 868 Arten auf den 21 Flächen gefunden. Ein für ein tropisch-montanes Gebiet mit extremer Artenvielfalt erstaunlich großer Anteil der Fänge konnte artgenau bestimmt werden (Arctiidae: 70,4 % der Arten, 76,1 % der Individuen; Geometridae: 65 % der Arten, 78,1 % der Individuen).

Auf der Grundlage diese Datenmaterials werden in der vorliegenden Dissertation die Alpha- und Beta-Diversität der Nachtfalter, Gemeinschaftsstrukturen, das äußere Erscheinungsbild und unterschiedliche Körpergrößenmerkmale (z. B. Flügellänge, Körperlänge, Flügelbeladung) sowie die zeitliche Dynamik der Artengemeinschaften beleuchtet. Ebenso wurde der Einfluss verschiedener Umweltfaktoren wie z. B. Temperatur, Kronenschluss der Vegetation und Höhenlage auf die Artenvielfalt und den Artenwechsel der Nachtfalter untersucht.

Die Lebensgemeinschaften der beiden ökologisch sehr unterschiedlichen Nachtfalterfamilien zeichnen sich beide durch wenige sehr häufige und viele sehr individuenarme Arten aus. Der Anteil der unikalen Einzeltiere (Singletons) betrug bei den Arctiidae 21,3 % und 18,6 % bei den Geometridae. Ebenso zeigten die beiden Taxa im Individuenanteil der dominantesten Arten ein einheitliches Bild. Dieser betrug, gemessen als Mittelwert über alle 21 Standorte, 14,7 % bei den Arctiidae und 13,1 % bei den Geometridae.

Fast die Hälfte aller beobachteten Arten kamen sowohl auf den gestören Flächen als auch im Naturwald vor (141 Arctiidae-Arten (49 %) und 410 Geometridae-Arten (47 %)). Hingegen war das Vorkommen von 109 Arctiidae-Arten (38 %) und 366 Geometridae-Arten (42 %) auf die Sukzessionsflächen beschränkt war, und 37 Bärenspinner (13 %) und 92 Spanner (11 %) wurden nur im Naturwald gefunden.

Faunenstruktur auf hohem systematischen Niveau

Die Arten- und Individuenanteile untergeordneter Taxa innerhalb der Arctiidae veränderten sich merklich entlang des Störungsgradienten. Ctenuchini nahmen anteilig mit zunehmender Bewaldung zu, wohingegen die Lithosiinae (Flechtenbären) zahlenmäßig abnahmen. Phaegopterini waren in etwa gleichmäßig entlang des Gradienten verteilt. Diese Unterschiede könnten mit der unterschiedlichen Lebensweisen der Arten in diesen Taxa in Zusammenhang stehen. Viele Larven des Tribus Ctenuchini sind

Futterpflanzenspezialisten, und auch die adulten Tiere leben oft pharmakophag an pyrrolizidinalkaloidhaltigen (PA) Pflanzen. Während Larven der Lithosiinae im Verdacht stehen an Flechten zu fressen, welche auf den frühen Sukzessionsstandorten besonders häufig vorkommen, sind die Larven der größten Tribus Phaegopterini eher polyphag mit einem breiten Futterpflanzenspektrum, und die meisten adulten Tiere haben einen robusten Körperbau und sind gute Flieger.

Alpha-Diversität der Gemeinschaften

Die Alpha-Diversität (Habitat-Diversität oder lokale Artenvielfalt) von Arctiidae und Geometridae, sowie innerhalb der Bärenspinner der Taxa Phaegopterini, Ctenuchini und Lithosiinae, wurde gemessen mittels Fishers Alpha und der „rarifizierten" Artenzahl. Die Muster der lokalen Artenvielfalt unterschied sich zwischen den beiden Familien, jedoch war die Diversität in beiden Familien hoch. Die Werte lagen bei den Arctiidae zwischen 21,7 und 53,6 (Fishers Alpha), bei den Geometridae zwischen 77,0 und 170,6. Die Familie Arctiidae zeigte einen Diversitätsabfall mit zunehmender Bewaldung, mit einem Maximum in den späten Sukzessionsstadien, wohingegen die Diversität der Geometridae in Richtung späte Sukzessionsflächen und Naturwald zunahm und dort die höchste Artenvielfalt aufwies. Die drei größeren untergeordneten Taxa der Arctiidae trugen unterschiedlich viel zu diesem Artenreichtum bei: Phaegopterini waren stets am artenreichsten, gefolgt von den Ctenuchini und den Lithosiinae.

Die Muster stimmen sehr gut mit der Erkenntnis überein, dass tropische Geometridae als Larven eher an Gehölzpflanzen gebunden sind und somit vor allem in Waldhabitaten artenreicher auftreten, wohingegen Arctiidae häufiger in Sukzessionsflächen und anthropogen gestörtem Gelände vorkommen.

Beta-Diversität (Artenwechsel) der Gemeinschaften

Die Ähnlichkeit zwischen den Gemeinschaften der Arctiidae, Geometridae und der untergeordneten Taxa (Phaegopterini, Ctenuchini und Lithosiinae) entlang des Sukzessionsgradienten wurde mit Hilfe des CNESS-Index für unterschiedliche Werte des Stichprobengrößen-Parameters *m* berechnet. Dadurch kann der Einfluss häufiger bzw. seltenere Arten auf Muster der Faunendifferenzierung exploriert werden. Ordinationen der Stichproben wurden mit dem Verfahren der nicht-metrischen multidimensionalen Skalierung (NMDS) durchgeführt. Die Unterschiede der Artengemeinschaften in den verschiedenen Habitattypen wurden mittels einer Randomisierungsstatistik (ANOSIM) untersucht.

Beide Nachtfalterfamilien zeigten ähnliche Muster in der Änderung der Artenzusammensetzung im Sukzessionsverlauf, obwohl sie sich in den Mustern der lokalen Diversität klar unterschieden. In Ordinationsdiagrammen trennten sich die Nachtfaltergemeinschaften der Naturwaldstandorte klar von denen der Sukzessionsstandorte ab. Die aufgelassenen Weiden wiesen dabei eine deutlich verarmte Nachtfaltergemeinschaft auf. Die Trennung der Standorte wurde desto deutlicher, je stärker die seltenen Arten betont wurden. Die erste Dimensionsachse der Ordinationen spiegelte den Kronenschluß der Vegetation, den Sukzessionsgrad sowie die Distanz der Standorte zum Naturwald wider. Die zweite Ordinationsachse (die einen kleineren Anteil der Varianz abbildet) war – deutlich schwächer – mit der Höhenlage der Standorte korreliert. Jedoch hatte die räumliche Nähe der Standorte zueinander keinen Einfluß auf die Ähnlichkeit der Gemeinschaften. Diese weitgehende Parallelität des Artenwechsels für beide Nachtfalterfamilien konnte auch durchweg in Matrix-Rang-Korrelationstests bestätigt werden. Generell reagierten dabei Geometriden-Gemeinschaften sensitiver auf die Umweltveränderungen im Sukzessionsgradienten als Arctiiden-Gemeinschaften.

Körpergröße, Rüssellänge und Erscheinungsbild

Unterschiedliche Körpermaße wie Vorderflügellänge, Körperlänge, Flügeloberfläche, Flügelflächenbelastung wurden in der Familie Arctiidae untersucht. Es gab ausgeprägte taxonspezifische Schwankungen, jedoch zeigten Analysen auf Artniveau keine Unterschiede in Bezug auf die Verteilung der Mittelwerte dieser Körpermaße entlang des Sukzessionsgradienten. Auf der Ebene der Falterindividuen war hingegen eine Abnahme der Vorderflügel- und

Körperlänge sowie der Flügeloberfläche entlang des Störungsgradienten zu beobachten. Die Verteilung der Größenklassen aller Arten und Individuen war unimodal, ähnlich einer Lognormal-Verteilung. Lediglich die Verteilung der Körpergröße basierend auf den Individuen war bimodal. Größere Phaegopterini waren relativ häufiger in den Sukzessionsflächen anzutreffen, wohingegen größere Ctenuchini und Lithosiinae hauptsächlich im Naturwald gefunden wurden. Ctenuchini zeigten eine breitere Größenklassenverteilung in den späten Sukzessionsstadien im Vergleich zu den frühen Sukzessionsstadien und dem Naturwald.

Arten mit teilweise oder sogar vollständig reduziertem Saugrüssel waren insgesamt selten (8,4 % der Arten, 5,3 % der Individuen), traten aber in den Sukzessionsflächen doppelt so häufig wie im Naturwald auf. Es wurden auch taxonspezifische Unterschiede in der Rüsselentwicklung gefunden. Vor allem in der Tribus Arctiini erwies sich der Verzicht auf Ressourcenzugang bei den Imagines als verbreitete Lebenszyklusstrategie.

Die gefundenen Arctiidae-Arten konnten zu etwa gleichen Teilen in die beiden verschiedenen Erscheinungsbildkategorien, kryptisch oder aposematisch, eingeordnet werden. Insgesamt gab es keine Änderung des relativen Anteils aposematisch gefärbter Tiere entlang des Störungsgradienten, jedoch ergaben sich Änderungen auf niedrigerem taxonomischen Niveau. Aposematisch gefärbte Arten der Phaegopterini und Lithosiinae waren auf den Sukzessionsflächen relativ häufiger, wohingegen aposematisch gefärbte Vertreter der Ctenuchini eher im Naturwald anzutreffen waren.

Zeitliche Dynamik der Gemeinschaften

Trotz deutlicher Abundanzschwankungen war die lokale Artenvielfalt der Arctiidae ziemlich konstant über die drei Sammelzeiträume, wohingegen die Individuenzahlen, beobachteten Artenzahlen sowie die lokale Diversität der Geometridae zeitlich stärker schwankten. Jedoch gab es in beiden Familien unter den individuenreichen Arten nur sehr wenige Vertreter, die eine ausgeprägte zeitliche Dynamik aufzeigten. Mehr als 50 % der Arten, die zusammen > 90 % der ausgewerteten Individuen umfassten, wurden bei den Arctiidae und den Geometridae in allen drei Fangperioden und damit sowohl in trockeneren als auch sehr niederschlagsreichen Jahreszeiten gefunden.

Multivariate Analysen der Artenzusammensetzung der Standorte ergaben in beiden Familien eine Auftrennung nach der Sammelperiode (regenreichere Zeit vs. trockenere Zeit) sowie der Habitatkategorie (frühe oder späte Sukzessionsstadien). Der Unterschied der Nachtfaltergemeinschaften der drei Sammelperioden war umso größer, je länger die zeitliche Distanz zwischen den einzelnen Sammelperioden wurde. Bei den Geometridae war die zeitliche Dynamik insgesamt stärker ausgeprägt als bei den Arctiidae und übertraf in ihrer Stärke auch die Differenzierung der Gemeinschaften der verschiedenen Habitate. Dies kann als Hinweis darauf gelten, dass Geometridae mehrheitlich (zumal als Larven) stärker auf ephemere Ressourcen (Blüten, Jungtriebe der Fraßpflanzen) angewiesen sind als Arctiidae.

Die lokale Artenvielfalt war in beiden Nachtfalter-Familien außergewöhnlich hoch, auch noch an stärker anthropogen gestörten Standorten. Demnach zeigten die Nachtfalter auf dieser kleinen räumlichen Skala ein gutes Ausbreitungspotential zur Wiederbesiedlung gestörter Standorte, die sich in unmittelbarer Nähe zum Naturwald befanden. Jedoch nahm die Diversität mit zunehmendem Abstand der Standorte zum Naturwald deutlich ab. Trotz der Unterschiede in Bezug auf die lokale Artenvielfalt zwischen den beiden Familien gab es eine unerwartet große Ähnlichkeit in ihren Beta-Diversitätsmustern. Daher erwies sich in dieser Studie die Beta-Diversität als besserer Indikator für die Auswirkung der Waldzerstörung, während die Alpha-Diversität im Sukzessionsverlauf sehr taxon-spezifische Muster aufwies. Diese taxon-spezifischen Muster erlaubten nicht, im Sinne einer „Biodiversitätsindikation“ von einer Nachtfaltergruppe auf eine andere – oder gar auf andere Organismen – zu extrapolieren. Jedoch erwiesen sich Nachtfalter, und hier insbesondere die Geometridae, selbst auf sehr kleinen räumlichen Skalen als außerordentlich sensitive Indikatoren für Umweltänderungen, wie sie mit der Störung bzw. Regeneration der andinen Naturwälder einhergehen.

10 Resumen

La diversidad de dos familias de polillas muy rica en especies arctiid y geometrid fue investigada en un área de la cordillera Andina del sur de Ecuador (Reserva Biológica San Francisco, 3°58´ S, 79°5´ W), a lo largo de un gradiente de sucesión que se extiende desde derrumbamiento con poca vegetación hasta bosque maduros entre los 1800 y 2005 m sobre nivel del mar. Este estudio es parte de un proyecto interdisciplinario sobre diversidad y de funcionamiento de un ecosistema de bosques lluviosos montañosos.

Los especímenes fueron recogidos durante tres etapas en 2002 (marzo a abril, octubre a noviembre) y en el 2003 (agosto a octubre) en 15 sitios en sucesión. Las polillas fueron colectada por atracción a fuente de luz débil (2 x 15 W: luz negra y luz mezclada) en un cilindro de gasa blanca a partir de la 18:45 hasta las 21:45 hora. Los datos de este estudio de 15 sitios con diferentes estadios de sucesión, fueron comparados con los datos de investigaciones realizadas anteriormente en seis sitios de bosques maduros ubicados a la misma altura.

Fueron colectada un total de 9.211 polillas de arctiid representada por 287 especies, de las cuales 135 pertenecen a Phaegopterini, seguido por Ctenuchini (82), Lithosiinae (54), Pericopini (9), y Arctiini (7), así como 23.720 polillas geometrid que representaban 868 especies, fue muestreado manualmente con trapas de luz en 21 sitios.

Este estudio trata la diversidad alfa y beta, fueron investigados la estructura de la comunidad, aspecto externo y diversos parámetros del cuerpo de las polillas arctiid y la dinámica temporal, así como el papel de diversos factores ambientales tales como temperatura, el hábitat, etc.

Las dos familias de polilla (Arctiidae, Geometridae) con diferencias ecológicas bien marcada fue caracterizado por algunas especies muy comunes y muchas especies pobres en individuos. La proporción de singletons únicos fue 21.3% en Arctiidae y 18.6% en Geometridae. Ambas familias también demostraron un cuadro uniforme en lo que respecta a la proporción de individuos que pertenecían a la especie más dominante. La proporción de la especie más común medida como valor medio en los 21 sitios era 14.7% en Arctiidae y 13.1% en Geometridae. La mayoría de las polillas de arctiid (70.4%) y una proporción grande de geometrids (65%) pudrieron ser identificadas la especie.

Casi la mitad de la especie observada fue encontrada en las áreas de sucesión, en bosque maduro (141 especies de arctiid (49%) y 410 especies de geometrid (47%)), mientras que arctiid 109 (38%) y 366 especies de geometrid (42%) fueron restringidos en los sitios de sucesión así como arctiid 37 (13%) y 92 especies de geometrid (11%) al bosque maduro.

Composición de la fauna

Las proporciones más altas de arctiid cambiaron distintamente a lo largo del gradiente de la sucesión. Ctenuchini contribuyó más fuertemente a los conjuntos en bosque natural, mientras que Lithosiinae disminuyó proporcionalmente con la recuperación del bosque. Phaegopterini fue distribuido aproximadamente igualmente a través del gradiente de sucesión. Estas observaciones se pueden ligar a los caracteres de la forma de vida de los grupos de polillas. Muchas larvas de Ctenuchini se han especializado en plantas al igual que las polillas de adultas que también son pharmacophagous en plantas con alto contenido de alcaloides de pyrrolizidine. Por el contrario, las larvas de Lithosiinae se sospechan que se alimentan (por lo menos en parte), de líquenes los cuáles crecen abundantemente en las etapas tempranas de sucesión de los bosques tropicales montañoso. Las especies grande Phaegopterini son con frecuencia polyphagous como larva, y las polillas del adulto de muchas especies son robustos y puede volar.

Diversidad alfa

Diversidad alfa (diversidad local) de las polillas de arctiid y de geometrid en su totalidad, así como las Phaegopterini, Ctenuchini y Lithosiinae fueron medidos usando la alfa Fisher y el números de especie raras. Los patrones locales de la diversidad son levemente diferentes entre estas dos familias, pero la diversidad es alta y en un rango entre 21.7 y 53.6 (Diversidad alfa) para las polillas de arctiid y 77.0-170.6 (Diversidad alfa) para Geometridae. Arctiidae demostró una disminución con la recuperación del bosque y un máximo pronunciado de la diversidad en las etapas posteriores de sucesión, mientras que la diversidad de geometrid aumentó con la recuperación del bosque y es similar entre la sucesión avanzada y los bosque maduros. Las tres especies subordinados más grandes del arctiid contribuyeron diferentemente a riqueza de la especie: Phaegopterini fue siempre la de mayor diversidad, seguido por Ctenuchini y Lithosiinae.

Esto corrobora con opinión de que geometrid tropical está limitado más a la vegetación de árboles maderables, mientras que un número de arctiids son más comunes en hábitat de sucesión.

Diversidad beta

Semejanzas de los conjuntos de todas las polillas arctiid y geometrid y de las especie que se subordinan Phaegopterini, Ctenuchini y Lithosiinae fueron calculados usando índice de CNESS (especie prevista acorde-normalizada compartida) con diversos valores de m. Las ordenaciones fueron realizadas usando la escala bidimensional no métrica (NMDS). La diferencia de la composición de especies en los diferentes tipos de hábitats fue investigada a través de un análisis estadístico de similaridad (ANOSIM).

Las dos especies de polilla demostraron patrones similares de diversidad beta, aunque diferencian en sus patrones de la diversidad alfa. El orden de las muestras de la polilla demostró una separación clara de arctiid (para la familia entera y para todos los especies subordinados más grandes) así como conjuntos de geometrid en los sitios de la sucesión contra los bosque maduro. Los pastos abandonados sostuvieron un empobrecido de las polillas. La segregación de la fauna fue más pronunciada con respecto a especie rara. Los ejes de ordenación reflejaron sobre todo el grado del disturbio del hábitat (la vegetación, grado de sucesión y de la distancia de los sitios al bosque maduro) y en un grado inferior la altitud. Sin embargo, las diferencias de la fauna no estuvieron relacionadas con la distancias geográficas entre los sitios del muestreo. Este paralelismo en el cambio de la especie de las dos polillas se pudo confirmar también en la matriz de correlaciones ($r > 0.58$, $P<0.001$).

Tamaño de cuerpo, desarrollo de la probóscide y aspecto externo

Diversos parámetros del cuerpo tales como longitud de las alas delanteras, longitud de cuerpo y área de la superficie de las alas fueron utilizados. Había variación específica en la taxonomía de estos parámetros del cuerpo tales como longitud de las alas delanteras, longitud de cuerpo, y área de la superficie de las alas, sin embargo, los análisis por especie no demostraron ninguna diferencia en rasgos relacionados tamaño del cuerpo a lo largo del gradiente. En el nivel individual, había una disminución en la longitud de las alas delanteras y del cuerpo así como el área de la superficie de las alas con la recuperación del bosque. La distribución por clase de toda la especie y el números individuos total demostró una distribución uní modal similar a una distribución de Log-normal, con una excepción: la longitud de cuerpo de los individuos la cual mostró una distribución bimodal. Phaegopterini más grande era común en los sitios de la sucesión, mientras que Ctenuchini y Lithosiinae eran más grandes principalmente en el bosque maduro y Ctenuchini mostró una distribución frecuencia más amplia en las etapas tardías de la sucesión en comparación con las sucesiones más temprana y bosque.

Especies con una reducción parcial o total del proboscidio fueron encontradas frecuentemente en las áreas de sucesión que en los bosques maduros y también había algunas diferencias taxonómicas en el desarrollo de los proboscidios.

El aspecto externo de la especie arctiid fue dividido igualmente en críptico o aposematico. La incidencia relativa del aposematismo en polillas arctiid no cambió a lo largo del gradiente de la sucesión; sin embargo, tales patrones llegaron a ser evidentes en niveles sistemáticos más bajos. Las especies aposematicas entre Phaegopterini y Lithosiinae eran más frecuentes en los sitios de la sucesión, mientras que Ctenuchini en los bosques.

Dinámica temporal

A pesar de fluctuaciones en la cantidad de polilla la diversidad local de arctiid en el periodo de recolección fue relativamente constante, mientras que las polillas geometrid fluctúan en el cantidad de individuos y especie así como en la diversidad local en los tres períodos de muestreo. Sin embargo existieron en ambas familias algunas de la especie comunes que mostraron cambios temporales más del 50% de la especie y el > 90% de individuos fueron encontrados en los tres períodos de muestreo para ambas familias. El análisis multivariado de las muestras de la polilla revelaron una separación de los conjuntos arctiid y geometrid según el período de muestreo así como las diversas de los hábitat. Sin embargo, el efecto del período de muestreo aumentó con el aumento del tiempo entre los períodos de muestreo.

La dinámica temporal para Geometridae en general fue alta comparada con Arctidae y la diferencia de la composición de especies en los hábitats también es muy fuerte. Esto indica, que la mayoría de especies de Geometridae (en estado larvario)depende más de recursos efímeros (como flores, yemas apicales juveniles de las plantas) que Arctiidae.

La diversidad local en ambas familias nocturnas fue excepcionalmente alta, también en los sitios con fuertes disturbios antropogénicos. Por consiguiente las familias nocturnas muestran en estas pequeñas áreas un alto potencial para extenderse y colonizar sitios disturbados, cercanos al bosque natural. Sin embargo la diversidad decrece con el incremento de la distancia entre estos sitios y el bosque natural. A pesar de las diferencias en la diversidad local entre ambas familias hubo una alta similitud inesperada en la beta-diversidad modelo. En este estudio la beta-diversidad fue un buen indicador de los impactos de los disturbios en los bosques, mientras que la alfa-diversidad en el desarrollo de la sucesión mostró patrones específicos taxonómicos. Estos patrones específicos taxonómicos no permitieron en este sentido “indicadores de biodiversidad” extrapolar de un grupo nocturno a otro nocturno u otros organismos en general. Sin embargo familias nocturnas especialmente Geometridae, resultan ser en pequeñas áreas extraordinarios indicadores sensitivos de los cambios del ambiente como: disturbios o bien sea la regeneración de los bosques andinos naturales.

Darstellung des Eigenanteils

Diese Doktorarbeit folgt dem allgemein gebräuchlichen internationalen Standard einer Ph.D.-Thesis. Sie ist in separate Kapitel gegliedert, die auch separat gelesen werden können, ohne vorhergehende Kapitel studieren zu müssen, und die dennoch in ihrer Gesamtheit eine geschlossene Einheit bilden (kumulative Form).

Kapitel 1: Im ersten Kapitel führe ich in die Thematik ein. Dieses Kapitel wurde ausschließlich von mir verfasst.

Sämtliche neue wissenschaftliche Orginaldaten wurden von mir selbst oder unter meiner unmittelbaren Anleitung erhoben. Bei der Aufsammlung und Präparation der Nachtfalter wirkten einige studentische Hilfskräfte mit, die jeweils namentlich in den Danksagungen erwähnt sind. Die Determination erfolgt bei den Arctiiden zu 100 % durch mich selbst, bei den Geometriden zu 90 %. Dr. G. Brehm half bei der Grobsortierung der Unterfamilien sowie bei einigen schwierigen Fällen (10 % der Geometriden-Arten). Die statistischen Auswertungen erfolgten ausschließlich durch mich; Prof. Dr. K. Fiedler trug hierzu diverse ergänzende Hinweise auf wenig bekannte, jedoch zur Ergebnisfindung beitragende statistische Verfahren bei.

Kapitel 2-4: Enthalten sämtliche Orginaldaten sowie aktualisierte Daten von Dr. D. Süßenbach. Letztere wurden von mir von Grund auf überarbeitet (taxonomische Neusortierung). Der Eigenanteil pro Kapitel beträgt in allen drei Fällen 70%. K. Fiedler trug intellektuell und mit Formulierungsvorschlägen zur Auswertung, Darstellungsweise und Diskussion bei (30 %).

Kapitel 5-6: Verwendung von eigenen Orginaldaten, sowie Daten von D. Süßenbach und G. Brehm. Eigenanteil bei Kapitel 5 ca. 80 % und Kapitel 6 ca. 75%. K. Fiedler trug intellektuell zur Diskussion und Auswertungen bei (Kapitel

5: 10 % und Kapitel 6: 20 %), ebenso G. Brehm, der seine Orginaldaten zur Verfügung stellte und intellektuell zur Diskussion beitrug (Kapitel 5: 10 % und Kapitel 6: 5 %).

Kapitel 7-9: In der Synopsis verbinde ich die einzelnen Kapitel miteinander und erläutere die Bedeutung der Ergebnisse. Diese Kapitel wurden ausschließlich von mir geschrieben.

Acknowledgements

First of all, I want to thank Prof. Dr. Konrad Fiedler for his kind support and for many fruitful discussions that helped to work out essential results and for statistical advice.

Thanks to Prof. Dr. Klaus H. Hoffmann, who allowed me to continue my work at the Department of Animal Ecology I after the relocation of my supervisor.

Dr. Christoph L. Häuser (Staatliches Museum für Naturkunde, Stuttgart) and Prof. Dr. Giovanni Onore (Ponificia Universidad Católica del Ecuador, Quito) supported the project logistically.

Many thanks to Daniel Bartsch, Dr. C. L. Häuser, Dr. Martin R. Honey, Dr. Linda M. Pitkin (Natural History Museum, London) and Dr. Axel Hausmann (Zoologische Staatssammlung, München) for providing access to reference collections and for their help during the work in the collections. Benoît Vincent (Paris) identified some arctiid species.

I thank Dr. Dirk Süßenbach who provided data from his samples from the natural forest.

Many thanks to Dr. Gunnar Brehm, Dr. Klaus Fischer, Dr. John Slogett and Dr. Christian Schulze for improving earlier drafts of this dissertation and for their assistance in some statistical problems.

The Deutsche Forschungsgemeinschaft financed our project (FOR 402/1-1 TP 15, FOR 402/2-1 TP A3).

The Ministerio del Medio Ambiente in Ecuador issued research permits, and the foundation Nature and Culture International (Loja, Ecuador) gave logistical support and allowed access to the study sites and their facilities.

Many thanks to Maria Feijoo and their family, who provided us with food and also provided us an insight into the Ecuadorian way of life.

Many colleagues, notably Dr. Jürgen Homeier (botanical data), Dr. Rütger T. Rollenbeck (meteorological data), Alfredo Martinez (botanical data), Nathalie Soethe, Matthias Oesker helped with their knowledge and have worked in the same study area as myself and made the time at the field station in Ecuador very enjoyable. Thanks to all occupants apart from those listed above. Special thanks to Dr. Felix Matt, who managed the life on the station and helped anytime.

Special thanks to Oscar Valdes and Alfredo Martinez for translating the Spanish summary.

Doreen Fetting, Jörg Hager, Georg Petschenka, Claudia Ramenda, Caroline Schulze, Annick Servant, Anna Spengler and Anne Walter helped with sampling and processing moths as well as assisted in databasing thousands of moths.

My colleagues from the University of Bayreuth, mainly Monika Körner, Dr. Stefan Dötterl, Siegfried Kehl, and Dr. Holger Daniels helped in various ways.

My warmest thanks go to my parents and sisters for their continuous support, and to Andrea Sieber for moral support. Last but not least Ronja and Ernesto for their love.

Appendix 1: List of all 250 arctiid species and 7717 individuals collected along a succession gradient in South Ecuador in the years 2002 and 2003, ordered by subfamily, genus and species. **ID** means identification number in corresponding database. A to I are the different sites ordered by their degree of succession. Total are the sum of all individuals of one species. **sp** undetermined species, **sp cf** (confronta) species that resemble, but are not identical with a described species. When more than one undetermined species was assigned to a genus, these species were numbered. [1] aposematic coloured, [2] Hymenoptera mimicry, [3] cryptic coloured, [4] metallic shine. * proboscis reduced, ° no proboscis.

ID	Genus	Species	A	B1	B2	C	D1	D2	E1	E2	F1	F2	G1	G2	H1	H2	I
	Arctiini																
198	*Chlorhoda*	*metamelaena* [1*]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
12	*Hypercompe*	*magdalenae* [1*]	-	1	-	-	-	-	-	-	-	1	1	-	-	-	3
8	*Hypercompe*	*nemophila* [3°]	5	5	6	-	2	-	-	1	5	7	5	4	2	4	19
9	*Hypercompe*	*pratincola* [3°]	-	-	-	-	-	-	-	-	1	-	-	-	-	2	1
11	*Hypercompe*	*robusta* [1*]	3	-	1	-	-	1	-	1	-	-	-	-	-	-	1
13	*Palaeomolis*	*metarhoda* [3*]	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-
160	*Virbia*	sp 1 [1*]	1	2	-	-	-	-	1		1	2	2	1	-	1	3
	Ctenuchini																
127	*Chrostosoma*	*rica* [2]	16	2	1	-	-	1	5	9	5	5	-	1	-	2	15
103	*Chrysocale*	sp 1 [4]	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
417	*Coreura*	*simsoni* [1]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
102	*Correbia*	*bricenoi* [3]	-	-	-	-	-	2	-	3	1	-	2	1	-	1	1
101	*Correbia*	*negrona* [3]	1	1	1	-	-	-	-	-	-	-	1	2	1	1	-
82	*Correbidia*	*fana* [3]	1	3	1	-	-	-	-	1	-	-	-	-	-	1	3
416	*Correbidia*	sp cf *terminalis* [3]	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
220	*Cosmosoma*	*carabayanum* [2]	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
126	*Cosmosoma*	*centralis* [2]	5	2	2	1	2	6	4	12	3	9	4	7	3	2	8
131	*Cosmosoma*	*flavothorax* [2]	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
125	*Cosmosoma*	*meridense* [2]	27	11	4	1	3	4		13	5	18	12	8	6	7	28
143	*Cosmosoma*	sp 15 [2]	25	24	17	5	7	10	6	11	4	20	58	38	8	15	33
137	*Cosmosoma*	sp 2 [2]	1	1	-	-	-	-	-	-	-	-	-	-	2	-	-
138	*Cosmosoma*	*stictinota*[2]	4	-	-	-	-	2	-	-	-	-	3	2	-	1	1
106	*Ctenucha*	sp cf *albipars*[1]	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-
98	*Cyanopepla*	*alonzo*[1]	1	-	-	2	-	-	-	-	-	-	-	-	-	1	-
130	*Dasysphinx*	*buckleyi*[2]	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
92	*Delphyre*	*discalis*[3]	7	1	5	6	5	1	4	12	2	8	13	9	7	4	10
222	*Delphyre*	*tetilla*[1]	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1
226	*Epectaptera*	*metochria*[1]	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1
132	*Epectaptera*	sp 1[1]	3	1	4	6		1	4	2	13	7	15	9	8	18	16
133	*Epectaptera*	sp 2[1]	1	1	-	-	-	-	1	2	6	4	5	3	2	5	6
2020	*Epectaptera*	sp 3[1]	-	-	-	-	-	-	-	1	-	-	-	1	-	1	1
414	*Epectaptera*	sp 4[1]	-	-	-	-	-	-	-	1	2	-	1	-	-	1	1
95	*Episcepsis*	*dodaba*[1]	1	-	1	2	5	-	4	-	2	1	3	2	-	1	1
218	*Euagra*	*chica*[4]	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-

ID	Genus	Species	A	B1	B2	C	D1	D2	E1	E2	F1	F2	G1	G2	H1	H2	I
119	*Eucereon*	*amazonum*[3]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
112	*Eucereon*	*casca*[3]	1	-	-	-	-	-	1	2	-	1	4	4	-	-	-
113	*Eucereon*	*coeruleocaput*[3]	2	4	1	-	1	-	2	4	4	2	5	8	-	1	3
225	*Eucereon*	*confine*[1]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3
117	*Eucereon*	*confinis*[1]	-	1	-	-	1	-	-	-	-	-	-	3	2	-	-
121	*Eucereon*	*consortum*[1]	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
120	*Eucereon*	*davidi*[3]	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-
118	*Eucereon*	*flavicaput*[3]	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-
413	*Eucereon*	*griseatum*[3]	-	-	1	-	-	-	-	-	-	-	2	-	-	1	-
115	*Eucereon*	*lineata*[3]	2	1	1	2	1	1	3	7	-	4	11	13	3	7	2
224	*Eucereon*	*mathani*[3]	-	-	1	-	-	-	1	-	-	-	-	-	-	1	-
900	*Eucereon*	*mitigata*[1]	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1
99	*Eucereon*	*myrtusa*[1]	-	3	-	-	1	1	-	2	-	1	6	1	4	2	3
116	*Eucereon*	*nebulosum*[3]	3	2	1	-	1	-	1	5	3	6	13	4	5	8	3
122	*Eucereon*	*ockendeni*[1]	4	4	4	-	-	-	-	4	-	2	3	4	4	2	7
231	*Eucereon*	*perstriata*[3]	-	-	-	-	1	-	1	-	-	-	-	-	1	2	-
111	*Eucereon*	*perstriatum*[3]	-	1	-	2	1	-	-	1	-	1	1	1	-	2	4
114	*Eucereon*	*pseudocasca*[1]	2	1	2	-	-	1	2	-	-	1	3	5	3	2	6
146	*Eucereon*	sp cf *flavicincta*[3]	-	-	-	-	1	-	-	-	-	-	1	1	-	-	-
261	*Eucereon*	sp cf *zizana*[3]	1	1	-	-	2		2	2	-	-	-	-	2	-	2
1020	*Eucereon*	sp 02[3]	-	-	-	3	-	-	1	1	1	-	-	-	-	-	-
142	*Eucereon*	sp 08[1]	-	-	-	2	-	-	1	-	-	-	3	4	1	3	2
419	*Eucereon*	sp 10[3]	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
990	*Eucereon*	*striatum pallenscens*[1]	-	-	-	-	-	-	-	1	-	-	1	-	1	-	-
123	*Eucereon*	*tigrata*[1]	1	2	3	-	1	1	1	4	3	1	3	8	1	17	4
161	*Eucereon*	*zizana*[3]	13	7	4	2	5	4	13	11	6	11	17	12	1	4	12
477	*Gymnelia*	sp cf *lyrcea*[2]	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
108	*Holophaea*	*endoleuca*[1]	18	10	8	2	2	8	14	29	7	27	19	15	13	20	36
128	*Homoeocera*	*crassa*[2]	-	-	-	-	1	-	-	1	-	-	-	1	-	-	-
129	*Homoeocera*	*staminea*[2]	-	-	1	-	-	-	-	-	-	-	-	-	2	-	1
23000	*Hyaleucerea*	*costinotata*[3]	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
139	*Loxophlebia*	sp 1[2]	1	2	1	-	1	2	-	3	-	3	1	2	-	-	1
219	*Macrocneme*	*cyanea*[4]	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
221	*Mesothen*	*roseifemur*[2]	-	-	-	-	-	1	-	-	-	-	1	1	1	-	-
100	*Mydropastea*	*cephalena*[1]	1	4	1	-	1	1	1	-	-	6	13	9	-	1	4
134	*Napata*	sp 1[1]	-	1	1	1	1	-	1	-	2	6	1	-	1	-	4
135	*Napata*	sp 3[1]	-	4	2	6	1	-	7	8	13	13	16	17	12	11	15
94	*Philoros*	*rubriceps*[1]	5	6	2	-	7	7	1	4	-	2	1	-	-	-	1
140	*Poecilosoma*	*vespoides*[2]	-	-	-	-	-	-	-	1	-	-	-	-	-	1	1
110	*Poliopastea*	*viridis*[3]	5	7	1	1	2	2	-	13	2	6	5	5	2	-	5
93	*Pseudaclytia*	*major*[3]	3	-	-	-	1	1	1	3	1	1	5	2	2	3	2
297	*Psilopleura*	sp cf *flavicans*[1]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
223	*Rhynchopyga*	*elongata*[1]	-	-	2	-	-	-	1	-	-	1	-	-	-	1	-
141	*Rhynchopyga*	*xanthospila*[2]	-	1	1	-	-	1	-	-	-	4	1	-	1	-	4
104	*Sagaropsis*	*elegans*[4]	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-
109	*Saurita*	sp 1[3]	5	1	4	3	-	1	3	6	4	6	-	2	-	4	6
	Pericopini																
395	*Chetone*	*histrio*[1]	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
85	*Dysschema*	*imitata*[3*]	-	-	-	-	-	-	-	-	-	2	-	-	-	-	1

ID	Genus	Species	A	B1	B2	C	D1	D2	E1	E2	F1	F2	G1	G2	H1	H2	I
285	*Dysschema*	*marginalis*^{1*}	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
84	*Dysschema*	*semirufa*$^{1\circ}$	7	11	11	-	2	1	1	9	7	9	5	2	3	3	11
255	*Dysschema*	sp cf *moseroides*$^{3\circ}$	-	-	-	-	-	-	-	-	1	-	-	-	-	-	2
83	*Hyalurga*	*urioides*$^{3\circ}$	-	1	1	-	-	-	-	1	1	-	-	1	2	4	1
1420	*Hypocrita*	*calida*^{1}	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1
418	*Hypocrita*	*celadon*^{4}	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
8000	*Xenosoma*	*progonum*^{3}	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Phaegopterini																
201	*Aemilia*	*crassa*^{3}	-	-	-	1	-	1	1	-	-	-	-	-	-	-	1
17	*Aemilia*	*mincosa*^{3*}	8	3	6	3	-	1	3	2	-	3	3	2	4	2	5
204	*Aemilia*	sp cf *brunneipars*^{3}	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
1	*Amastus*	*aconia*^{1}	10	6	1	5	4	1	7	12	4	5	5	3	1	2	8
1540	*Amastus*	*albipuncta*^{1}	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
7	*Amastus*	*coccinator*^{1}	6	6	-	2	-	-	2	6	3	3	8	1	1	4	8
3	*Amastus*	*collaris*^{1}	2	1	-	1	-	-	-	1	-	-	1	-	2	1	-
6	*Amastus*	*erganoides*^{3}	-	-	-	-	-	-	-	1	1	2	3	-	-	-	1
1560	*Amastus*	*hampsoni*^{1}	-	1	-	-	-	-	1	-	-	-	-	-	-	-	1
2500	*Amastus*	*oleagina*^{1}	5	3	1	2	1	-	5	-	-	1	-	-	-	-	3
1500	*Amastus*	sp cf *rosenbergi*^{1}	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1
473	*Amastus*	sp 08^{1}	2	-	-	1	-	1	1	-	1	-	-	-	-	1	-
2	*Amastus*	*umber*^{1}	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-
3700	*Amaxia*	*pardalis*^{1*}	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
39	*Amaxia*	*pulchra*^{1*}	-	3	1	-	1	-	-	-	-	1	-	1	-	-	2
18	*Bernathonomus*	*piperita*^{1}	1	2	-	-	-	-	-	-	-	-	-	-	-	-	4
274	*Bernathonomus*	sp 02^{1}	-	1	-	-	-	1	-	-	-	-	-	1	-	-	-
69	*Bertholdia*	*flavidorsata*^{1}	-	6	1	-	-	-	2	-	1	-	1	1	1	-	4
71	*Bertholdia*	*griseopalpis*^{1}	1	1	2	-	1	-	-	2	-	-	-	2	-	-	1
70	*Bertholdia*	*myosticta*^{1}	4	2	7	-	-	-	3	5	4	8	2	3	1	1	6
472	*Bertholdia*	sp 1^{1}	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
72	*Bertholdia*	*specularis*^{1}	-	2	1	-	-	-	1	-	-	2	-	-	-	-	1
24	*Cissura*	*unilineata*^{1}	1	-	1	-	-	-	1	4	-	-	-	-	-	-	2
80	*Echeta*	*grandis*^{1}	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
46	*Echeta*	sp cf *rubrireta*$^{3\circ}$	1	1	1	-	-	-	5	-	-	-	1	6	2	1	3
15	*Elysius*	*atrata*^{1}	1	-	-	2	-	1	-	-	2	1	1	1	1	1	1
234	*Elysius*	*carbonarius*^{3}	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
206	*Elysius*	*hades*^{3}	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-
53	*Elysius*	*lavinia*^{3}	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
14	*Elysius*	*melanoplaga*^{3}	3	3	-	-	-	-	1	3	4	5	7	1	9	-	15
47	*Elysius*	*ochrota*^{3}	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-
45	*Elysius*	sp cf *hades*^{3}	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
16	*Elysius*	*terra*^{3}	-	1	-	-	1	-	-	-	1	1	3	-	1	-	-
79	*Gorgonidia*	*buckleyi*^{1}	-	2	1	-	-	-	-	-	-	2	-	1	1	1	1
22	*Graphea*	*marmorea*^{1}	1	1	1	-	-	-	-	-	-	-	3	-	-	2	-
21	*Halysidota*	*atra rindgei*^{3}	-	-	1	-	1	1	-	-	1	1	3	1	1	-	-
199	*Halysidota*	*underwoodi*^{1}	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1
4	*Hemihyalea*	*minerva*^{1}	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
5	*Hemihyalea*	*watkinsi*^{1}	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
23	*Hyperthaema*	*sanguineata*^{1}	-	-	1	1	-	-	-	-	-	-	-	1	2	-	-
243	*Hyponerita*	*persimilis*^{1}	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-

ID	Genus	Species	A	B1	B2	C	D1	D2	E1	E2	F1	F2	G1	G2	H1	H2	I
74	*Idalus*	*dorsalis*[1]	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
76	*Idalus*	*erythronata*[1]	2	1	-	1	-	-	-	-	-	-	1	-	-	-	-
73	*Idalus*	*herois*[1]	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
75	*Idalus*	*pichesensis*[1]	2	-	1	-	-	-	-	1	-	-	-	-	-	-	3
91	*Ischnocampa*	*celer*[3]	-	1	-	-	-	-	-	-	-	-	2	1	1	1	-
86	*Ischnocampa*	*mamona*[3]	3	6	3	4	-	4	3	7	7	12	20	13	7	9	12
87	*Ischnocampa*	*sordida*[3]	1	3	6	-	-	2	4	4	21	6	34	9	10	14	34
213	*Ischnocampa*	*sordidior*[3]	-	-	-	1	-	-	-	1	-	1	4	-	-	3	1
216	*Ischnocampa*	sp cf *ferrea*[3]	1	1	1	-	-	-	-	2	-	-	-	-	-	1	-
89	*Ischnocampa*	sp cf *nubilosa*[3]	1	-	1	-	-	-	-	1	1	1	-	-	-	-	1
217	*Ischnocampa*	sp cf *tristis*[3]	-	-	1	-	-	-	1	4	-	-	1	-	-	3	1
90	*Ischnocampa*	sp 1[3]	-	-	1	-	-	-	-	-	-	3	2	3	3	-	5
88	*Ischnocampa*	sp 2[3]	2	5	2	-	-	-	-	2	3	5	9	6	2	3	3
51	*Ischnocampa*	*tristis*[3]	2	-	-	-	-	-	-	3	1	1	9	1	-	1	2
124	*Lampruna*	*punctata*[3]	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
64	*Leucanopsis*	*apicepunctata*[3]	3	2	2	2	-	-	1	1	2	1	6	2	5	6	3
212	*Leucanopsis*	*bipartita*[3]	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1
59	*Leucanopsis*	*boliviana*[3]	1	2	-	1	-	-	-	-	1	1	4	4	1	-	1
61	*Leucanopsis*	*luridioides*[3]	-	1	2	1	-	1	-	2	3	3	2	7	5	8	7
65	*Leucanopsis*	*nayapana*[3]	5	11	2	6	2	7	9	14	1	8	6	4	2	1	4
232	*Leucanopsis*	*notodontina*[3*]	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
1180	*Leucanopsis*	*nubilosus*[3]	2	-	-	-	-	-	-	-	-	-	-	1	-	-	1
60	*Leucanopsis*	*quadrata*[3]	-	1	1	1	-	-	1	2	2	2	3	1	2	2	-
209	*Leucanopsis*	sp cf *boliviana*[3]	1	-	2	-	-	-	-	1	-	1	-	-	-	1	-
205	*Leucanopsis*	*subterranea*[3*]	-	-	1	-	-	-	-	-	-	1	3	-	1	1	5
20	*Lophocampa*	*atriceps*[3]	-	-	-	1	-	-	-	-	-	-	-	-	-	-	3
67	*Lophocampa*	*distincta brunnescens*[3]	6	1	-	-	-	1	1	1	2	3	5	3	-	2	6
66	*Lophocampa*	*distincta distincta*[3]	-	-	-	-	-	-	-	-	-	1	1	-	1	-	-
68	*Lophocampa*	*dognini*[3]	-	-	3	-	-	-	-	-	-	1	-	-	-	1	-
42	*Melese*	*babosa*[1]	3	1	2	1	-	-	-	-	-	-	1	1	3	3	3
41	*Melese*	*endopyra*[1]	5	5	1	-	-	-	4	2	9	9	23	5	9	6	14
474	*Melese*	*intensa*[1]	-	-	-	1	-	-	-	1	-	-	-	-	1	-	-
203	*Melese*	*nebulosa*[1]	-	-	1	2	-	-	-	-	-	2	1	-	1	-	-
19	*Neidalia*	*villacresi*[1°]	-	-	1	-	-	-	-	1	1	1	-	2	-	-	-
96	*Neritos*	sp 03[1]	-	1	-	1	-	-	-	-	-	2	-	-	-	-	-
54	*Onthyes*	*flavicosta*[3]	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
52	*Onythes*	*pallidicosta*[3]	5	3	4	1	1	-	1	2	-	-	12	1	1	2	4
48	*Opharus*	*consimilis*[1]	-	1	1	1	1	1	-	3	-	-	1	3	1	2	1
57	*Opharus*	*polystrigata*[3]	-	-	-	-	-	-	-	1	-	-	1	1	-	-	-
78	*Opharus*	*rhodosoma*[1]	-	1	-	-	-	-	-	-	-	1	-	-	-	1	-
81	*Ormetica*	*ameoides*[1]	-	1	-	-	1	-	-	1	2	1	3	3	-	2	3
26	*Pachydota*	*nervosa*[3]	-	1	1	-	-	1	-	1	2	-	1	-	-	-	2
77	*Pachydota*	*saduca*[1]	-	-	1	-	1	3	-	3	-	-	-	2	-	1	3
27	*Pachydota*	*striata*[1]	1	-	-	2	-	-	-	-	-	-	-	-	-	-	-
43	*Parevia*	sp 03[1]	3	-	2	-	-	-	2	1	4	4	8	4	-	1	10
55	*Pelochyta*	*arontes*[3]	-	-	-	-	-	-	-	-	-	1	1	-	-	1	-
49	*Pelochyta*	sp cf *lystra*[1]	-	1	1	2	-	1	-	-	2	1	3	4	1	1	-
56	*Pelochyta*	sp cf *pallida*[3]	3	-	-	1	-	1	-	2	-	-	2	-	-	-	-
50	*Pelochyta*	sp 10[3]	1	1	-	-	-	1	-	-	-	2	1	3	2	2	1

ID	Genus	Species	A	B1	B2	C	D1	D2	E1	E2	F1	F2	G1	G2	H1	H2	I
214	*Pelochyta*	sp 14[3]	-	-	-	-	-	-	-	1	-	-	1	2	-	1	2
58	*Pelochyta*	sp 2[3]	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-
284	*Phaegoptera*	*discisema*[3]	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
62	*Phaegoptera*	sp 01[3]	1	1	3	-	-	1	-	-	-	1	1	-	1	1	3
211	*Phaegoptera*	sp 04[3]	-	1	-	-	1	-	-	-	2	1	3	-	-	-	-
63	*Phaegoptera*	sp 05[3]	1	-	-	-	-	-	-	1	-	-	5	-	1	1	-
210	*Phaegoptera*	sp 06[3]	3	2	1	-	-	-	1	1	-	4	-	1	1	-	9
476	*Phaegoptera*	sp 07[3]	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
475	*Phaegoptera*	sp 08[3]	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
105	*Pseudopharus*	*amata*[1]	-	-	-	1	2	-	-	1	1	-	2	-	-	-	3
1780	*Psychophasma*	*erosa*[3]	1	-	-	1	1	1	1	12	6	-	-	-	-	-	4
25	*Selenarctia*	*elissa*[1]	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
207	*Sychesia*	*dryas*[1]	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
202	*Symphlebia*	*citrarius*[1]	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1
35	*Symphlebia*	*fulminans*[1°]	2	-	-	-	-	-	-	-	-	-	-	-	1	-	-
40	*Symphlebia*	*juvenis*[1]	2	1	1	-	1	1	2	-	-	-	1	2	-	-	1
37	*Symphlebia*	*primulina*[3]	-	1	1	-	-	-	-	-	1	-	1	-	-	1	1
28	*Symphlebia*	*similis*[1°]	3	8	1	-	2	1	1	1	2	8	1	5	1	6	8
230	*Symphlebia*	sp cf *catenata*[3]	1	-	-	-	1	1	-	1	1	3	-	1	-	-	1
34	*Symphlebia*	sp cf *citrarius*[3]	-	-	-	-	-	-	-	-	1	1	-	-	-	-	1
32	*Symphlebia*	sp 01[1]	2	-	1	-	-	-	-	-	-	1	-	1	-	-	1
330	*Symphlebia*	sp 03[1*]	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-
31	*Symphlebia*	sp 04[3]	1	-	-	-	-	-	-	-	-	-	1		-	-	-
36	*Symphlebia*	sp 111[1]	1	2	-	-	-	-	-	1	1	1	3	1	-	-	2
415	*Symphlebia*	sp 211[1]	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
	Lithosiinae																
195	*Agkonia*	*pega*[3]	3	10	3	2	6	1	4	2	-	14	19	22	5	17	19
186	*Agylla*	*argentea*[3]	-	1	-	-	-	-	2	1	-	2	-	-	-	1	-
172	*Agylla*	*argentifera*[3]	7	-	1	1	-	3	-	-	4	-	-	1	-	1	2
169	*Agylla*	*auraria*[1]	-	-	-	-	-	-	-	-		1	-	-	-	-	2
227	*Agylla*	*dentifera*[3]	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
194	*Agylla*	*flavitincta*[3]	26	22	5	8	1	4	14	11	7	30	22	23	5	24	7
178	*Agylla*	*foyi*[3]	1	5	-	-	-	1	-	-	-	-	-	-	-	1	4
173	*Agylla*	*fulvithorax*[3]	-	1	-	-	2	2	-	1	1	-	1	-	-	2	1
185	*Agylla*	*fusciceps*[3]	1	2	3	-	-	-	1	1	1	1	1	-	-	3	12
192	*Agylla*	*hampsoni*[3]	61	28	21	11	7	2	21	11	9	24	12	9	8	5	23
170	*Agylla*	*hermanilla*[1]	1	4	-	-	-	-	-	1	1	3	-	1	-	2	6
229	*Agylla*	*marcata*[3]	-	-	-	-	-	-	-	-	2	2	-	-	-	1	1
171	*Agylla*	*nitridalis*[3]	19	9	9	2	6	-	10	12	6	7	12	4	2	5	9
180	*Agylla*	*nivea*[3]	4	12	6	3	4	3	7	23	7	13	5	5	1	8	8
176	*Agylla*	*nochiza*[3]	2	2	1	-	-	3	1	1	-	1	1	1	-	-	-
188	*Agylla*	*rotunda*[3]	11	3	5	-	-	1	4	1	-	2	-	-	-	-	-
191	*Agylla*	*separata*[3]	16	13	11	10	5	3	7	21	6	15	18	19	5	21	10
175	*Agylla*	sp 01[3]	5	5	1	-	-	3	1	1	-	1	1	-	-	-	4
179	*Agylla*	sp 02[3]	-	3	-	-	-	-	2	1	-	1	-	-	-	-	1
190	*Agylla*	sp 14[3]	11	18	16	1	3	3	8	7	6	36	28	23	1	17	36
375	*Agylla*	sp 18[3]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
181	*Agylla*	sp 19[3]	25	11	7	16	-	-	15	13	5	13	5	11	4	7	7
177	*Agylla*	sp 20[3]	1	6	1	-	2	2	-	5	2	7	1	4	-	1	10

ID	Genus	Species	A	B1	B2	C	D1	D2	E1	E2	F1	F2	G1	G2	H1	H2	I
167	*Agylla*	sp 25[3]	5	8	7	2	-	3	3	3	5	11	19	17	2	4	15
168	*Agylla*	sp 26[3]	2	2	6	-	2	-	1	1	-	3	3	1	-	-	8
189	*Agylla*	sp 6[3]	4	4	1	-	2	1	2	2	1	4	3	1	2	-	3
228	*Agylla*	*subochracea*[3]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
183	*Agylla*	*tobera*[3]	4	2	1	3	-	1	1	2	3	2	2	3	-	-	1
182	*Agylla*	*zucarina*[3]	22	41	17	5	2	2	22	9	11	48	27	23	6	15	27
163	*Areva*	*albogrisea*[3]	4	7	1	2	-	-	5	2	9	15	34	17	22	26	1
144	*Chrysochlorosia*	sp cf *magnifica*[4]	1	1	4	-	-	1	1	1	1	7	2	10	-	8	2
107	*Cloesia*	*parthia*[4]	1	2	-	-	-	-	1	2	-	2	1	1	-	-	6
158	*Diarhabdosia*	*laudamia*[3]	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-
97	*Gardinia*	*paradoxa*[4]	2	-	-	7	5	2	9	4	-	1	2	1	-	4	-
145	*Illice*	*interrupta*[1]	-	-	-	-	-	-	1	1	-	1	3	4	-	4	1
157	*Illice*	*sexalata*[1*]	1	-	-	-	-	1	2	-	1	4	3	5	2	1	1
152	*Illice*	sp cf *minuta*[1]	3	-	3	-	-	-	-	1	-	3	1	6	-	2	2
151	*Illice*	sp 1[1*]	2	5	-	-	1		1	5	2	11	8	13	1	3	22
148	*Illice*	sp 2[1]	2	-	1	-	-	-	-	1	-	-	-	-	-	-	1
156	*Illice*	sp 3[1]	2	5	8	-	-	-	-	4	-	4	7	8	-	4	8
149	*Lycomorpha*	*splendens*[1]	-	1	-	-	-	-	-	3	1	1	1	-	1	-	1
159	*Lycomorphodes*	*suspecta*[3]	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
196	*Macroptila*	*laniata*[3]	93	145	49	33	22	17	78	77	39	170	83	89	16	62	76
155	*Metalobosia*	*holophaea*[4]	3	18	6	-	3	5	16	9	11	32	48	36	2	23	37
150	*Nodozana*	*fifina*[1]	-	1	1	-	-	2	1	1	-	4	2	6	2	1	3
154	*Pronola*	*magniplaga*[3]	1	-	-	-	-	-	2	1	-	2	3	9	5	3	1
153	*Pronola*	*perdiffusa*[3]	-	1	-	-	-	1	1	1	1	-	1	2	1	1	-

Appendix 2: List of all 775 species and 20,670 individuals collected along a succession gradient in South Ecuador in the years 2002 and 2003, ordered by subfamily, genus and species. **ID** means identification number in corresponding database. A to I are the different sites ordered by their degree of succession. Total are the sum of all individuals of one species. Taxonomy of the subfamily Ennominae follows Pitkin (2002), and Brehm *et al*. (2005) (for references see chapter5). **sp** undetermined species, **sp cf** (confronta) species that resemble, but are not identical with a described species. When more than one undetermined species was assigned to a genus, these species were numbered after Brehm *et al*. (2005) or they get their ID number.

ID	Genus	Species	A	B1	B2	C	D1	D2	E1	E2	F1	F2	G1	G2	H1	H2	I
	Ennominae																
2003	*Achagua*	*obsoleta*	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
938	*Acrosemia*	*vulpecularia*	1	-	2	-	1	1	3	2	3	1	3	7	1	4	1
69	*Acrotomia*	*muta*	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-
1095	*Acrotomodes*	*clota*	-	1	1	4	1	-	1	-	-	1	-	-	-	-	5
941	*Acrotomodes*	*kunoi*	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
104	*Aenictes*	*sororcula*	1	-	-	-	-	-	-	-	1	1	-	-	1	-	1
2007	*Anisoperas*	*cervinicolor*	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
2085	*Anisoperas*	*clotilda*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
2090	*Apiciopsis*	*angusta*	-	-	-	-	-	-	-	-	12	2	8	3	-	-	6
292	*'Apiciopsis'*	sp cf *maciza*	-	-	-	-	-	-	-	-	-	-	1	3	-	2	1
740	*Aplogompha*	*lafayi*	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-
304	*Aragua*	*bistonaria*	-	1	-	-	-	-	1	-	-	3	3	6	2	4	5
73	*Argyrotome*	*prospectata*	33	16	11	118	4	27	27	24	11	23	54	11	9	6	15
2076	*Argyrotome*	*tenebrosa*	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
221	*Astyochia*	*cloelia*	3	-	1	18	-	-	1	1	1	-	1	-	1	-	-
2028	*Astyochia*	*lechula*	2	-	-	5	1	3	1	-	-	-	-	-	1	-	1
224	*Astyochia*	*paulina*	1	-	-	2	-	-	-	1	-	-	1	-	-	-	-
222	*Astyochia*	sp cf *marginea*	1	1	-	-	1	-	-	-	-	-	2	1	-	-	5
223	*Astyochia*	*vitrea*	-	1	1	12	-	2	-	-	-	1	1	-	-	-	1
745	*Ballantiophora*	sp cf *gibbiferata*	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
254	*'Bassania'*	*crocallinaria*	-	1	-	2	1	-	1	-	1	2	2	2	-	1	2
53	*Bassania*	*goleta*	-	-	-	-	-	-	-	-	-	1	1	1	-	1	-
7	*Bassania*	*olivacea*	1	1	-	1	-	-	-	-	-	-	1	-	-	-	1
57	*Bassania*	sp	1	-	-	-	2	-	-	-	-	-	-	-	-	-	-
80	*Bonatea*	*duciata*	-	1	-	-	-	-	1	-	-	2	-	3	1	1	5
81	*Bonatea*	*funerea*	-	-	-	-	-	-	-	-	-	-	1	1	-	2	1
76	*Bonatea*	*viridilinea*	1	6	2	13	-	1	3	1	2	9	13	7	42	9	10
78	*Bonatea*	*viridirufa*	-	6	4	2	2	1	-	-	6	6	1	3	-	1	5
273	*Bryoptera*	*basisignata*	1	-	-	6	2	-	1	-	1	-	1	1	1	-	1
267	*Bryoptera*	*canidentata*	3	7	10	7	-	2	1	7	9	16	21	13	1	8	18
268	*Bryoptera*	*friaria*	3	1	1	-	1	-	1	3	2	-	1	2	-	1	-
780	*Bryoptera*	*fulvisquamosa*	-	-	1	-	-	2	2	8	1	8	15	30	4	11	5
266	*Bryoptera*	*injunctata*	-	-	-	1	-	-	2	1	-	-	3	-	4	4	2

ID	Genus	Species	A	B1	B2	C	D1	D2	E1	E2	F1	F2	G1	G2	H1	H2	I
274	*Bryoptera*	sp	-	1	-	-	-	-	-	-	-	-	-	2	7	-	-
779	*Bryoptera*	sp cf *friaria*	-	-	-	-	-	2	4	3	1	2	6	-	4	4	1
774	*Budara*	*partita*	5	6	4	1	-	-	2	4	8	15	1	7	1	3	25
1093	*Budara*	sp 1093	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
1083	*Callipseustes*	*bivittata*	-	-	-	-	1	-	-	-	-	-	1	-	3	2	-
339	*Callipseustes*	*semifimbriata*	-	-	-	-	1	-	-	1	-	1	-	1	1	2	-
2094	*Callipseustes*	sp 2094	-	-	-	-	1	-	1	-	-	-	1	2	1	10	-
800	*Callipseustes*	sp cf *pullaria*	1	-	-	-	-	1	-	-	-	-	-	1	1	-	-
338	*Callipseustes*	sp cf *trisecta*	-	3	-	3	1	1	3	1	1	1	6	-	6	2	2
2093	*Callipseustes*	sp cf *variegata*	1	1	-	-	-	-	-	1	-	1	1	1	-	2	2
2071	*Callipseustes*	*variegata*	-	-	-	-	-	-	-	-	-	-	-	1	3	-	-
75	*Cargolia*	*arana*	2	2	1	7	-	-	1	1	3	5	12	4	8	13	4
74	*Cargolia*	*pruna*	2	-	5	-	-	-	1	-	-	2	3	1	-	4	9
2161	*Cargolia*	sp 2161	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1
1078	*Carpella*	*aequidistans*	1	2	1	1	-	-	-	-	-	3	1	1	1	-	1
1348	*Cartellodes*	*levis*	-	-	-	-	-	1	-	1	-	-	3	-	-	3	-
749	*Certima*	*espuma*	1	2	-	3	2	-	2	-	3	2	4	7	-	1	2
936	*Certima*	*esquina*	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-
1080	*Certima*	*eximia*	-	-	-	-	-	-	-	-	-	1	2	-	1	1	-
2080	*Certima*	*jelskii*	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1
95	*Certima*	*lojanata*	7	-	4	18	1	2	6	1	4	4	3	3	7	4	2
253	*Certima*	*miligina*	-	-	1	-	-	-	-	1	-	-	1	1	-	-	1
2072	*Certima*	*nivisparsa*	-	1	-	-	-	-	1	-	-	1	-	-	-	-	2
133	*Certima*	sp 01N	9	9	3	26	4	8	9	2	3	6	8	5	1	8	3
97	*Certima*	sp 02	-	-	-	2	-	-	-	1	2	1	2	3	2	1	1
2165	*Certima*	sp 2165	-	-	-	-	-	-	2	-	-	1	-	-	-	-	-
2008	*Certima*	*strigifera*	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
94	*Certima*	*unilineata*	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-
96	*Certima*	*xylinochroma*	-	-	-	1	-	-	-	-	-	1	-	1	-	-	1
717	*Charca*	*fulminea*	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-
718	*Charca*	*ornata*	1	-	-	1	-	-	-	-	-	-	-	1	3	-	1
307	*Charca*	sp 02	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1
2055	*Cidariophanes*	*brigitta*	-	-	-	-	-	-	-	-	-	-	-	3	-	-	1
2057	*Cidariophanes*	*psittacaria*	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-
1264	*Cimicodes*	*albicosta*	-	-	-	2	1	-	-	-	-	-	-	-	-	2	1
1165	*Cimicodes*	*ferruginea*	-	-	-	-	-	-	-	-	-	1	2	2	8	1	-
90	*Cimicodes*	sp	3	-	-	1	-	-	1	2	7	1	2	2	18	2	7
294	*Cirsodes*	*acuminata*	-	-	-	-	-	-	1	1	-	-	3	-	-	-	2
291	*Cirsodes*	*casta*	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1
290	*Cirsodes*	*meridaria*	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
126	*Cosmophyga*	*privataria*	-	3	-	2	-	1	1	2	1	-	1	1	1	-	-
127	*Cosmophyga*	*sociodes*	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-
755	*Cratoptera*	*vestianaria*	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
200	*'Cyphoedma'*	*transvolutata*	-	1	-	1	-	-	-	2	1	2	3	2	1	3	6
1051	*Devarodes*	sp 1051	1	-	-	-	-	-	-	-	-	1	-	6	1	1	1
2163	*Ennominae*	sp 2163	-	-	-	2	-	-	-	-	-	-	-	-	1	-	-
252	*Epimecis*	*diffundaria*	1	-	-	-	-	1	1	1	-	1	2	-	1	-	4
2024	*Epimecis*	sp cf *fumistrota*	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
945	*Erosina*	*rusticata*	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-

ID	Genus	Species	A	B1	B2	C	D1	D2	E1	E2	F1	F2	G1	G2	H1	H2	I
817	*Eusarca*	*colorifera*	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-
2092	*Eusarca*	sp	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
181	*Eusarca*	sp	-	-	1	1	-	-	1	-	25	1	5	10	3	-	17
2073	*'Eustenophasma'*	*constricta*	-	-	-	-	-	-	-	3	-	-	-	-	9	10	-
2075	*'Eustenophasma'*	*fuscata*	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-
2074	*'Eustenophasma'*	sp cf *violacea*	1	-	1	-	-	-	-	-	-	-	1	-	1	-	-
314	*Eutomopepla*	*rogenhoferi*	1	-	-	3	-	-	-	-	2	-	-	-	-	-	-
2040	*Fulgurodes*	*mayor*	1	2	-	4	-	-	-	-	-	-	1	-	-	2	1
2039	*Fulgurodes*	*panopea*	-	-	-	-	-	-	-	-	-	-	-	2	-	1	-
738	*Fulgurodes*	*perasata*	-	1	-	6	-	-	-	-	-	1	-	1	-	-	1
296	*Furcijuxta*	*emilia*	-	-	-	-	-	-	-	-	-	2	2	-	-	-	2
295	*Furcijuxta*	sp cf *mathilda*	-	1	-	-	-	-	-	-	-	2	-	2	-	-	-
265	*Glena*	sp cf *juga*	1	-	-	-	-	-	1	-	-	1	-	1	-	1	-
933	*Glena*	sp	-	-	-	-	-	-	1	-	-	-	2	-	3	1	-
808	*Gypsara*	*exularia*	5	5	-	5	1	1	1	3	1	5	3	-	8	4	-
86	*Herbita*	*aglausaria flavidiscata*	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
2037	*Herbita*	*hypolizon*	-	-	-	-	-	-	-	-	-	-	2	3	-	1	1
2035	*Herbita*	*ochriplaga*	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
2095	*Herbita*	sp 2095	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
2096	*Herbita*	sp cf *tucumana*	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
2088	*Herbita*	sp cf *reducta*	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
85	*Herbita*	*zarina*	1	-	-	-	-	1	-	-	3	1	2	2	-	1	8
84	*Herbita group 2*	*chiomaria*	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1
88	*Herbita group 3*	*decurtaria*	-	1	-	1	1	1	-	1	4	-	4	1	1	1	-
82	*Herbita group 3*	*dognini*	-	1	3	1	-	-	-	5	1	3	13	12	2	4	7
940	*Herbita group 3*	*opalizans*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
87	*Herbita group 3*	*tenebrica*	-	1	-	1	1	-	-	-	1	-	-	-	3	1	-
70	*Hygrochroma*	*nondina*	-	1	-	-	-	-	1	1	-	-	-	2	-	-	1
939	*Hygrochroma*	*olivinaria*	-	-	-	-	-	-	-	-	-	-	2	-	-	-	1
83	*Ira*	*somnolenta*	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-
730	*Iridopsis*	*anaisaria*	1	1	-	2	2	-	-	-	-	-	3	-	3	-	-
257	*Iridopsis*	*gaujoni*	4	3	4	1	2	1	-	3	-	3	2	2	2	2	1
260	*Iridopsis*	*huambaria*	-	-	-	2	-	-	-	-	1	-	-	-	-	-	-
263	*Iridopsis*	*litharia*	-	-	-	1	-	-	-	-	2	-	1	-	-	-	1
258	*Iridopsis*	*muscinaria*	-	-	-	3	-	-	1	-	-	-	-	-	1	-	1
261	*Iridopsis*	*nephotessares*	-	-	1	-	-	-	-	-	1	1	1	1	-	-	1
259	*Iridopsis*	*scolancala*	-	-	-	-	-	-	-	2	-	-	1	2	1	2	-
2098	*Iridopsis*	sp 2098	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
256	*Iridopsis*	sp cf *subnigrata*	4	-	5	-	2	2	1	2	-	5	5	4	3	2	3
262	*Iridopsis*	*subnigrata*	1	3	-	3	1	1	1	-	1	3	2	6	2	5	2
308	*Ischnopteris*	*brehmi*	-	-	-	-	-	-	-	-	-	1	2	2	-	4	2
1861	*Ischnopteris*	*chryses*	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
99	*'Isochromodes'*	*atristicta*	-	1	-	-	-	-	-	-	1	1	-	-	-	-	-
828	*Isochromodes*	*brumosa*	-	-	-	-	-	-	-	-	1	3	11	4	4	4	1
842	*Isochromodes*	*duplicata*	1	-	-	1	-	-	-	-	-	-	-	1	1	3	-
112	*Isochromodes*	*extimaria*	4	4	1	2	1	-	-	-	-	3	19	17	1	8	8
668	*Isochromodes*	*fallax*	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
109	*Isochromodes*	*fraterna*	1	3	-	5	-	-	1	1	9	-	9	10	3	10	7
103	*Isochromodes*	*palumbata*	2	4	4	-	1	1	-	-	4	4	19	19	7	4	3

ID	Genus	Species	A	B1	B2	C	D1	D2	E1	E2	F1	F2	G1	G2	H1	H2	I
113	*Isochromodes*	*pectinicornata*	-	2	1	-	-	-	-	-	2	1	3	5	2	3	-
98	*Isochromodes*	*polvoreata*	-	1	-	-	-	-	-	1	-	-	-	3	-	1	-
2123	*Isochromodes*	*rasata*	-	-	-	-	-	-	-	-	1	1	1	9	3	1	3
149	*Isochromodes*	*sabularia*	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-
105	*Isochromodes*	sp 04	-	-	-	-	-	-	-	1	2	-	1	1	2	4	2
106	*Isochromodes*	sp 05	3	4	3	4	-	-	1	1	5	6	20	14	6	6	9
115	*Isochromodes*	sp 14	-	-	-	-	-	-	-	-	1	-	2	2	-	2	2
693	*Isochromodes*	sp 24	-	-	-	-	-	-	-	-	-	-	1	1	-	1	-
829	*Isochromodes*	sp 26	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-
101	*Isochromodes*	sp cf *duplicata*	-	-	-	-	-	-	-	-	-	1	-	-	-	-	2
117	*Isochromodes*	sp cf *pectinicornata*	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
744	*Leuciris*	*institata*	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
301	*Leuculopsis*	sp cf *pulverulenta*	5	1	5	2	1	1	-	1	-	5	-	3	1	1	-
157	*Lobopola*	*cimarrona*	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
684	*Lobopola*	sp 04	1	-	1	-	-	-	1	-	-	-	-	-	-	1	-
690	*Lomographa*	*albifrons*	1	1	2	17	-	1	1	-	2	2	1	10	-	-	2
187	*Lomographa*	*bicineta*	4	1	-	2	-	-	-	2	1	8	2	7	-	3	5
190	*Lomographa*	*chartularia*	1	-	-	-	-	-	-	1	-	3	3	1	2	3	6
691	*Lomographa*	*circumvallaria*	1	3	4	-	-	-	-	-	1	6	8	25	1	4	11
2081	*Lomographa*	*rufifrons*	10	3	3	11	-	1	1	1	2	7	-	4	-	3	-
191	*Lomographa*	sp cf *chartularia* 01	-	-	1	-	-	-	1	2	1	3	9	15	-	-	6
2087	*Lomographa*	sp cf *chartularia* 02	-	-	-	-	-	-	-	-	1	1	1	-	-	-	1
192	*Lomographa*	*tributaria*	6	4	2	53	1	7	9	9	10	9	34	39	1	9	11
322	*'Loxaspilates'*	*torcida*	3	1	-	7	-	-	-	-	-	2	1	-	-	3	-
767	*Macaria*	*acutaria*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
685	*Macaria*	*bejucoaria*	-	-	1	1	1	-	-	-	-	-	1	-	1	-	1
172	*Macaria*	*lapidata*	-	1	3	1	-	-	-	3	2	2	6	4	7	2	1
768	*Macaria*	*lydia*	3	1	8	-	9	10	-	7	2	5	3	1	-	2	7
173	*Macaria*	*ostia*	2	-	-	-	1	-	1	3	-	1	4	6	3	3	3
2019	*Macaria*	*pernicata*	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
655	*Macaria*	*regulata*	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
763	*Macaria*	sp	-	-	-	-	-	1	-	2	-	2	-	1	-	-	-
174	*Macaria*	sp cf *indentata*	2	-	-	-	1	-	-	3	-	4	1	-	2	1	-
937	*Mallomus*	*galbanata*	1	-	-	1	6	2	1	2	2	1	5	1	2	3	2
790	*Mallomus*	*synopsioides*	2	3	-	9	-	-	1	1	-	2	-	1	-	2	-
2103	*Melanolophia*	*corza*	-	-	-	1	-	-	-	1	-	-	1	-	-	-	-
2066	*Melanolophia*	*mallea*	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-
974	*Melanolophia*	*musarana*	13	4	4	5	9	5	6	5	-	1	1	4	-	2	7
765	*Melanolophia*	*muscosa*	1	-	-	1	-	-	-	1	1	1	11	3	5	1	-
269	*Melanolophia*	*reducta meridiana*	-	1	-	1	-	-	-	-	-	-	-	-	2	-	-
271	*Melanolophia*	sp 01	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1
2110	*Melanolophia*	sp cf *trisurca*	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
270	*Melanolophia*	*trisurca*	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
220	*Melanoscia*	*felina*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
219	*Melanoscia*	*thiaucourti*	-	1	-	-	-	-	-	-	-	-	-	-	-	-	4
918	*Melinodes*	*albarita*	-	-	-	1	-	-	1	-	-	1	1	-	-	-	2
160	*Melinodes*	*detersaria*	1	-	-	-	-	-	-	2	-	-	1	-	-	-	-

ID	Genus	Species	A	B1	B2	C	D1	D2	E1	E2	F1	F2	G1	G2	H1	H2	I
331	*Melinodes*	*saeta*	5	1	4	11	-	1	5	5	31	13	34	6	16	14	13
916	*'Melinodes'*	sp cf *ignea*	1	-	-	-	-	-	-	-	-	-	2	2	5	7	3
182	*Mesedra*	*attenuata*	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
177	*Mesedra*	*munda*	-	1	-	-	-	-	-	-	1	1	1	-	1	1	1
180	*Mesedra*	sp 01	-	2	2	1	1	1	-	-	-	1	2	8	-	-	4
178	*Mesedra*	sp cf *confinis* 03N	1	-	-	-	-	1	1	-	2	1	-	2	1	-	2
159	*Microxydia*	*colorata*	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-
2045	*Microxydia*	*orsitaria*	2	-	-	1	-	-	1	2	4	2	-	3	2	1	3
1833	*Microxydia*	*ruficomma*	10	28	2	12	1	5	23	38	9	14	18	15	2	9	5
838	*Mimosema*	sp cf *sobrina*	12	9	5	25	1	4	6	10	15	15	8	6	2	5	4
805	*Microxydia*	*strigosa*	10	2	-	2	-	-	2	1	5	1	13	9	1	10	2
2046	*Microxydia*	*trigonifera*	1	2	1	6	2	2	1	15	40	7	8	33	1	4	6
129	*Mimosema*	*versilinea*	-	-	-	-	-	-	-	-	2	1	1	3	2	-	3
2069	*Minyolophia*	sp 2069	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
166	*Mychonia*	*corticinaria*	-	-	1	-	-	-	-	-	-	1	-	-	2	-	-
215	*Mychonia*	*galanata*	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
2070	*Mychonia*	*graphica*	-	-	-	-	-	-	-	-	1	-	1	-	-	-	1
546	*Mychonia*	sp 546	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-
921	*Mychonia*	*violacea*	-	1	-	3	-	-	2	3	3	4	14	5	2	2	5
722	*Myrmecophantes*	*albifascia*	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-
861	*Narragodes*	*ochreata*	1	-	-	-	-	-	-	8	-	1	4	2	1	3	2
303	*Nazca*	*indentata*	1	1	3	-	-	-	-	-	1	2	6	4	2	2	12
170	*Neazata*	*fragilis*	-	-	-	-	-	-	-	-	-	-	-	1	-	1	1
2162	*Neazata*	*stabilis*	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
130	*Nematocampa*	sp cf *falsa*	1	-	2	1	-	-	1	1	-	1	6	2	7	2	2
332	*'Nematocampa'*	sp cf *confusa*	1	-	3	1	-	-	-	-	2	2	7	4	2	2	2
287	*Neodora*	*costinotata*	-	-	-	-	-	1	-	2	-	-	1	-	-	-	1
286	*Neodora*	*glaucularia*	7	2	3	3	1	2	3	3	-	8	12	10	4	4	8
500	*Neofidonia*	*nigristigma*	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2100	*Neotherina*	*consequens*	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
810	*Nephodia*	*clara*	2	1	2	3	-	-	2	1	1	7	5	5	10	9	1
769	*Nephodia*	*crata*	3	1	1	-	-	-	-	3	-	1	1	-	-	-	5
2064	*Nephodia*	*exclamationis*	-	1	-	2	-	-	1	1	-	-	3	-	-	2	6
218	*Nephodia*	*fumilinea*	1	-	-	-	-	1	-	-	-	-	1	4	1	5	2
213	*'Nephodia'*	*fumosata*	-	1	-	-	-	-	-	1	2	1	3	4	3	5	-
212	*Nephodia*	*illota*	1	1	-	-	2	1	2	1	-	-	-	-	-	-	1
849	*Nephodia*	*nudata*	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
2125	*Nephodia*	*panacea*	1	1	-	3	-	-	-	-	1	2	4	2	1	2	1
205	*Nephodia*	*pania*	1	3	-	2	-	-	-	1	1	-	4	1	1	7	4
203	*Nephodia*	*pecalba*	1	-	-	1	-	-	-	1	-	1	1	-	2	1	4
207	*Nephodia*	*pellucenta*	5	-	-	1	-	-	-	-	-	-	-	-	-	-	-
206	*Nephodia*	*sororcula*	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
209	*Nephodia*	sp 03	1	1	-	1	-	-	-	1	1	1	2	4	5	3	1
2124	*Nephodia*	sp 2124	6	2	-	1	-	-	1	1	-	-	-	-	-	-	2
299	*Nephodia*	sp cf *astyochiodes*	3	-	3	-	1	-	-	1	2	2	4	2	3	1	9
214	*Nephodia*	sp cf *exclamationis*	2	-	1	13	-	1	-	-	-	-	-	-	-	1	3
204	*'Nephodia'*	sp cf *organa*	4	3	1	3	1	-	-	5	-	-	5	5	4	12	6
2063	*Nephodia*	*transducta*	-	-	1	-	-	-	-	-	-	-	-	-	1	-	1
770	*Nephodia*	*trisecta*	-	-	-	2	-	-	-	-	-	1	-	3	1	2	-

ID	**Genus**	**Species**	**A**	**B1**	**B2**	**C**	**D1**	**D2**	**E1**	**E2**	**F1**	**F2**	**G1**	**G2**	**H1**	**H2**	**I**
688	*Nephodia*	*turpis*	-	-	1	-	-	-	-	-	2	-	1	1	-	-	-
773	*Nephodia*	*vestigiata*	1	2	1	-	-	-	-	-	-	1	-	-	-	2	4
2014	*Nepitia*	*detractaria*	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-
2002	*Neuromelia*	*sericea*	1	-	-	-	-	-	1	-	-	1	-	-	-	-	-
145	*Oenoptila*	*costata*	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
131	*'Oenoptila'*	*leprosata*	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
981	*Oenoptila*	*recessa*	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
2047	*Oenoptila*	sp 2047	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
132	*'Oenoptila'*	sp cf *filata*	2	-	-	1	1	1	-	1	2	4	1	4	-	-	5
2048	*Oenoptila*	sp cf *prunicolor*	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
142	*Oenoptila*	sp cf *separata*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
231	*Opisthoxia*	*archidiaria*	-	-	-	-	-	-	-	1	-	1	2	4	3	3	2
233	*Opisthoxia*	*branickiaria*	-	-	-	-	-	-	1	-	-	-	3	-	-	1	-
234	*Opisthoxia*	*descimoni*	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-
228	*Opisthoxia*	*metargyria*	-	-	1	-	-	-	-	-	-	-	1	-	1	-	-
232	*Opisthoxia*	sp cf *danaeata*	3	3	-	1	-	-	-	1	3	2	8	2	2	1	8
2077	*Opisthoxia*	sp cf *laticlava*	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1
2041	*Oxydia*	*affinis*	-	-	-	-	-	-	-	-	1	1	-	-	1	1	2
59	*Oxydia*	*augusta*	2	1	1	16	-	2	4	-	-	-	-	-	-	1	3
1013	*Oxydia*	*distichata*	-	-	-	-	-	-	-	1	1	-	1	-	-	1	-
60	*Oxydia*	*geminata*	6	4	3	5	2	1	4	3	3	8	4	8	1	4	11
67	*Oxydia*	*herbertina*	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2004	*Oxydia*	*insolita*	-	-	1	-	1	-	-	-	-	-	-	2	-	-	-
65	*Oxydia*	*mexicata*	-	1	-	1	-	-	-	2	2	1	3	-	-	-	1
673	*Oxydia*	*nimbata*	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
61	*Oxydia*	*olivata*	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
71	*Oxydia*	*optima*	2	1	2	3	-	-	1	1	-	2	4	2	3	5	1
72	*Oxydia*	*scriptipennaria*	1	1	-	8	1	1	3	3	1	1	2	4	8	4	2
2009	*Oxydia*	sp 2009	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
64	*Oxydia*	sp cf *agliata*	-	-	-	-	-	-	-	-	-	-	1	-	-	2	-
2018	*Oxydia*	sp cf *agliata* 1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
68	*Oxydia*	*subdecorata*	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-
58	*Oxydia*	*trychiata*	8	4	10	13	2	5	9	14	6	15	45	11	29	38	38
297	*Pantherodes*	*colubraria viperaria*	25	24	4	1	21	26	-	33	6	9	7	5	4	3	14
298	*Pantherodes*	*conglomerata*	511	204	114	90	269	175	64	468	42	131	58	73	137	116	133
644	*Paragonia*	*cruraria*	-	1	-	-	-	-	-	-	1	-	1	-	-	-	-
313	*Patalene*	sp cf *hamulata*	-	-	-	1	-	-	-	1	-	1	2	1	1	-	2
649	*Patalene*	sp cf *hamulata*	1	-	-	1	-	-	-	-	-	-	-	1	1	1	2
164	*Periclina*	*apricaria*	-	1	-	1	-	-	-	1	1	-	-	-	-	-	-
162	*Periclina*	*rumiaria*	1	-	1	-	-	-	-	-	-	-	-	-	1	-	-
165	*Periclina*	sp cf *merana*	-	1	-	1	-	-	-	-	-	-	-	-	-	2	-
732	*Periclina*	sp cf *rumiaria*	3	-	-	1	-	-	1	-	-	-	1	-	1	-	-
2022	*Perissopteryx*	*delusa*	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
912	*Perissopteryx*	*raveni*	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
2020	*Perissopteryx*	sp 2020	-	1	-	-	-	-	-	-	1	-	1	1	-	2	1
2021	*Perissopteryx*	sp 2021	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
989	*Perissopteryx*	sp 989	-	-	-	1	1	1	-	-	2	-	1	3	4	3	1
995	*Perissopteryx*	sp 995	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-
154	*Perissopteryx*	sp cf *nigricomata*	6	9	10	1	8	15	3	20	2	9	29	75	22	29	8

ID	Genus	Species	A	B1	B2	C	D1	D2	E1	E2	F1	F2	G1	G2	H1	H2	I
2015	*Pero*	*alboculata*	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-
2013	*Pero*	*boa*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
239	*Pero*	*buckleyi*	2	5	9	15	-	5	2	3	5	7	10	4	4	4	14
248	*Pero*	*caustomeris*	1	-	-	-	2	2	-	1	-	2	6	7	-	-	8
686	*Pero*	*cyclodaria*	1	1	-	-	-	1	-	1	-	1	3	4	-	-	3
251	*Pero*	*maculicosta*	-	3	-	1	1	1	4	5	-	5	11	15	-	1	1
2012	*Pero*	*nucleata*	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-
472	*Pero*	*obtusaria*	-	1	-	-	21	14	-	-	-	-	-	-	-	-	-
245	*Pero*	*periculosaria*	-	2	-	19	-	1	-	3	-	-	-	-	-	-	1
237	*Pero*	*plenilunata*	5	7	6	6	-	-	2	4	5	9	12	12	11	18	17
2038	*Pero*	*poaphilaria*	2	-	1	1	-	-	1	2	1	2	3	1	-	-	-
924	*Pero*	*pretensa*	-	-	-	-	1	-	-	-	-	1	4	-	-	-	2
2122	*Pero*	*saturara*	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
246	*Pero*	*scitaria*	-	1	1	2	1	4	-	-	1	2	-	2	-	1	2
942	*Pero*	*semiusta*	-	17	3	4	2	8	3	4	6	13	15	8	2	6	9
833	*Pero*	*semiusta*	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1
928	*Pero*	sp 928	-	1	1	-	-	-	-	1	-	1	-	-	-	-	-
2097	*Pero*	sp cf *lindigi*	-	1	-	-	1	-	1	-	-	-	-	-	-	-	-
2079	*Pero*	sp cf *participa*	4	3	2	-	2	1	-	3	-	2	2	-	-	-	2
238	*Pero*	sp cf *rapinaria*	1	2	4	4	1	1	-	-	-	-	3	1	-	2	-
242	*Pero*	sp cf *tabitha*	1	3	-	-	3	-	-	-	1	2	6	2	-	2	2
244	*Pero*	*speciosata*	-	-	-	2	-	-	1	-	-	1	-	1	-	-	1
243	*Pero*	*trena*	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
247	*Pero*	*tricaria*	1	-	-	5	-	4	1	1	-	2	-	4	-	-	2
793	*Pero*	*tridenta*	-	3	-	-	4	-	1	-	-	1	1	3	-	1	3
792	*Pero*	*unfortunata*	-	4	1	-	1	2	-	4	-	1	3	5	-	1	2
2044	*Perusia*	*complicata*	-	-	-	3	-	-	-	-	-	-	-	-	-	1	-
812	*Perusia*	*praecisaria*	-	-	-	-	-	-	1	2	1	1	2	1	-	2	-
135	*Perusia*	sp 05N	1	-	-	1	-	-	1	2	-	-	-	1	-	-	-
136	*Perusia*	sp 06N	-	1	1	-	-	-	-	-	-	1	1	1	1	2	2
328	*Perusia*	*verticata*	2	9	1	9	6	8	6	11	8	8	7	19	-	1	14
147	*'Petelia'*	*anagogaria*	-	-	-	-	-	-	-	-	-	-	1	1	-	-	1
155	*'Petelia'*	*binigrata*	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
608	*'Petelia'*	*nigriplaga*	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
140	*'Petelia'*	*nummifera*	-	-	1	-	-	-	-	2	-	-	-	-	-	-	-
138	*'Petelia'*	*plagiata*	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
156	*'Petelia'*	*purpurea*	-	1	-	-	-	1	-	-	-	1	-	1	-	-	1
146	*'Petelia'*	sp	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-
121	*'Petelia'*	sp 02N	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
152	*'Petelia'*	sp 11	-	-	-	-	-	-	-	-	-	2	-	-	1	-	2
1025	*'Petelia'*	sp cf *interrupta*	1	-	1	-	-	-	-	-	-	-	-	1	-	-	-
2016	*Phaludia*	sp cf *xanthomelaena*	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1
802	*Phaludia*	*xanthomelaena*	1	-	1	1	-	-	-	-	-	-	5	1	2	2	4
716	*Pherotesia*	*coiffaiti*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
1183	*Pherotesia*	*potens*	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
197	*Pherotesia*	*subjecta*	-	-	3	-	-	-	-	-	-	1	-	1	-	-	2
226	*Phrygionis*	*flavilimes*	-	-	-	-	-	1	-	-	-	1	-	-	1	-	-
227	*Phrygionis*	*platinata*	-	2	2	-	-	-	-	1	1	1	5	4	-	3	2
225	*Phrygionis*	*polita*	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-

ID	Genus	Species	A	B1	B2	C	D1	D2	E1	E2	F1	F2	G1	G2	H1	H2	I
128	*Phyle*	*transglauca*	2	1	-	-	1	-	-	-	1	1	1	1	-	1	1
49	*Phyllodonta*	*caninata*	1	2	-	3	1	-	-	-	1	1	2	2	1	-	2
51	*Phyllodonta*	*cataphracta*	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
45	*Phyllodonta*	*flabellaria*	-	-	-	-	-	-	-	-	2	1	3	4	1	-	13
137	*Phyllodonta*	*muscilinea*	1	3	-	1	-	-	-	-	-	2	1	-	3	1	1
50	*Phyllodonta*	*obscura*	2	-	2	8	-	-	1	-	-	-	-	1	-	-	-
47	*Phyllodonta*	*semicava*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
1045	*Phyllodonta*	*songaria*	-	-	1	-	-	-	-	-	1	-	1	1	-	-	2
46	*Phyllodonta*	sp cf *flabellaria*	-	-	-	-	-	-	-	-	-	-	1	1	-	-	2
48	*Phyllodonta*	*succedens*	1	1	-	2	-	-	-	-	2	-	1	-	10	-	1
277	*Physocleora*	*castaneata*	-	-	-	-	-	-	1	-	-	-	3	-	3	-	-
281	*Physocleora*	*celosoides*	-	-	-	-	1	-	1	1	-	1	6	2	1	1	4
335	*Physocleora*	*enana*	-	-	1	-	1	-	3	-	-	2	1	-	1	-	4
336	*Physocleora*	*flaviplaga*	1	-	-	-	-	-	2	6	1	4	4	4	3	2	4
2084	*Physocleora*	*grisescens*	1	3	3	-	3	3	1	1	11	4	6	4	5	5	8
279	*Physocleora*	*latimedia*	-	-	-	3	-	1	-	1	-	-	2	1	3	2	1
334	*Physocleora*	*mniophilaria*	2	4	3	-	-	1	4	3	4	4	8	3	5	2	12
285	*Physocleora*	*piperacea*	1	-	2	-	-	-	-	-	1	4	-	-	-	-	2
333	*Physocleora*	*pulverata*	1	5	3	-	3	2	6	2	7	11	8	6	8	6	7
887	*Physocleora*	sp 07	9	21	8	3	9	6	9	7	28	37	40	21	27	29	30
2101	*Physocleora*	sp 2101	2	-	-	-	-	-	1	1	1	-	1	1	-	-	-
280	*Physocleora*	sp cf *accessilinea*	-	-	-	-	-	-	-	-	1	-	4	-	3	2	-
275	*Physocleora*	sp cf *delgada*	1	-	2	5	-	-	2	1	3	2	20	5	24	3	2
282	*Physocleora*	*warreni*	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1
230	*Pityeja*	*histrionaria*	-	-	-	1	-	-	-	-	-	-	1	-	-	-	1
89	*Prochoerodes*	*pilosa*	-	-	1	-	1	1	-	2	1	1	10	10	4	3	7
2027	*Pyrinia*	*cerocampata*	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
323	*Pyrinia*	*coearia*	-	2	8	-	1	1	-	-	4	4	1	-	-	1	-
839	*Pyrinia*	*divalis*	1	3	3	3	-	-	-	1	1	3	2	1	1	1	3
318	*Pyrinia*	*gallaria*	2	-	-	-	-	-	1	-	1	1	-	-	5	1	-
317	*Pyrinia*	*megara*	23	12	5	2	7	3	5	1	2	12	21	9	1	2	7
316	*Pyrinia*	sp 01	2	3	5	1	2	2	-	-	-	3	1	1	-	1	-
2108	*Pyrinia*	sp 2108	-	-	-	-	-	-	-	1	-	-	-	2	-	-	-
315	*Pyrinia*	sp cf *sanitaria*	3	1	-	-	1	-	-	-	1	-	1	-	-	-	2
309	*Rucana*	*abnormipalpis*	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-
660	*Rucana*	*bisecta*	-	-	-	-	-	-	-	-	1	-	-	-	1	1	-
2058	*Rucana*	*brunneoviridis*	1	-	-	-	1	-	-	-	-	-	1	-	1	-	1
311	*Rucana*	*degener*	-	1	-	-	-	-	-	-	1	-	2	1	-	-	-
2059	*Rucana*	*fidelis*	-	-	-	-	-	-	-	1	-	-	-	-	-	-	3
759	*Sabulodes*	*boarmidaria*	1	-	1	-	-	-	1	1	2	2	2	2	2	2	-
92	*Sabulodes*	*boliviaria*	-	-	1	-	-	1	1	-	1	2	5	1	1	4	3
93	*Sabulodes*	*caberata oberthuri*	1	3	-	1	-	-	8	4	4	8	15	14	1	6	4
2034	*'Sabulodes'*	*colombiata*	1	-	-	5	-	3	2	4	1	1	4	1	-	1	1
934	*'Sabulodes'*	*mima*	-	-	-	1	-	1	-	-	-	-	4	3	-	-	-
873	*'Sabulodes'*	*muscistrigata*	2	-	-	5	1	-	2	-	-	-	-	2	2	7	1
944	*Sabulodes*	*prolata*	-	-	3	1	-	1	-	1	-	4	4	8	-	2	5
2164	*Sabulodes*	sp 2164	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
990	*Sabulodes*	sp cf *carbina* 2	-	3	1	-	-	-	-	-	-	1	1	4	4	-	-
122	*Sabulodes*	sp cf *carbina* 3	2	2	3	-	-	-	-	3	2	2	22	33	2	9	5

ID	Genus	Species	A	B1	B2	C	D1	D2	E1	E2	F1	F2	G1	G2	H1	H2	I
183	*'Sabulodes'*	sp cf *lineata*	-	-	-	-	-	-	-	-	-	-	1	1	-	3	2
125	*Sabulodes*	*thermidora*	73	184	121	201	37	29	20	20	29	64	24	49	6	42	15
176	*'Semiothisa'*	*mayana*	1	2	1	-	1	2	-	-	6	8	1	-	-	-	-
175	*Semiothisa*	*radiata*	-	-	-	-	-	-	1	1	1	-	2	-	-	1	-
319	*'Semiothisa'*	*regressa*	3	-	2	5	-	-	3	-	2	5	2	1	2	1	2
202	*Sericoptera*	*mahometaria*	-	2	2	2	-	-	2	11	2	5	7	15	2	3	7
2005	*Sicya*	*dognini*	-	1	-	-	-	-	-	-	-	-	1	-	-	-	-
2006	*Sicya*	*inquinata*	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
689	*Sicya*	*pomona*	2	2	-	5	-	-	1	-	2	2	1	-	1	5	1
2036	*Simopteryx*	*liodesaria*	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2017	*Sphacelodes*	*studiosa*	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
91	*Sphacelodes*	*vulneraria*	-	-	-	-	-	-	-	-	2	-	1	-	-	-	2
310	*Stegotheca*	*costiplaga*	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
217	*Tarma*	*theodora*	-	1	1	-	-	-	-	1	-	-	1	1	-	-	2
2001	*'Thysanopyga'*	*fractimacula*	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
	Geometrinae																
370	*Cathydata*	*batina*	2	3	-	-	-	-	1	1	-	-	2	-	1	1	3
364	*Chavarriella*	*psittacina*	-	1	-	-	-	-	-	-	1	-	3	-	2	3	-
358	*Chloropteryx*	*opalaria*	7	27	3	3	4	1	14	34	10	25	50	34	4	23	10
959	*Chloropteryx*	sp cf *stigmatica*	-	2	-	1	2	-	1	3	2	4	9	11	2	8	3
343	*Hyalochlora*	*nadia*	1	4	-	1	1	-	-	-	-	4	1	3	-	-	6
368	*Hydata*	*projiciens*	2	-	-	-	-	-	-	-	-	1	-	-	-	-	-
369	*Hydata*	*stigmatica*	-	-	-	1	-	-	1	2	1	-	3	4	4	5	3
692	*Hydata*	*subfenestraria*	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
761	*Lissochlora*	*cecilia*	6	8	4	4	-	-	1	6	6	12	27	14	11	11	12
354	*Lissochlora*	*diarita*	-	2	1	-	1	-	1	1	1	-	12	2	1	5	6
351	*Lissochlora*	*hoffmannsi*	2	6	-	4	-	-	3	6	2	1	14	3	6	4	5
352	*Lissochlora*	*latuta*	5	7	10	2	-	-	1	4	4	17	36	24	18	21	21
2052	*Lissochlora*	*quotidiana*	1	2	-	1	-	-	1	2	-	-	2	-	1	3	-
2049	*Lissochlora*	*rufiguttata*	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
2051	*Lissochlora*	sp 2051	1	3	-	3	-	1	1	5	4	1	5	6	4	5	1
371	*Neagathia*	*corruptata*	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1
355	*Nemoria*	*aturia scotocephala*	9	6	11	2	3	-	1	2	-	6	9	6	3	2	5
353	*Nemoria*	*delicataria*	3	2	3	3	-	-	1	4	5	4	10	3	2	4	13
757	*Nemoria*	*erina*	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
340	*Nemoria*	*heterograpta*	1	1	2	-	-	-	1	1	1	1	-	-	1	1	1
346	*Nemoria*	*imitans*	2	1	1	7	-	-	2	5	1	1	6	2	-	3	-
345	*Nemoria*	*nigrisquama*	36	13	11	61	-	-	2	3	-	13	20	24	2	8	8
777	*Nemoria*	sp 04	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
1474	*Nemoria*	sp cf *aturia*	-	-	-	-	1	-	-	-	-	-	5	-	4	2	1
882	*Nemoria*	sp cf *erina*	-	1	1	1	-	1	-	2	2	-	1	1	-	-	2
349	*Nemoria*	sp cf *sellata*	1	2	-	-	1	1	-	5	-	3	4	3	-	3	6
363	*Oospila*	*asmura*	1	-	-	-	-	-	-	-	-	-	1	-	1	-	-
366	*Oospila*	*atroviridis*	2	-	1	-	-	2	1	-	-	2	-	-	-	1	1
362	*Oospila*	*concinna*	1	-	3	1	-	2	-	3	1	-	1	-	1	-	5
344	*Oospila*	*ecuadorata*	2	-	3	2	-	-	1	1	4	2	6	2	-	3	8
1427	*Oospila*	*holochroa*	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-
365	*Oospila*	*lacteguttata*	-	-	2	-	-	-	1	2	-	-	-	-	-	1	-
367	*Oospila*	*lunicincta*	2	2	-	-	-	-	-	-	1	-	2	-	3	-	3

ID	Genus	Species	A	B1	B2	C	D1	D2	E1	E2	F1	F2	G1	G2	H1	H2	I
1423	*Oospila*	*stagonata*	2	-	-	-	-	-	-	2	-	-	2	1	-	-	-
2050	*'Phrudocentra'*	*niveiceps*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3
360	*Phrudocentra*	*subaurata*	5	3	3	1	1	1	2	4	1	1	3	3	-	1	2
341	*Poecilochlora*	*minor*	1	1	2	-	-	-	-	-	1	-	1	-	2	1	2
1438	*Pyrochlora*	*rhanis*	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
342	*Rhodochlora*	*roseipalpis*	1	8	1	4	-	-	4	1	1	4	5	4	1	3	21
347	*Synchlora*	*amplimaculata dependens*	6	8	2	1	-	1	4	8	4	6	6	6	3	5	10
611	*Synchlora*	*tumefacta*	5	8	7	5	3	2	3	11	6	21	23	12	7	5	15
350	*Synchlora*	*gerularia*	2	2	-	-	2	1	2	1	2	-	3	3	-	2	4
359	*Telotheta*	*muscipunctata*	3	5	1	4	1	-	3	2	3	14	9	1	11	8	1
	Larentiinae																
438	*Brabirodes*	*cerevia*	-	-	-	-	-	-	-	1	-	1	2	-	-	-	1
429	*Callipia*	*parrhasiata*	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
2120	*Callipia*	*rosetta*	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1
985	*Callipia*	sp	1	-	-	-	-	-	-	-	-	2	-	-	-	-	3
458	*Deinoptila*	*penicula*	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-
439	*Dyspteris*	*breviataria*	-	1	-	-	-	-	-	-	-	-	-	2	-	-	2
391	*Eois*	*amarillada*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
376	*Eois*	*angulata*	1	-	-	-	-	-	-	1	-	1	3	1	2	-	-
799	*Eois*	*antiopata*	1	-	-	-	-	-	-	-	-	-	1	-	-	-	1
397	*Eois*	*azafranata*	2	1	-	2	-	-	-	2	2	4	4	17	2	1	6
401	*Eois*	*basaliata*	2	-	-	3	1	-	2	-	2	-	2	-	1	-	1
710	*Eois*	*binaria*	-	-	-	-	-	-	-	-	1	1	2	2	3	4	1
410	*Eois*	*biradiata*	2	-	-	-	-	-	-	-	-	-	1	1	3	-	1
396	*Eois*	*borrata*	8	12	5	4	2	-	-	2	8	19	8	7	10	14	28
385	*Eois*	*burla*	8	3	3	3	2	1	-	2	6	15	2	10	2	10	24
386	*Eois*	*cancellata*	1	1	-	1	-	-	-	1	1	-	-	-	-	-	1
389	*Eois*	*carrasca*	-	-	-	-	-	-	-	-	-	1	-	1	1	1	2
392	*Eois*	*chasca*	1	1	3	1	-	-	1	3	-	3	1	2	6	1	7
1029	*Eois*	*chrysocraspedata*	4	3	3	2	1	1	-	1	-	10	11	6	143	8	2
403	*Eois*	*ciocolatina*	2	1	-	6	2	-	3	1	2	2	4	2	20	25	1
1695	*Eois*	*concatenata*	-	-	-	-	-	-	-	-	-	-	-	7	4	-	-
378	*Eois*	*encina*	1	-	-	-	-	-	-	1	1	1	2	-	6	1	1
390	*Eois*	*escamata*	-	-	-	-	-	-	-	-	-	1	1	-	1	2	1
374	*Eois*	*golosata*	3	2	3	2	-	-	-	1	-	4	2	1	1	2	9
381	*Eois*	*goodmani*	1	2	2	4	1	-	2	-	2	7	12	11	16	8	5
2031	*Eois*	*hermosaria*	-	1	-	1	-	1	-	-	-	-	-	1	-	1	-
384	*Eois*	*lucivittata*	1	1	2	-	-	2	-	4	3	-	4	1	-	2	-
398	*Eois*	*margarita*	4	9	6	4	-	2	1	5	3	8	12	10	3	5	32
413	*Eois*	*mediostrigata*	4	-	-	9	1	-	-	1	1	-	1	-	3	1	-
803	*Eois*	*muscosa*	1	-	-	-	-	-	-	1	-	2	1	1	7	7	1
387	*Eois*	*nigricosta*	7	2	-	-	-	-	-	4	-	2	-	1	1	1	2
388	*Eois*	*nigrosticta*	-	-	-	-	-	-	-	-	-	1	-	-	-	1	1
404	*Eois*	*obada*	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
818	*Eois*	*odatis*	1	-	-	-	1	-	1	-	1	3	1	1	-	1	-
416	*Eois*	*olivacea*	2	4	1	5	3	4	4	7	2	6	7	7	11	6	8
1023	*Eois*	*pallidicosta*	-	1	-	-	-	-	-	-	-	2	-	-	-	-	3
424	*Eois*	*paraviolascens*	10	4	5	1	1	1	5	5	2	35	44	15	162	10	11
696	*Eois*	*paulona*	-	-	1	-	1	-	-	4	1	3	5	7	2	4	5

ID	Genus	Species	A	B1	B2	C	D1	D2	E1	E2	F1	F2	G1	G2	H1	H2	I
425	*Eois*	*plana*	4	1	2	2	1	2	-	4	4	8	5	3	56	2	4
383	*Eois*	*planetaria*	-	-	-	-	-	-	-	-	-	-	2	-	-	-	1
2030	*Eois*	*rubiada*	-	1	1	-	-	1	1	2	-	-	-	1	-	-	2
377	*Eois*	*sagittaria*	5	1	-	-	-	-	-	-	-	2	-	2	-	-	-
382	*Eois*	sp	-	-	1	-	-	-	-	-	-	-	-	-	-	-	2
409	*Eois*	sp 09	1	1	-	2	-	-	3	-	-	-	-	1	4	2	1
420	*Eois*	sp 14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
427	*Eois*	sp 16	-	-	-	-	-	-	-	-	-	-	-	2	1	2	-
708	*Eois*	sp 18	1	-	-	-	-	-	-	2	-	-	-	-	3	-	2
706	*Eois*	sp 19	-	-	-	1	-	-	-	-	-	1	1	-	1	-	-
2117	*Eois*	sp 2117	-	1	-	-	-	-	-	1	1	-	-	-	9	4	1
2126	*Eois*	sp 2126	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
2127	*Eois*	sp 2127	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
2128	*Eois*	sp 2128	2	-	-	-	1	-	-	3	-	-	1	-	1	2	2
2129	*Eois*	sp 2129	-	1	-	-	1	1	-	-	-	-	-	-	-	2	-
2130	*Eois*	sp 2130	1	-	-	-	-	-	-	-	-	1	-	-	-	-	-
2131	*Eois*	sp 2131	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
2132	*Eois*	sp 2132	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2133	*Eois*	sp 2133	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-
820	*Eois*	sp 30	5	-	1	1	5	1	1	5	-	3	3	8	1	1	3
399	*Eois*	sp cf *adimaria*	-	1	2	-	-	-	-	1	-	-	-	-	1	-	-
1033	*Eois*	sp cf *apyraria*	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-
426	*Eois*	sp cf *catana*	1	3	1	1	-	-	-	1	-	1	-	-	-	-	-
423	*Eois*	sp cf *dorisaria*	-	-	-	-	-	-	-	-	-	1	-	-	6	2	1
412	*Eois*	sp cf *encina*	9	-	-	2	1	1	-	2	1	1	-	1	6	2	-
394	*Eois*	sp cf *fucosa*	2	2	-	5	-	2	2	-	4	1	11	18	31	12	1
402	*Eois*	sp cf *inflammata*	1	1	-	-	-	2	-	-	-	-	-	-	-	-	3
515	*Eois*	sp cf *inflammata*	1	2	-	1	-	-	-	1	1	-	3	-	3	1	-
935	*Eois*	sp cf *insignata*	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
411	*Eois*	sp cf *lunifera*	-	-	-	-	-	-	-	-	-	-	1	3	2	2	1
419	*Eois*	sp cf *odatis*	1	3	-	-	2	-	-	-	2	1	5	9	10	9	3
408	*Eois*	sp cf *olivaria*	1	-	-	1	-	-	-	1	-	-	-	-	1	1	1
379	*Eois*	sp cf *sagittaria*	-	-	-	1	-	-	-	1	-	-	-	-	-	1	-
961	*Eois*	sp cf *tegularia*	-	-	-	-	-	-	-	-	-	1	1	1	1	2	-
889	*Eois*	*subpallida*	1	-	-	-	-	-	-	2	-	-	-	-	-	-	-
836	*Eois*	*tegularia*	3	3	3	2	1	1	-	6	3	4	23	40	16	12	3
414	*Eois*	*trillista*	1	1	-	2	-	-	-	-	-	1	-	4	-	1	2
709	*Eois*	*vinosata*	-	-	-	-	-	-	-	-	-	1	3	5	1	-	1
422	*Eois*	*xanthoperata*	-	-	-	-	2	-	-	-	-	1	-	-	2	-	-
1059	*Erateina*	*artabates*	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
2118	*Erebochlora*	*cerasii*	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
2042	*Eubaphe*	sp 2042	-	1	-	-	-	-	-	-	-	-	1	6	1	5	3
1049	*Eubaphe*	*tritonia*	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
482	*Euphyia*	*aguada*	1	3	-	-	84	39	2	4	-	1	-	2	-	1	-
480	*Euphyia*	*alboscripta*	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
457	*Euphyia*	*cinerascens*	-	-	-	1	-	-	1	-	-	1	3	1	5	6	-
1043	*Euphyia*	*cocama*	-	-	-	-	1	-	-	1	-	-	-	-	-	1	-
453	*Euphyia*	*consequata*	-	-	-	-	-	-	-	1	1	-	1	3	1	4	1
2104	*Euphyia*	*gustosa*	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-

ID	Genus	Species	A	B1	B2	C	D1	D2	E1	E2	F1	F2	G1	G2	H1	H2	I
952	*Euphyia*	*infundibulata*	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1
2054	*Euphyia*	*kirschi*	-	-	1	-	-	-	-	-	-	-	-	-	-	1	-
830	*Euphyia*	*porraceata*	-	-	1	-	-	-	-	-	-	-	1	7	2	1	1
466	*Euphyia*	*rojiza*	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
2067	*Euphyia*	sp 2067	1	-	-	-	1	1	-	1	-	-	-	-	-	-	-
2107	*Euphyia*	sp 2107	-	-	-	-	-	-	-	-	-	-	-	-	2	1	-
2155	*Euphyia*	sp 2155	-	1	-	-	-	-	-	-	-	-	-	3	-	-	-
2156	*Euphyia*	sp 2156	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
2157	*Euphyia*	sp 2157	-	-	-	1	1	1	-	-	-	-	-	1	-	-	-
841	*Euphyia*	sp cf *acerbata*	-	3	-	-	-	-	-	4	-	1	-	-	-	-	1
462	*Euphyia*	sp cf *fringillata*	-	-	-	-	1	-	-	-	-	3	-	-	-	1	1
1504	*Euphyia*	*sturnularia*	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
2116	*Euphyia*	*subalbata*	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
460	*Euphyia*	*subguttaria*	13	1	6	4	13	12	2	19	2	6	1	1	3	2	8
2060	*Euphyia*	*subtersignata*	1	1	3	1	3	2	1	2	2	1	5	19	4	11	3
2109	*Euphyia*	*subvinosa*	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
452	*Euphyia*	*trujillaria*	-	1	-	2	-	-	1	1	-	-	2	5	2	6	2
813	*Euphyia*	*violetta*	1	-	-	-	-	2	-	4	-	-	4	2	2	1	1
471	*Euphyia*	*zara*	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
577	*Eupithecia*	*albirasa*	-	1	-	-	-	-	-	-	-	1	-	1	1	-	-
623	*Eupithecia*	*anita*	1	12	1	9	-	5	2	13	1	-	14	32	3	4	8
705	*Eupithecia*	*bullata*	-	-	-	-	-	1	2	6	-	-	4	2	1	1	-
554	*Eupithecia*	*casta*	-	1	1	-	-	-	-	-	-	-	2	-	-	-	1
566	*Eupithecia*	*cunina*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
652	*Eupithecia*	*cupreata*	1	-	-	-	2	-	-	-	-	-	1	-	-	-	1
575	*Eupithecia*	*drastica*	-	2	2	2	-	1	-	-	2	1	1	1	-	2	3
556	*Eupithecia*	*duena*	3	2	9	1	8	3	-	1	7	3	-	1	-	1	9
557	*Eupithecia*	*galepsa*	1	3	-	-	-	-	-	1	-	2	2	1	-	-	3
677	*Eupithecia*	*higa*	6	5	3	5	2	-	2	1	3	1	1	2	-	2	1
617	*Eupithecia*	*hippolyte*	1	-	1	-	-	2	-	3	-	-	2	-	2	1	3
569	*Eupithecia*	*hormiga*	19	2	-	8	-	7	5	7	4	7	3	1	1	1	4
563	*Eupithecia*	*lachaumei*	-	6	4	2	6	6	2	9	5	9	11	2	2	5	15
681	*Eupithecia*	*linda*	1	1	-	-	-	-	-	-	-	-	-	-	4	-	-
661	*Eupithecia*	*nigrithorax*	3	1	19	2	7	7	4	5	4	25	7	7	1	1	6
653	*Eupithecia*	*nigrodiscata*	-	-	-	-	-	2	1	1	-	2	7	7	-	1	4
614	*Eupithecia*	*ochrosoma*	-	2	3	1	-	-	-	-	-	-	-	1	-	-	1
648	*Eupithecia*	*pallidicosta*	-	-	1	-	1	1	-	-	2	2	3	-	1	2	7
607	*Eupithecia*	*parallaxis*	2	2	1	2	-	1	1	1	-	5	9	9	2	6	1
562	*Eupithecia*	*penicilla*	-	-	-	-	1	1	1	-	-	6	-	2	1	3	1
896	*Eupithecia*	*philippis*	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
550	*Eupithecia*	*rubellicincta*	11	11	2	9	1	1	-	3	-	3	5	11	-	6	8
560	*Eupithecia*	*scione*	-	-	-	-	-	-	-	-	-	1	2	1	-	1	1
674	*Eupithecia*	*sobria*	13	7	6	5	4	3	-	1	-	1	-	3	-	-	1
663	*Eupithecia*	*sorda*	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
578	*Eupithecia*	sp 02	24	18	12	7	10	10	2	8	5	8	6	9	5	4	13
580	*Eupithecia*	sp 04	-	-	-	1	1	-	-	-	-	2	3	3	2	2	1
581	*Eupithecia*	sp 05	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
585	*Eupithecia*	sp 09	-	-	-	-	1	-	-	-	-	-	2	-	2	-	-
899	*Eupithecia*	sp 127	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-

ID	Genus	Species	A	B1	B2	C	D1	D2	E1	E2	F1	F2	G1	G2	H1	H2	I
900	*Eupithecia*	sp 128	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-
2137	*Eupithecia*	sp 2137	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2138	*Eupithecia*	sp 2138	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
2139	*Eupithecia*	sp 2139	-	4	1	-	4	-	-	2	-	-	3	1	-	1	2
2140	*Eupithecia*	sp 2140	-	-	-	-	-	-	1	-	-	-	2	-	-	-	-
2141	*Eupithecia*	sp 2141	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1
2142	*Eupithecia*	sp 2142	-	-	2	2	-	-	-	-	2	2	1	4	7	-	1
2143	*Eupithecia*	sp 2143	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
2144	*Eupithecia*	sp 2144	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
2145	*Eupithecia*	sp 2145	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
2146	*Eupithecia*	sp 2146	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
2147	*Eupithecia*	sp 2147	1	-	-	-	-	-	-	-	1	-	1	-	-	-	-
2148	*Eupithecia*	sp 2148	-	-	-	-	-	1	1	-	-	1	-	2	-	-	-
599	*Eupithecia*	sp 23	1	-	-	-	-	-	-	-	-	-	-	-	1	1	1
602	*Eupithecia*	sp 26	-	-	-	-	-	-	1	-	-	1	-	-	-	1	-
522	*Eupithecia*	sp 27	-	-	1	-	-	-	-	-	-	1	-	3	1	1	-
609	*Eupithecia*	sp 32	-	-	-	5	-	-	-	-	-	1	-	-	1	-	-
651	*Eupithecia*	sp 34N	1	2	-	-	-	1	-	-	-	1	-	1	1	-	2
620	*Eupithecia*	sp 43	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
622	*Eupithecia*	sp 45	4	4	-	2	4	-	1	4	9	6	2	8	1	-	12
624	*Eupithecia*	sp 47	1	4	4	7	8	-	5	7	-	8	4	2	-	2	4
629	*Eupithecia*	sp 52	3	4	2	-	3	1	-	1	-	-	2	1	-	1	1
635	*Eupithecia*	sp 58	-	-	2	-	-	-	-	-	-	2	1	-	-	-	-
645	*Eupithecia*	sp 67	-	4	1	1	3	1	3	2	3	2	1	4	3	2	3
646	*Eupithecia*	sp 68	-	-	-	-	-	-	2	-	-	1	-	1	-	-	1
658	*Eupithecia*	sp 80	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
662	*Eupithecia*	sp 84	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
664	*Eupithecia*	sp 86	-	3	10	2	5	1	1	8	1	7	5	4	-	6	9
666	*Eupithecia*	sp 88	-	1	6	3	6	3	1	4	2	9	-	1	-	1	5
669	*Eupithecia*	sp 91	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
671	*Eupithecia*	sp 93	2	-	6	3	2	-	1	1	1	3	-	2	3	2	-
572	*Eupithecia*	sp cf *contexta*	5	-	5	1	1	2	-	-	-	8	6	3	1	3	10
573	*Eupithecia*	sp cf *contexta* 1	-	-	2	1	1	1	-	1	2	3	-	2	3	1	3
574	*Eupithecia*	sp cf *contexta* 2	4	1	-	3	2	-	1	-	-	1	2	2	-	2	-
576	*Eupithecia*	sp cf *idalia*	-	2	-	3	-	-	-	1	2	1	2	6	3	1	-
565	*Eupithecia*	sp cf *junctifascia*	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-
552	*Eupithecia*	sp cf *madura*	2	2	1	-	5	-	1	-	1	1	5	-	-	-	2
2082	*Eupithecia*	sp cf *muralla*	-	-	-	-	1	-	-	-	-	-	-	1	-	-	1
561	*Eupithecia*	sp cf *penicilla*	1	1	1	3	1	-	2	1	3	-	-	-	3	-	1
551	*Eupithecia*	sp cf *rubellicincta* 1	1	3	-	-	-	1	1	-	2	-	1	4	-	1	-
702	*Eupithecia*	sp cf *rubellicincta* 3	13	10	7	21	1	2	6	5	3	6	2	7	3	4	2
555	*Eupithecia*	sp cf *sobria*	9	15	6	3	4	2	3	8	3	5	4	2	2	1	4
2083	*Eupithecia*	sp cf *subtilis*	1	-	1	-	-	-	1	-	-	-	-	-	1	-	1
1581	*Eupithecia*	*tremula*	-	-	1	-	-	-	-	-	-	1	-	-	1	-	-
558	*Eupithecia*	*triangulifera*	-	-	1	-	-	-	-	1	1	-	-	-	-	-	1
568	*Eupithecia*	*trigenuata*	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-
2111	*Eupithecia*	*turbanata*	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1
570	*Eupithecia*	*versiplaga*	-	1	-	-	2	-	1	1	-	1	1	3	-	1	1

ID	Genus	Species	A	B1	B2	C	D1	D2	E1	E2	F1	F2	G1	G2	H1	H2	I
667	*Eupithecia*	*yangana*	15	30	14	18	9	6	1	3	3	17	2	8	3	2	4
430	*Graphidipus*	*flaviceps*	4	15	2	4	6	1	7	14	13	8	5	2	2	10	4
2113	*Graphidipus*	*fulvicostaria*	-	2	-	-	-	-	-	-	-	-	-	-	-	1	-
431	*Graphidipus*	*graphidiparia*	1	-	-	3	1	-	1	-	-	-	-	-	-	-	-
435	*Hagnagora*	*anicata*	-	2	1	-	-	-	1	4	-	-	5	2	2	2	4
434	*Hagnagora*	*croceitincta*	3	11	1	-	1	-	-	5	1	9	12	-	1	3	16
433	*Hagnagora*	*ephestris*	1	7	7	-	-	5	1	18	2	8	17	11	3	1	8
436	*Hagnagora*	*mortipax*	1	3	-	-	-	-	-	1	-	5	14	4	2	6	4
2078	*Hagnagora*	sp 2078	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
1042	*Hammaptera*	*ignifera*	-	-	-	-	-	-	-	1	-	3	2	9	1	3	-
468	*Hammaptera*	*praderia*	-	-	1	1	2	1	-	3	1	1	-	5	1	4	1
956	*Hammaptera*	*repandaria*	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-
2115	*Hammaptera*	sp 2115	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
469	*Hammaptera*	sp 469	1	1	-	-	1	3	-	3	2	1	9	31	-	9	3
2091	*Heterusia*	sp 2091	-	-	1	1	1	-	-	-	6	1	4	1	2	-	-
479	*Hydriomena*	*praelatata*	2	3	-	1	-	-	-	3	-	3	-	-	-	-	3
478	*Hydriomena*	sp 03	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
476	*Hydriomena*	sp cf *algosa*	1	2	-	2	-	1	-	-	-	1	-	5	3	1	2
475	*Hydriomena*	sp cf *cydra*	8	1	2	8	2	-	1	1	3	2	3	1	7	1	4
474	*Hydriomena*	sp cf *polyphonta*	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-
1068	*Hydriomena*	*vanonaria*	-	-	-	-	-	1	-	-	-	-	2	10	6	11	5
2150	*Larentiinae*	sp 2150	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2151	*Larentiinae*	sp 2151	-	-	-	1	1	1	-	1	1	-	1	-	-	1	-
2154	*Larentiinae*	sp 2154	-	-	-	-	-	-	-	-	1	-	-	-	-	-	2
2158	*Larentiinae*	sp 2158	1	-	-	-	-	-	-	-	-	1	-	-	-	-	-
951	*Obila*	*umbrinata*	-	-	2	1	1	-	-	-	1	2	1	-	-	-	-
1279	*Oligopleura*	*aulaeata*	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
442	*Orthonama*	*coneja*	1	-	-	1	-	1	-	-	-	-	-	-	1	1	-
441	*Orthonama*	*effluata*	6	2	2	2	5	10	5	10	1	1	1	5	-	-	5
2152	*Orthonama*	sp 2152	-	-	-	-	-	1	-	-	-	-	1	-	1	1	1
445	*Orthonama*	sp 445	2	1	-	4	5	2	-	2	-	-	-	-	-	1	-
984	*Perizoma*	*arcillata*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
492	*Perizoma*	*basiplaga*	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-
537	*Perizoma*	*cinerolimitata*	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-
486	*Perizoma*	*emmelesiata*	3	1	5	45	12	12	16	28	8	14	2	5	1	2	7
487	*Perizoma*	*zenobia*	29	15	39	39	6	3	9	11	7	40	3	3	-	3	6
894	*Pocophora*	*rufisticta*	-	-	-	-	1	1	-	3	-	3	-	3	-	-	-
489	*Psaliodes*	*albifascia*	1	1	-	1	-	-	-	2	-	-	-	-	3	-	4
511	*Psaliodes*	*aurativena*	-	1	-	-	-	-	-	-	-	2	-	1	1	-	-
549	*Psaliodes*	*biconalis*	-	-	-	-	-	-	-	-	2	1	-	2	2	-	5
524	*Psaliodes*	*castanea*	-	-	-	-	-	-	-	-	1	2	2	1	1	1	-
496	*Psaliodes*	*catenifera*	-	6	1	-	1	3	-	-	4	5	-	-	3	-	3
539	*Psaliodes*	*cedaza*	1	4	3	1	2	-	2	1	3	3	5	3	1	3	14
538	*Psaliodes*	*confusa*	1	-	-	-	-	-	-	-	2	-	1	3	-	-	-
532	*Psaliodes*	*crassinota*	2	-	1	-	1	-	-	-	-	-	1	-	-	-	1
545	*Psaliodes*	*cupreipennis*	-	-	-	-	1	-	-	-	1	1	-	-	7	1	3
523	*Psaliodes*	*cynthia*	1	2	2	-	-	-	-	-	1	2	8	6	9	5	3
531	*Psaliodes*	*detractata*	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-
100	*Psaliodes*	*infantula*	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-

ID	Genus	Species	A	B1	B2	C	D1	D2	E1	E2	F1	F2	G1	G2	H1	H2	I
488	*Psaliodes*	*inundulata*	6	6	9	2	9	8	3	12	17	27	9	7	1	-	15
542	*Psaliodes*	*liebra*	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
863	*Psaliodes*	*lignosata*	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
509	*Psaliodes*	*miniata*	1	1	2	-	-	-	-	-	1	3	3	7	2	3	8
699	*Psaliodes*	*nexilinea*	-	-	-	-	-	-	-	1	1	-	-	-	2	-	-
698	*Psaliodes*	*nictitans*	-	-	-	1	-	-	-	-	-	-	2	-	-	-	4
2032	*Psaliodes*	*nivestrota*	-	-	-	2	-	-	1	-	-	-	-	1	-	-	-
534	*Psaliodes*	*ocreata*	-	2	1	-	-	-	-	3	10	22	35	26	1	4	22
867	*Psaliodes*	*ossicolor*	-	-	-	-	-	-	-	-	-	-	-	1	-	2	-
541	*Psaliodes*	*perfuscata*	2	-	-	1	-	1	2	-	1	1	-	2	1	2	5
540	*Psaliodes*	*picta*	-	-	3	10	-	-	3	-	3	1	2	1	4	-	1
521	*Psaliodes*	*plumbescens*	2	-	2	2	-	2	-	1	-	2	-	2	-	-	2
498	*Psaliodes*	*rica*	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
503	*Psaliodes*	*semirasa*	-	-	-	-	-	-	-	-	1	-	1	-	1	1	2
2033	*Psaliodes*	*serratilinea*	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
501	*Psaliodes*	sp 06	1	-	-	-	-	-	-	-	1	1	-	1	-	1	4
1069	*Psaliodes*	sp 1069	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
510	*Psaliodes*	sp 15	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
2134	*Psaliodes*	sp 2134	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
2135	*Psaliodes*	sp 2135	-	-	-	-	-	-	-	-	-	-	2	1	-	-	-
2136	*Psaliodes*	sp 2136	2	-	-	1	-	-	-	-	1	-	-	1	-	6	-
2149	*Psaliodes*	sp 2149	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
517	*Psaliodes*	sp 22	1	-	-	1	-	-	-	-	-	-	1	-	-	1	-
544	*Psaliodes*	sp cf *cedaza* 2	1	-	1	-	-	-	-	3	4	5	4	-	-	7	14
526	*Psaliodes*	sp cf *disrupta*	8	-	19	3	-	-	1	4	-	3	1	2	-	-	-
499	*Psaliodes*	sp cf *endotrichiata*	1	-	-	-	-	1	-	-	-	-	-	-	1	-	1
865	*Psaliodes*	sp cf *inundulata*	1	-	1	-	1	-	-	-	-	-	1	-	-	-	-
548	*Psaliodes*	sp cf *picta* 1	-	-	-	1	1	-	1	-	-	1	1	1	-	-	-
497	*Psaliodes*	sp cf *tripita*	2	-	-	1	-	-	-	-	-	1	-	-	4	2	-
518	*Psaliodes*	*strigosa*	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-
533	*Psaliodes*	*trilunata*	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-
444	*Ptychorrhoe*	*blosyrata confirmata*	-	-	-	-	-	-	-	-	1	1	-	-	-	1	-
815	*Ptychorrhoe*	*rayada*	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
437	*Rhinura*	*populonia*	-	1	-	-	2	-	-	-	-	3	-	6	4	2	1
2153	*Rhinura*	sp 2153	1	3	-	1	-	2	1	2	1	1	1	5	-	7	-
2114	*Rhopalodes*	*ebriola*	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
443	*Rhopalodes*	sp 01	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
33	*Scotopteryx*	*fulminata*	2	-	-	-	-	-	-	-	-	-	1	-	2	-	1
2102	*Spargania*	*commutata*	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
448	*Spargania*	*cultata*	3	4	5	-	4	2	6	7	4	2	4	7	1	4	1
2112	*Spargania*	*denguera*	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-
451	*Spargania*	*narangilla*	1	2	-	6	1	2	3	2	3	-	1	3	1	2	13
2053	*Spargania*	*rufifimbria*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
789	*Spargania*	sp 11	-	-	-	1	-	-	-	1	-	-	1	-	-	1	-
2099	*Spargania*	sp 2099	2	1	2	-	-	-	-	1	-	1	-	1	-	-	-
2119	*Spargania*	sp 2119	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
2056	*Spargania*	sp cf *perpendiculata*	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-
2061	*Stamnodes*	*anthocharidaria*	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-

ID	Genus	Species	A	B1	B2	C	D1	D2	E1	E2	F1	F2	G1	G2	H1	H2	I
447	*Trichozoma*	*picaria*	1	-	-	3	-	1	2	3	-	1	-	-	2	1	1
440	*Triphosa*	*affirmata*	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-
	Sterrhinae																
29	*Cyclophora*	*acutaria*	1	5	1	1	1	4	2	2	1	3	-	2	-	-	2
2043	*'Cyclophora'*	*aequalipunctata*	2	1	-	-	-	-	-	-	-	-	1	-	1	1	-
6	*'Cyclophora'*	*aurantiata aurantiata*	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2
28	*Cyclophora*	*coecaria*	-	5	2	-	2	1	5	4	-	2	-	1	-	2	-
1	*'Cyclophora'*	*costinotata*	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-
844	*'Cyclophora'*	*fastidiosa*	2	-	1	1	-	-	-	-	-	-	-	-	-	-	-
3	*'Cyclophora'*	*flavicornis*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
15	*'Cyclophora'*	*gigantula*	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
13	*'Cyclophora'*	*globaria*	-	-	1	-	-	-	-	1	-	1	1	1	-	-	-
8	*'Cyclophora'*	*gracililinea*	3	-	-	1	-	1	-	-	-	-	-	-	-	-	-
5	*'Cyclophora'*	*griseomixta griseomixta*	3	4	1	1	-	1	1	-	-	1	1	-	-	-	1
2029	*'Cyclophora'*	*hieroglyphica*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
11	*'Cyclophora'*	*lancearia*	1	-	-	-	-	-	-	1	-	-	1	-	-	-	-
2026	*'Cyclophora'*	*lateritiaria*	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
16	*'Cyclophora'*	*rhodostigma*	-	-	-	-	-	-	-	-	-	-	-	-	-	1	4
2010	*'Cyclophora'*	*rufulata*	-	-	-	-	1	-	-	-	2	-	2	-	-	-	-
14	*'Cyclophora'*	*seposita*	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1
630	*Cyclophora*	sp 630	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-
2086	*'Cyclophora'*	sp cf *rhodostigma*	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
2025	*'Cyclophora'*	sp cf *subaenescens*	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
18	*'Cyclophora'*	sp cf *torsivena*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
12	*'Cyclophora'*	*sypharia*	-	-	1	-	-	-	-	-	-	-	-	-	1	-	1
17	*'Cyclophora'*	*torsivena*	-	1	-	1	-	1	1	1	1	-	3	2	3	2	2
44	*Dithecodes*	*distracta*	1	-	1	-	2	-	2	1	-	1	1	1	5	4	1
36	*Idaea*	*arhostiodes*	7	9	2	-	-	1	3	2	1	6	15	21	7	12	4
40	*Idaea*	*fimbriata*	1	1	6	-	-	-	-	-	1	5	8	7	-	4	4
34	*Idaea*	*recrinita*	10	7	9	7	-	-	4	4	8	10	28	27	5	7	12
971	*Idaea*	sp 04	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
2159	*Idaea*	sp 2159	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
2160	*Idaea*	sp 2160	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-
35	*Idaea*	sp cf *iridaria*	3	5	10	3	3	1	5	3	9	12	14	31	10	21	14
37	*Idaea*	sp cf *subvestita*	1	1	2	-	-	-	2	1	6	2	6	7	3	1	5
634	*Idaea*	sp cf *triangulata*	-	-	-	-	-	-	-	-	-	-	2	-	3	4	-
38	*Lobocleta*	*costalis*	-	1	1	-	-	-	2	1	2	2	2	-	5	2	1
373	*Odontoptila*	*mimica*	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
972	*Pleuroprucha*	sp 972	9	1	2	13	8	1	1	20	31	1	2	2	-	1	29
2121	*Pleuroprucha*	sp 2121	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1
26	*Scopula*	sp 02	-	-	1	1	1	-	-	-	-	-	5	3	6	1	2
321	*Scopula*	sp 03	1	-	-	3	-	1	2	1	1	-	-	1	-	1	-
595	*Scopula*	sp 595	-	-	-	3	2	15	4	1	-	2	-	-	1	2	-
704	*Scopula*	sp 704	-	-	-	-	-	-	-	-	-	1	2	-	2	-	-
987	*Scopula*	sp 987	3	3	5	1	4	1	-	-	-	-	-	-	-	-	-
27	*Scopula*	sp cf *subquadrata*	-	4	-	2	4	13	4	-	2	1	4	-	2	4	2
713	*Semaeopus*	*bimacula*	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-

ID	Genus	Species	A	B1	B2	C	D1	D2	E1	E2	F1	F2	G1	G2	H1	H2	I
2023	*Semaeopus*	*bottgeri*	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-
20	*Semaeopus*	*calavera*	1	1	1	-	2	-	1	1	1	1	3	2	-	1	1
23	*Semaeopus*	*dentilinea*	2	-	1	-	1	-	2	1	4	2	3	7	3	3	5
1000	*Semaeopus*	*hypoderis*	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-
22	*Semaeopus*	*ladrilla*	2	-	1	-	-	-	-	-	-	-	1	-	-	1	-
2062	*Semaeopus*	*mira*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
2011	*Semaeopus*	*rubida*	-	-	-	-	-	-	-	-	-	-	1	-	1	3	-
783	*Semaeopus*	sp 783	-	-	-	-	-	-	-	-	1	-	-	1	2	1	1
21	*Semaeopus*	*verbena*	-	1	-	-	-	-	-	-	1	1	-	-	-	-	1
1075	*Tricentra*	*allotmeta*	1	1	-	-	-	-	-	-	2	-	-	1	1	-	-
714	*Tricentra*	*gavisata*	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
43	*Tricentra*	sp cf *ascantia*	-	-	1	1	-	-	-	-	-	-	-	-	-	-	1
42	*Tricentrogyna*	*collustrata*	6	6	2	2	7	11	3	3	2	3	8	10	2	5	2
39	*Tricentrogyna*	*nigricosta*	5	1	1	3	3	3	2	1	-	1	2	3	-	-	1
	Oenochrominae																
196	*Racasta*	*rhodosticta*	2	-	-	-	-	-	-	-	-	1	-	1	-	-	-
195	*Racasta*	*spatiaria*	-	-	-	-	-	-	-	1	1	1	1	-	-	-	1

Erklärung

Hiermit erkläre ich, dass ich die vorliegende Arbeit selbständig verfasst und dabei keine anderen als die angegebenen Hilfsmittel und Quellen verwendet habe.

Ferner erkläre ich, dass ich diese Arbeit weder einer anderen Prüfungsbehörde vorgelegt noch anderweitig mit oder ohne Erfolg versucht habe, eine Dissertation einzureichen oder mich der Doktorprüfung zu unterziehen.

N. Hilt

Bayreuth, den 17.10.2005

(Nadine Hilt)