Diversity of geometrid moths in a montane rainforest in Ecuador

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Summary

The diversity of the very species-rich family of geometrid moths was investigated in a montane forest at the border of the Podocarpus National Park in southern Ecuador along an altitudinal gradient ranging from 1,040 m to 2,677 m above sea level. This study is part of a larger interdisciplinary project on diversity and functioning of a montane forest ecosystem. A total of 13,938 moths representing 1,010 species were sampled in light-traps at eleven elevational levels (two replicate sites each). Most species belonged to the subfamily Ennominae (500 sp.), followed by Larentiinae (391 sp.), Sterrhinae (58 sp.), Geometrinae (57 sp.), Oenochrominae (3 sp.), and Desmobatrinae (1 sp.). The study covers aspects of host-plant relationships, community structure, endemism, alpha-, beta-, and gamma-diversity. The role of different environmental factors as mechanisms for the diversity of the moths is discussed. Furthermore, methodological aspects of light-trap sampling, and selection of appropriate diversity measures and analytical tools are considered in this study.

<u>Host-plant relationships</u> Host-plant data covering 226 Neotropical geometrid species is reviewed, and new original records of larvae of 19 species collected in the study area are presented. In most species (66%), only single records are available, but the interpretation of large-scale patterns is possible. Larval biologies of the subfamily Ennominae are better documented than those of Larentiinae, and arboreal plants are used by ennomines more frequently than herbaceous plants. Polyphagy appears to be rather widespread whereas specialism towards a narrow range of hosts occurs less frequently. Important components of the montane forest flora, such as mosses, ferns, orchids or bromeliads, are insignificant as food resources for geometrid larvae. These patterns are similar to those found in geometrid moths in northern temperate regions and contradict the assumption of high host specificity in the tropics.

<u>Sampling and processing</u> Light-traps are commonly used to sample nocturnal arthropods, in particular Lepidoptera. As with most other methods applied in animal ecology, light-trap samples reflect activity rather than abundance in the habitat. However, such distortions can be accepted because this problem is expected to be equal at each site. In the present study, it is improbable that moths were attracted to the trap from far distances because only weak light sources (2 × 15 W) were utilised. The activity of moths peaks soon after dusk and decreases thereafter. This decrease is stronger at high altitudes rather than at low elevations, possibly because species

are more restricted in their activity by lower temperatures. The position of the light trap (ground vs. canopy) might have an influence on the results, but the differences are expected to be of minor importance because the canopy layer should be inside the attraction radius of the light traps (tree heights <25 m). Fluctuations in the abundance of species must generally be considered in the analyses of the data, but thus far, there are no hints for the occurrence of marked seasonal effects in the study area. A total of 52% of all taxa and 67% of all specimens could be identified to species level. A higher proportion could be identified in Ennominae (57%), and Geometrinae (79%), whereas a lower proportion was determined in Larentiinae (41%). Freezing of the material during storage might help to accelerate the processing of specimens. The genitalia structures of 47 doubtful “morphospecies” were reanalysed. In 57% (27 sp.) the status was confirmed, whereas the remainder was split into two species (10 → 20 sp.), or fused to one species (10 → 5 sp.). Hence, this “worst case scenario” shows that the same magnitude of species numbers is achieved by both sorting methods, and the differentiation by wing patterns is sufficient for diversity studies such as those performed in this dissertation.

<u>Faunal composition and endemism</u> The proportional contribution of subtaxa to the local geometrid fauna changes at all systematic levels considered. While the proportions of species of the subfamilies Ennominae, Sterrhinae and Geometrinae significantly decrease, the proportion of Larentiinae increases as altitude increases. This phenomenon has already been observed in other regions of the world. There is a remarkable similarity between the altitudinal patterns in Ecuador and those found along a latitudinal gradient in Europe. Species of the subfamily Larentiinae seem to be particularly well adapted to harsh environmental conditions. They might disproportionately profit from low predation pressure by ants, birds and bats at higher altitudes. As relatively weak fliers, they might particularly benefit from lower predation risks from insectivorous bats. Changes also occur within the subfamilies Ennominae and Larentiinae. The specialist ennomine tribes Cassymini, Macariini, and Palyadini completely vanish, and the proportion of the tribe Boarmiini decreases at high altitudes. In contrast, the remaining tribes (mostly comprising polyphagous species) either do not show proportional changes (Azelini, Nacophorini, Nephodiini, Ourapterygini), or even increase (Caberini, “*Cratoptera*-group”). Within Larentiinae, the species proportion of the genus *Eois* decreases, whereas concomitantly the proportion of *Eupithecia* increases. Many of these changes in the faunal composition can be explained by expected host-plant requirements of the species involved. My results show that diversity estimates based on taxon ratios which are assumed to be

constant must be regarded with caution because such ratios can change rapidly along environmental gradients. A rough estimate of endemism can be achieved by the analysis of the type localities of taxa that could be identified to species level. Species which were originally described in Ecuador and Peru increase in their proportion, whereas species that were described from other countries in the Neotropical region decrease as altitude increases. Hence, species collected at lower altitudes are relatively more widespread than those collected at higher altitudes. These results indicate a high incidence of locally restricted species in montane cloud forests and provide arguments why effective conservation of these threatened ecosystems is important.

Alpha diversity hotspot The alpha-diversity (intra-habitat diversity) of geometrid moths as a whole, ennomines and larentiines was measured using (1) species number, (2) Fisher’s alpha, (3) rarefied species number, and (4) extrapolated species number (Chao 1 estimator). When applied to the empirical data set, it can be shown that (1) and (4) strongly depend on the sample size, whereas (2) and (3) turned out to be suitable and reliable measures of diversity. The total geometrid species number of 1,010 is the highest ever counted in a small geographical area. At single sites, up to 292 species were observed, and extrapolation estimates range from 244 to 445 species per site. Since exclusively diurnal species also occur in the study area, and the geometrid ensembles are incompletely sampled, the actual total species number in the study area is estimated to be ca. 1,200 to 1,300. Values for Fisher’s alpha are among the highest ever measured, and range from 69 to 131 per site, while the value for the whole elevational range covered is 250. In contrast to theoretical assumptions and studies in other regions of the world, the diversity of geometrid moths remains consistently high throughout the entire gradient studied. The subfamily Larentiinae increases from the lowest elevations and reaches a high diversity at elevations above 1,800 m. The subfamily Ennominae has previously been assumed to be a group which is mainly found at low and medium elevations. A high diversity of both groups is maintained at high elevations despite a decrease in the diversity of potential host-plants, a decrease in structural complexity of the vegetation, and increasingly unfavourable climatic conditions. A relatively low predation pressure is discussed as a possible advantage of high-altitude habitats. Furthermore, the physiognomy of the Andes (folded mountains, large areas at high altitudes) might have improved speciation events and the development of a species-rich high-altitude fauna. There is evidence that the species-richness of other groups of herbivorous insects declines as altitude increases. This emphasises difficulties that are associated with biodiversity indicator groups, and calls for caution when generalising from case studies.

Appropriate ordination methods and similarity indices The analysis of beta-diversity (inter-habitat diversity) of species-rich communities requires the choice of appropriate statistical tools. The metric ordination methods correspondence analysis (CA) and detrended correspondence analysis (DCA), as well as non-metric multidimensional scaling (NMDS) are frequently applied, and their performance on an empirical data set was compared. All methods depict the same, well interpretable patterns. Both CA and NMDS show an arch-like structure, which hints to an underlying coenocline data pattern, whereas this arch is computationally eliminated in DCA. CA shows the clearest ordinations, while the DCA ordination is more scattered. NMDS is recommended because of its minimal statistical assumptions, compared with metric techniques. Ordination appears to be superior over classification approaches such as single-linkage cluster analysis in depicting gradual changes of communities. Of the large number of similarity indices available, the Sørensen and the NESS index were performance tested. The clearest NMDS ordinations were achieved by the NESS index with the parameter m set to its maximum ($m_{\max}$). Performance was measured by comparing stress, a measure of goodness-of-fit in NMDS. The lowest values of stress were achieved with NESS $m_{\max}$. In contrast, NESS with the parameter m set to 1 (identical with the Morisita index), had consistently higher stress values and performed worse than the Sørensen index. Hence, if high values of m can be achieved, such as in large data sets, the NESS index with $m_{\max}$ is recommended.

Beta-diversity Similarities of ensembles of all geometrid moths and of the subfamilies Ennominae and Larentiinae were calculated using the Sørensen and NESS index ($m = 1$, $m_{\max}$). Ordinations were performed with NMDS, CA and DCA. All ordinations clearly depict a gradual change of the ensembles along the altitudinal gradient. Since no sharp boundaries occur, a classification of the moth ensembles into distinct faunal groups or zones does not seem to be appropriate. Extracted ordination scores significantly correlate with altitude as well as with ambient temperature. All correlations for all investigated taxa (Geometridae, Ennominae, Larentiinae), by any index and ordination, range between $r = 0.89$ and $r = 0.99$ (all $p<0.001$). Climatic factors are assumed to be the most important factors responsible for the species turnover among geometrid moths. Mantel tests were performed in order to compare faunal matrices with matrices derived from further environmental factors. Both tree diversity and vegetation structure significantly correlate with faunal data, but tree diversity explains considerably more of the data variability (range:

Mantel r = 0.73 to 0.85, all $p<0.001$) than vegetation structure (range: Mantel r = 0.23, $p<0.05$ to r = 0.43, $p<0.001$). Hence, vegetation changes might also play an important but less pronounced role in beta-diversity patterns of geometrid moths than climatic factors. Simulated model data was developed in order to explain the complex empirical patterns. The models assume a consistent turnover of species and equal elevational ranges of all species involved. They fit empirical data very well (Mantel r >0.80 and $p<0.001$ in all models), and do not support Rapoport's rule of increasing elevational ranges with rising altitude.

Body size patterns Wingspan was measured in 2,282 males of geometrid moths in order to investigate body size patterns along the elevational gradient. Body sizes of the whole family are weakly correlated with altitude (r = -0.06, $p<0.001$). No consistent patterns were found in seven subordinated large taxa (Ennominae with the tribes Boarmiini and Ourapterygini, and Larentiinae with the genera *Eupithecia*, *Eois* and *Psaliodes*). The relationship between body size and altitude in Geometridae is probably spurious because larentiines are significantly smaller than ennomines and simultaneously increase in their proportion along the gradient. In most taxa studied, body size variation increases with altitude, suggesting that constraints acting in canalising body size (such as predation) are weaker at high elevations. The result is in accordance to previous studies that could not detect any consistent body size patterns in insects along climatic gradients. Phylogenetical relatedness is briefly discussed as important factor in the analysis of body size data.

Zusammenfassung

Die Diversität der sehr artenreichen Familie Geometridae wurde entlang eines Höhengradienten (1040 – 2677 m Meereshöhe) in einem montanen Bergregenwald am Rand des Podocarpus-Nationalparks in Südecuador untersucht. Die vorliegende Studie ist in die Arbeit einer interdisziplinären Forschergruppe eingebunden, die die Diversität sowie funktionale Zusammenhänge in einem Bergregenwald-Ökosystem untersucht. Insgesamt wurden 13938 Falter mit Hilfe von Lichtfallen auf elf Höhenstufen (mit je zwei Standorten pro Stufe) gesammelt und ausgewertet. Die Zahl der nachtaktiven Arten beläuft sich auf insgesamt 1010. Die meisten Arten gehören der Unterfamilie Ennominae an (500 sp.), gefolgt von Larentiinae (391 sp.), Sterrhinae (58 sp.), Geometrinae (57 sp.), Oenochrominae (3 sp.) und Desmobathrinae (1 sp.). Die Dissertation umfasst Alpha-, Beta- und Gamma-Diversität, Wirtspflanzenbeziehungen, Gemeinschaftsstrukturen und Endemismus. Die Rolle verschiedener Umweltfaktoren als zugrundeliegende Mechanismen der Diversität der Geometridae wird ebenso diskutiert wie die Veränderung der Körpergrößen entlang des Höhengradienten. Außerdem werden methodische Probleme des Lichtfangs und der Wahl geeigneter Diversitätsmaße und Auswertungsverfahren erörtert.

<u>Wirtspflanzenbeziehungen</u> Von 226 neotropischen Geometridenarten wurden Wirtspflanzenangaben aus der Literatur ausgewertet; von 19 Arten, deren Raupen im Arbeitsgebiet gesammelt wurden, konnten neue Kenntnisse gewonnen werden. Von den meisten Arten (66%) stehen nur Einzelnachweise zur Verfügung. Eine Interpretation von Mustern auf höherer taxonomischer Ebene ist dennoch möglich. Über die Wirtspflanzen der Raupen der großen Unterfamilie Ennominae ist mehr bekannt als über diejenigen der anderen großen Unterfamilie, der Larentiinae. Ennominen-Raupen ernähren sich offenbar eher von Gehölzpflanzen als von krautigen Pflanzen. Polyphagie scheint weit verbreitet zu sein, wohingegen Spezialisierung auf ein enges Wirtsspektrum seltener auftritt. Moose, Farne und Bromelien, die vor allem als Epiphyten die Vegetation tropischer andiner Bergregenwälder prägen, spielen als Nahrungspflanzen allenfalls eine sehr untergeordnete Rolle. Diese Muster ähneln denen aus gemäßigten Regionen. Die Ergebnisse widerlegen die verbreitete Annahme, dass herbivore Insekten in tropischen Regionen grundsätzlich sehr spezialisiert sind.

<u>Falterfang und weitere Bearbeitung</u> Insbesondere nachtaktive Schmetterlinge lassen sich mit Hilfe von künstlichen Lichtquellen effektiv anlocken. Wie andere Erfas-

sungsmethoden in der Tierökologie spiegeln die Stichproben aus Lichtfängen eher die Aktivität der Insekten als deren tatsächliche Häufigkeiten wider. Die dadurch entstehenden Verzerrungen sind aber hinnehmbar, da der auftretende Fehler an allen Standorten gleich ist. Es ist unwahrscheinlich, dass die Falter in der vorliegenden Studie aus weiter Entfernung angelockt werden, da nur schwache Lichtquellen (2 × 15 W) verwendet wurden. Die Aktivität der Falter erreicht bald nach Eintritt der Dunkelheit ihren Höhepunkt und sinkt danach ab. Die Abnahme ist an den höhergelegenen Standorten stärker ausgeprägt als an den tief gelegenen und hängt vermutlich mit den insgesamt tieferen Temperaturen in den Hochlagen zusammen. Die Position der Lichtfallen (Boden oder Kronenraum) hat vermutlich nur einen geringen Effekt auf die Ergebnisse, da der Kronenraum innerhalb des Einzugsbereiches der Lichtfallen liegt (Baumhöhen <25 m). Die Häufigkeiten der Arten schwanken, aber es gibt bislang keine Hinweise auf ausgeprägte saisonale Effekte im Gebiet. Insgesamt konnten 52% der Taxa und 67% der Individuen auf Artniveau bestimmt werden. Relativ höhere Proportionen wurden bei den Ennominen (57%) und Geometrinen (79%) erreicht, während geringere Anteile der Larentiinen (41%) artgenau bestimmt werden konnten. Das Einfrieren der Falter während der Lagerung des Materials wird empfohlen, da es die spätere Präparation deutlich erleichtert. Bei 47 Arten (Morphospezies), deren Zuordnung zuvor nicht eindeutig geklärt werden konnte, wurden zusätzlich die Genitalstrukturen untersucht. In 57% der Fälle wurde die bisherige Zuordnung beibehalten, während die verbleibenden Arten aufgespalten wurden (10 → 20 sp.) oder zu einer Art zusammengefasst werden konnten (10 → 5 sp.). Daraus ergibt sich, dass selbst in besonders schwierigen Bestimmungsfällen durch verschiedene Methoden der Artabgrenzung die gleiche Größenordnung der Artenzahl erreicht wird. Für breit angelegte Diversitätsstudien wie die vorliegende erscheint damit die Bestimmung aufgrund der Flügelzeichnungen bei Geometriden in der Regel ausreichend.

<u>Faunenstruktur und Endemismus</u> Die Arten- und Individuenanteile untergeordneter Taxa innerhalb der Geometridae verändern sich entlang des Höhengradienten. Der Anteil der Unterfamilien Ennominae, Sterrhinae und Geometrinae nimmt mit der Höhe signifikant ab, der der Larentiinen zu. Dieses Phänomen ist bereits aus anderen biogeographischen Regionen bekannt. Die Ergebnisse aus Ecuador weisen eine verblüffende Ähnlichkeit zu den Mustern auf, die die Analyse der Geometridenfauna entlang eines latitudinalen Gradienten in Europa ergibt. Larentiinen scheinen beson-

ders gut an schwierige Umweltbedingungen angepasst zu sein. Sie profitieren vermutlich von einem geringen Feinddruck durch Ameisen, Fledermäuse und Vögel in großen Höhen und hohen Breiten. Für die relativ schwach fliegenden Larentiinen könnte insbesondere die geringe Fledermausdiversität der Hochlagen eine wichtige Rolle spielen. Strukturelle Veränderungen zeigen sich auch innerhalb der großen Unterfamilien. Mit zunehmender Höhe verschwinden bei den Ennominen die spezialisierten Tribus Cassymini, Macariini und Palyadini. Während der Anteil der Boarmiini signifikant abnimmt, bleibt der der eher polyphagen Tribus Azelini, Nacophorini, Nephodiini und Ourapterygini konstant oder nimmt signifikant zu (Caberini, „*Cratoptera*-Gruppe“). Bei den Larentiinen sinkt der Anteil der Gattung *Eois*, während die Gattung *Eupithecia* an Bedeutung zunimmt. Viele der Veränderungen in der Faunenstruktur lassen sich durch Wirtspflanzenansprüche erklären. Die Ergebnisse zeigen, dass Diversitätsschätzungen, die auf konstanten Proportionen von Taxa beruhen, mit Vorsicht betrachtet werden müssen. Eine grobe Schätzung des Endemismusgrades kann durch die Auswertung der Typenlokalitäten derjenigen Taxa erreicht werden, die bis auf das Artniveau bestimmt wurden. Der Anteil der Arten, die aus Ecuador und Peru beschrieben wurden, nimmt mit der Höhe zu. Im Gegensatz dazu nimmt der Anteil von Arten, die aus anderen neotropischen Ländern beschrieben wurden, ab. Der höhere Anteil lokal verbreiteter Arten in den hohen Lagen unterstreicht, wie bedeutsam der effektive Schutz der gefährdeten Bergregenwald-Ökosysteme für den Erhalt der Biodiversität ist.

„Hotspot” der Alpha-Diversität Die Alpha-Diversität (Habitat-Diversität) von Geometridae, Ennominae und Larentiinae wurde gemessen mittels (1) der Artenzahl, (2) Fishers alpha, (3) der „rarifizierten” Artenzahl (rarefied species number) und (4) der extrapolierten Artenzahl (Chao 1-Schätzer). Es wurde gezeigt, dass die Maße (1) und (4) stark von der Größe der Stichproben abhängig sind, wohingegen sich die Maße (2) und (3) als geeignet und verlässlich erwiesen. Die Gesamtzahl von 1010 Arten von Geometriden ist die höchste jemals in einem kleinen geographischen Gebiet nachgewiesene Zahl. Bis zu 292 Arten wurden an einzelnen Standorten registriert. Die extrapolierten Werte liegen zwischen 244 und 445 Arten pro Standort. Da weitere, ausschließlich tagaktive Arten im Gebiet vorkommen und die Proben unvollständig sind, wird die tatsächliche Gesamt-Artenzahl der Geometridae auf ca. 1200 bis 1300 geschätzt. Die Werte für Fishers alpha gehören zu den höchsten je gemessenen und variieren je nach Standort zwischen 69 und 131, während der Wert für alle Standorte zusammen 250 beträgt. Im Gegensatz zu theoretischen Annahmen und Studien in anderen Regionen der Erde bleibt die Diversität der Familie über den gesamten Gradienten konstant hoch. Die Unterfamilie Larentiinae ist im unteren Bereich weniger divers als in den Lagen oberhalb 1800 m. Entgegen den Erwartungen bleibt die Diversität der Ennominen auch in den höchsten Lagen auf sehr hohem Niveau. Die hohe Diversität der Falter steht im Gegensatz zur abnehmenden Artendiversität potentieller Wirtspflanzen, zur abnehmenden strukturellen Vielfalt der Vegetation sowie zu schwieriger werdenden Umweltbedingungen. Ein geringer Prädationsdruck als Vorteil von andinen Hochlagen wird diskutiert. Weiterhin könnte die Physiognomie der Anden (Faltengebirge, große Areale auf großer Meereshöhe) die Artbildung und die Ausprägung einer artenreichen Gebirgsfauna begünstigt haben. Die Diversität anderer Gruppen herbivorer Insekten nimmt hingegen ab. Anhand dieser Ergebnisse wird die Problematik der Verwendung von Biodiversitäts-Indikatoren aufgezeigt und vor unzulässigen Generalisierungen gewarnt.

<u>Geeignete Methoden zur Ordinierung und Ähnlichkeitsindizes</u> Die Analyse der Beta-Diversität artenreicher Gemeinschaften erfordert die Wahl geeigneter statistischer Methoden. Die metrischen Ordinierungsverfahren Korrespondenzanalyse (correspondence analysis, CA) und detrended correspondence analysis (DCA) sowie das nicht-metrische Verfahren der multidimensionalen Skalierung (NMDS) werden oft angewendet. Mit Hilfe eines großen empirischen Datensatzes wurden die Verfahren im Hinblick auf ihre Brauchbarkeit untersucht. Alle Methoden ergeben die gleichen, gut interpretierbaren Muster. Sowohl CA als auch NMDS zeigen ein hufeisenförmiges Muster, das auf eine zugrundeliegende zoenokline Datenstruktur schließen lässt. In der DCA ist dieses Muster hingegen eliminiert. Die Ordinierungen sind dabei weniger deutlich als diejenigen in CA. Wegen der im Vergleich zu den metrischen Verfahren geringen statistischen Annahmen erscheint NMDS insgesamt am empfehlenswertesten. Ordinierungsverfahren zeigen gegenüber Klassifizierungsverfahren (single-linkage cluster) deutliche Vorteile in der Darstellung gradueller Veränderungen von Gemeinschaften. Unter den zahlreichen verfügbaren Ähnlichkeitsindizes wurden der Sørensen-Index sowie der NESS-Index getestet. Die deutlichsten Ordinierungsmuster wurden mit dem NESS-Index erreicht, wenn dessen Parameter m auf sein Maximum eingestellt wurde (m_{max}). Das Verhalten der Indizes wurde mit Hilfe von Stress gemessen. Stress ist ein Maß der Güte der Anpassung in der NMDS. Die niedrigsten Stress-Werte wurden dabei mit m_{max} erreicht. Im Gegensatz

dazu war der Stress durchgehend höher als in den anderen getesteten Indizes, wenn *m* im NESS-Index auf 1 gesetzt wurde (dann identisch mit Morisitas Index). Wenn hohe *m*-Werte erreicht werden können, wie z. B. in großen Datensätzen, ist die Verwendung des NESS-Index empfehlenswert.

Beta-Diversität Ähnlichkeiten der Gemeinschaften von Geometriden und der Unterfamilien Ennominae und Larentiinae wurden mit Hilfe des Sørensen-Index sowie der NESS-Indizes (m = 1, m_{max}) errechnet. Die Ordinationsverfahren NMDS, CA und DCA (s.o.) wurden angewendet. Alle Ordinierungen zeigen deutliche graduelle Veränderungen der Gemeinschaften entlang des Höhengradienten. Da keine scharfen Grenzen auftreten, erscheint eine Klassifizierung in diskrete Kategorien nicht sinnvoll. Extrahierte Werte aus den Ordinierungen für alle Taxa (Geometridae, Ennominae, Larentiinae) korrelieren hochsignifikant mit der Meereshöhe und mit der Umgebungstemperatur der Standorte (alle $p<0{,}001$, $0{,}89 \leq r \leq 0{,}99$). Klimatische Faktoren sind vermutlich in erster Linie für den beobachteten Artenwechsel entlang des Höhengradienten verantwortlich. Mantel-Tests wurden durchgeführt, um Ähnlichkeitsmatrizen der Fauna mit Matrizen zu vergleichen, die aus biotischen und abiotischen Umweltfaktoren errechnet wurden. Sowohl Matrizen der Baumartendiversität als auch diejenigen der Vegetationsstruktur korrelierten signifikant mit den Fauna-Matrizen. Deutlich mehr der Variabilität der Daten wurde dabei durch die Baumartendiversität erklärt (Mantel-Test: $0{,}73 \leq r \leq 0{,}85$, alle $p<0{,}001$) als durch die Vegetationsstruktur (Mantel-Test: Werte zwischen $r = 0{,}23$, $p<0{,}05$ und $r = 0{,}43$, $p<0{,}001$). Vegetationsmerkmale spielen damit eine wichtige Rolle, werden aber in der Bedeutung von klimatischen Faktoren übertroffen. Simulationsmodelle wurden entwickelt, um die komplexen empirischen Muster zu erklären. Die Modelle nehmen einen konstanten Umsatz an Arten und gleiche Verbreitungsamplituden aller beteiligten Arten an. Sie erreichen dabei sehr hohe Ähnlichkeiten zu den empirischen Datensätzen (Mantel r-Werte >0.8, alle p<0.001). Rapoports Regel steigender Arealgrößen von Arten mit zunehmender Höhe wird damit nicht unterstützt.

Muster der Körpergrößen Die Flügelspannweite von 2282 Geometriden-Männchen wurde gemessen, um die Muster der Körpergrößen entlang des Höhengradienten zu untersuchen. Außer der gesamten Familie wurden die Ennominae mit den Tribus Boarmiini und Ourapterygini sowie die Larentiinae mit den Gattungen *Eupithecia*, *Eois* und *Psaliodes* getrennt betrachtet. Die Körpergröße der gesamten Familie ist schwach negativ mit der Höhe korreliert ($r = -0{,}06$, $p<0{,}001$). In den untersuchten

Subtaxa zeigen sich insgesamt nur schwache und uneinheitliche Muster. Die Beziehung zwischen der Körpergröße der Geometriden und der Höhe beruht auf einer Verschiebung der Anteile der artenreichen Unterfamilien. Larentiinen haben dabei eine signifikant geringere Körpergröße als Ennominen. Überraschenderweise nimmt in den meisten Taxa die Variabilität der Körpergrößen mit der Höhe zu. Dies könnte ein Hinweis auf geringere Zwänge sein, die die Körpergröße beeinflussen (kanalisieren, z.B. Prädation). Die Ergebnisse stimmen mit vorhergehenden Studien überein, die keine konsistenten Muster der Körpergrößen von Insekten entlang klimatischer Gradienten fanden. Die phylogenetische Verwandtschaft als ein wichtiger Faktor in der Analyse von Körpergrößendaten wird diskutiert.

Resumen

La diversidad de los Geometridae, una familia de mariposas muy rica en especies, fue investigada a lo largo de un gradiente altitudinal (1040 – 2677 m.s.n.m.) en un bosque de montaña en el sur del Ecuador (al límite del Parque Nacional Podocarpus). La presente tesis forma parte de un proyecto multidisciplinario sobre diversidad y relaciones funcionales en este ecosistema. En total fueron colectadas 13938 mariposas utilizando trampas de luz en once niveles altitudinales (dos sitios de cada uno). La mayoría de las 1010 especies pertenece a la subfamilia Ennominae (500 esp.), seguida de Larentiinae (391 esp.), Sterrhinae (58 esp.), Geometrinae (57 esp.), Oenochrominae (3 esp.) y Desmobathrinae (1 esp.). La tesis cubre aspectos de relaciones con plantas huéspedes, estructura de comunidad, endemismo, y diversidad alfa, beta y gamma. El papel de diferentes factores ambientales como mecanismos de la diversidad de las mariposas es discutado, igual como el cambio del tamaño de cuerpo a lo largo del gradiente altitudinal. Además son considerados problemas metódicos de trampas de luz y la elección de medidas adecuadas para la diversidad.

<u>Relaciones con plantas huéspedes</u> Datos sobre plantas alimentarias publicados para 226 especies neotropicales de Geometridae fueron analizados, y datos adicionales de 19 especies colectadas en el área de investigación son presentados. Para la mayoría de las especies (66%) solamente hay comprobaciones singulares. Pero una interpretación de interrelaciones en escalas grandes si es posible. La biología larval de la subfamilia Ennominae es mejor documentada como la de los Larentiinae, los Ennominae preferiendo plantas arbóreas sobre herbáceas. Una amplia ‘carta de menú’ al parecer es común, mientras menos especies muestran una especialización a un espectro angosto de plantas. Estos resultados son muy parecidos a aquellos encontrados en Geometridae de zonas templadas del hemisferio norte, y contradicen a la hipótesis que insectos herbivóros de regiones tropicales fuesen muy especializados.

<u>Captura y procesamiento de mariposas</u> Especialmente mariposas nocturnas se dejan atraer efectivamente con trampas de luz. Como otros métodos en la ecolología animal, las muestras asi colectadas reflejan más bien la actividad de los insectos que sus frecuencias. Pero las desfiguraciones implicadas son aceptales, debido a que este problema supuestamente afecta igualmente a todos los sitios. Es improbable que las mariposas fueron atraidos de distancias largas, ya que se utilizaron fuentes de luz tenues (2 × 15 W). La actividad de las mariposas llega a un

máximo pronto después del crepúsculo y luego disminuye. Esta disminución es más fuerte en los sitios ubicados más altos y depende probablemente de las temperaturas bajas allí. La posición de las trampas de luz (suelo o dosel) presumiblemente tiene un efecto insignificante. Hay que considerar que las frecuencias de la especies oscilan, pero los datos muestran ningún indicio de pronunciados efectos estacionales. En total 52% de las especies y 67% de los especímenes se pudo identificar hasta el nivel especifico. A proporciones más altas se llegó con los Ennominae (57%) y Geometrinae (79%), mientras una parte pequeña de los Larentiinae (41%) fue identificada. La congelación de las mariposas durante el almacenamiento es recomendable pues facilita la preparación posterior. En 47 especies que anteriormente no se pudo clasificarlas inequívocamente, fueron adicionalmente analizados sus estructuras genitales. En 57% de los casos la clasificación inicial fue mantenida, mientras las demás especies fueron escindidas (10 → 20 esp.) o reunidas en una sola especie (10 → 5 esp.). De esto resulta que incluso en casos de identificación particularmente difíciles se llega a la misma dimensión de especies con ambos procedimientos. Con ello es suficiente la clasificación según el debujo de las alas para estudios de diversidad como la presente.

Composición faunistica y endemismo La contribución proporcional de los subtaxa dentro de los geométridos cambia a lo largo del gradiente altitudinal. Mientras las proporciones da las subfamilias Ennominae, Sterrhinae y Geometrinae disminuyen significantemente con la altura, incrementa la parte de los Larentiinae. Este fenómeno ya es conocido de otros regiones del mundo. Los resultados de Ecuador muestran una similaridad notable a estudios de un gradiente latitudinal en Europa. Los Larentiinae aparecen particularmente adaptados a condiciones ambientales difíciles. Posiblemente aprovechan disproporcionadamente de una reducida depredación de hormigas, aves y murciélagos en alturas elevadas. Como voladores relativamente débiles, los Larentiinae profitarian particularmente de la diversidad minima de murciélagos insectivoros en grandes alturas. Cambios estructurales se encuentran también en las subfamilias Ennominae y Larentiinae. Subiendo en la altura dentro de los Ennomiinae desaparecen las tribus especialistas Cassymini, Macariini y Palyadini. La proporción de la tribu Boarmiini disminuye significantemente, mientras en las tribus mayormente polifagas Azelini, Nacophorini, Nephodini y Ourapteygini queda constante, y en las Caberini y el ‘grupo *Cratoptera*’ incrementa significantemente con la altura. Dentro de las Larentiinae disminuye la proporción del genero *Eois*, mientras la del genero *Eupithecia* crece. Muchos de estos cambios en la composición faunistica se puede explicar con exigencias acerca de plantas huéspedes. Según estos resultados hay que tener cuidado con estimaciones sobre la diversidad basadas en estructuras taxonómicas constantes, las cuales cambiando rapidamente a lo largo de gradientes ambientales. Una estimación del endemismo se consigue con el análisis de localidades típicas de las especies identificadas. La proporción de species descritas de Ecuador y Perú aumenta con la altura, a diferencia de aquella de especies descritas de otros paises neotropicales que disminuye. Por lo tanto especies colectadas en alturas bajas son distribuidas más ampliamente que aquellas encontradas más arriba. La parte grande de especies locales en el bosque de montaña subraya la importancia de la conservación de esta ecosistema amenazada.

‘hotspot’ de la diversidad La diversidad alfa (diversidad intra-hábitat) de los geométridos y sus subfamilias Ennominae y Larentiinae fue medida como (1) número de especies, (2) ‘Fisher’s alpha’, (3) el número de especies ‘rarificado’ (con métodos de ‘rarefaction’) y (4) el número de especies extrapolado (estimado Chao 1). Aplicado a los datos empíricos se muestra que las medidas (1) y (4) dependen del tamaño de las pruebas, mientras (2) y (3) se demostraron adecuadas y fiables. El total de 1010 especies de geométridos es el número más grande jamás comprobado para una área geograficamente pequeña. Hasta 292 especies fueron colectadas en sitios particulares, con los estimados (Chao 1) entre 244 y 445 especies por sitio. Porque hay más especies exclusivamente diurnas en el área de investigación, y las pruebas quedaron incompletas, el número total verdadero de especies se estima entre 1200 y 1300. Los valores de ‘Fisher’s alpha’ se ubican entre los más altos jamás medidos y llegan de 69 a 131 dependiente al sitio y a 250 para todos sitios juntos. A diferencia de suposiciones teóricas y estudios de otras regiones del mundo la diversidad de esta familia de mariposas queda constantemente alta en todo el gradiente investigado. La subfamilia Larentiinae es menos diversa en zonas bajas como más arriba que 1800 m.s.n.m. De los Ennominae se ha expectado que fuera un grupo que se encuentra principalmente en niveles altitudinales bajas e intermedias. Ambas subfamilias mantienen una diversidad alta en zonas altas a pesar del descenso de la diversidad de potenciales plantas huéspedes, la reducida complejidad estructural de la vegetación, y condiciones climáticas cada vez más desfavorables. La presión de depredación relativamente baja en grandes alturas es discutida como una ventaja. Además la fisonomía de los Andes podria haber favorecido la especiación y la evolución de una fauna de montaña muy diversa. La diversidad de otros grupos de insectos herbivoros disminuye en cambio con la altura, lo que acentua dificultades asociadas con ciertos grupos como indicadores de biodiversidad y advierte de generalizaciones.

Métodos de ordinación apropiados e indices de similaridad El análisis de la diversidad beta en comunidades ricas en especies requiere la elección de métodos estadísticos apropiados. Los procedimientos metricos de ordinación ‘análisis de correspondencia’ (correspondence analysis, CA) y ‘detrended correspondence analysis’ (DCA), además procedimientos non-metricos de la ‘escalización multidimensional’ (NMDS) son frecuentemente utilizados y aqui analizados con una base de datos grande. Todos los métodos dan los mismos resultados bien interpretables. Tanto CA como NMDS presentan una estructura en forma de herradura, indicando una estructura de datos ‘coenoclina’. DCA elimina esta ‘herradura’. CA presenta las ordinaciones más claras, mientras la ordinación DCA es más esparcida. Se recomienda NMDS porque en comparación a procedimientos metricos requieren pocas suposiciones estadísticas. Métodos de ordinación aparecen superiores a semejantes de clasificación (como ‘single-linkage cluster analysis’) debido a la mejor representación de cambios graduales en comunidades. De la gran cantidad de indices de similaridad disponibles, los de Sørensen y NESS fueron analizados. Las ordinaciones NMDS más claras fueron obtenidas con el index NESS con el parámetro m puesto al maximo $m_{\max}$. El comportamiento de los indices fue medido comparando ‘stress’, una medida para la calidad de adaptación (‘goodness-of-fit’) en NMDS. Los valores más bajos de ‘stress’ fueron obtenidos con NESS $m_{\max}$. Contrastando con esto, NESS con el parámetro m puesto a 1 (asi identico con el index Morisita), el ‘stress’ tenia consistentemente valores más altos que en otros indices analizados. Entonces cuando se pueden obtenir valores altos para m, como en bases de datos grandes, se recomienda el uso del index NESS.

Diversidad beta Similitudes de comunidades de geométridos y las subfamilias Ennominae y Larentiinae fueron calculadas usando los indices de Sørensen y NESS ($m = 1$, $m_{\max}$). Ordinaciones fueron llevadas a cabo con NMDS, CA y DCA. Todas las ordinaciones muestran claramente cambios graduales en las comunidades a lo largo del gradiente altitudinal. Como no hay límites bien marcados, una clasificación de las comunidades de mariposas en categorías distintivas no aparece apropiada. Valores extraidos de las ordinaciones correlacionan significantemente con la altura y con la temperatura ambiental de los sitios. Todas las correlaciones de todas las taxa investigadas (Geometridae, Ennominae, Larentiinae), con todos los indices de similitud y procediminetos de ordinación son altamente significantes (todos $p<0.001$, $0.89 \leq r \leq 0.99$). Principalmente factores climáticos probablemente son responsables para la diversidad beta de los geométridos. ‘tests Mantel’ fueron llevados a cabo para comparar matrices faunisticas con matrices calculadas con más factores ambientales. La diversidad de árboles y la estructura vegetal correlacionan significantemente con datos faunisticos, pero la diversidad de árboles explica considerablemente más de la variabilidad de datos (valores Mantel: $0.73 \leq r \leq 0.85$, todos $p<0.001$) que la estructura vegetal (valores Mantel entre $r = 0.23$, $p<0.05$ y $r = 0.43$, $p<0.001$). Por lo tanto cambios en la vegetación podrian jugar un papel importante pero menos pronunciado que factores climáticos para la diversidad beta de los geométridos. Se desarollaron modelos de simulación, para explicar los resultados empiricos. Estos modelos presumen un cambio uniforme de especies y amplitudes iguales de sus distribuciones altitudinales. Las simulaciones son muy similares a los datos empíricos (test Mantel: $r>0.80$ y $p<0.001$ en todos modelos) y no confirman la regla de Rapoport según la cual las extensiones altitudinales de las especies aumentasen con la altura.

<u>Tamaños de las mariposas</u> La envergadura de alas fue medida en 2282 geométridos machos, para investigar los tamaños en el gradiente altitudinal. Los tamaños de la familia entera declinan con la altura ($r = -0.06$, $p<0.001$). En las subfamilias grandes Ennominae y Larentiinae en cambio no fue encontrado ningúna relación. La correlación entre tamaño y altura presumiblemente no es auténtica, porque larentiinos son significantemente más pequeños que ennominos, y simultáneamente la proporción de los primeros incrementa con la altura. Este resultado coincide con estudios anteriores que no pudieron detectar una relación consistente entre tamaño de insectos a lo largo de gradientes climáticos. Parentesco filogenético es discutado como factor importante en el análisis de datos de tamaño.

1 General introduction

The tropical rainforests are probably the most species-rich of all terrestrial ecosystems (Myers 1992). Yet these systems are often poorly understood and there is a scarcity of even fundamental inventory data about all kinds of organisms (e.g. Henderson et al. 1991). For example, it was not known until the 1980’s that the Neotropical lowland rainforests of Iquitos (Peru) are the most species-rich in the world, with 300 tree species per ha (Gentry & Smith 1988). Botanical studies in western Ecuador revealed samples which were by far the most species-rich yet recorded, even excluding tree species from the data (Gentry & Dodson 1987). In the Neotropics, research has been largely focused on lowland rainforests, e.g. in the vicinity of Manaus, where the effects of large scale deforestation and fragmentation have been investigated in long-term projects (Bierregaard et al. 1992, Turner 1996, Didham et al. 1998). In recent years it has been recognised that the rainforests of the Andean region are of particular interest, since they have a flora as rich as or even richer than that of the much larger Amazon basin (Henderson et al. 1991). With 20,000 endemic vascular plants and 1,567 endemic vertebrates (respectively 6.7% and 5.7% of the global total), the northern Andes are one of the two “hottest hotspots” of diversity on earth for these groups, and probably for other taxa as well (Myers et al. 2000). Since an understanding of these threatened ecosystems is essential to their preservation, an interdisciplinary research project about the diversity and functioning of a montane rainforest ecosystem has been established in 1997 in South Ecuador. It currently involves 20 projects from a variety of biological and geographical disciplines (Beck & Müller-Hohenstein 2001, Fiedler 2001).

Only about ten percent of Andean ecosystems are still undisturbed and there is serious concern that the remaining ecosystems, such as the montane rainforests, will be destroyed within a short period of time (Henderson et al. 1991, Doumenge et al. 1995). Rates of loss by deforestation in the tropical rainforests are estimated at 0.8 – 2% per annum (Purvis & Hector 2000, see also Stokstad 2001); the Andean montane rainforests are particularly threatened because of fast growing human populations migrating into remote parts of these regions. For Ecuador, the dramatic loss of natural vegetation is illustrated by Sierra (1999).

Arthropods dominate rainforest ecosystems in terms of species numbers (Erwin 1982, Ødegaard 2000). Only few studies on arthropods have been conducted in the Andean region. For example, of the 89 studies on canopy arthropods reviewed by Basset (2001), none was carried out in the Andes. Arthropods are highly important elements of tropical forest ecosystems because of the many processes in which they are involved as detrivores, herbivores, predators and parasitoids. Insects account for a major proportion of arthropod diversity, and within insects the herbivores dominate in terms of species numbers (e.g. Brown 1989). As a consequence, herbivorous insects play a central role in many discussions on global species diversity. There has been an intense debate about the order of magnitude of species richness since Erwin's first estimates in 1982 that on a global scale arthropods might reach as many as 30 million species, many more than the two million previously thought to exist. Since then the database has been significantly improved, and the species number of herbivorous insects is currently estimated to be lower, from five to ten million species (Ødegaard 2000). As can be seen from this large range, these estimates still depend on many assumptions and much research needs to be carried out before a more precise number can be determined (May 1988, Ødegaard 2000). Although a number of studies on tropical insect diversity have been performed in the past (Basset 2001 and references therein), these still seem to be "drops in the ocean".

Herbivorous insects are not only species-rich: they also have important functions within ecosystems. On the one hand, by consuming large quantities of plant material, and on the other by acting as prey or hosts for predators and parasitoids, they determine structural relationships within ecosystems (Janzen 1987). It is known that herbivorous insects play a major role as regulators of primary production and nutrient cycling in temperate forest ecosystems (Mattson & Addy 1975, Swank et al. 1981, Lovett & Ruesink 1995). Folivorous insects have been recognised as the most important consumers in tropical forests (Coley & Barone 1996). Not only do parasitoids essentially depend on herbivorous insects as a food resource, but so also do a significant proportion of insectivorous bats and birds. However, the quantification of the functional roles that herbivorous insects play remains a major challenge because of the complexity, species-richness and lacking autecological information on insect communities in most tropical ecosystems.

Since sampling effort is necessarily limited in any field study, investigations have to be restricted either to guilds or taxonomic units. For example, Basset & Novotný (1999) and Diserud & Ødegaard (2000) investigated all the herbivorous insects of a few focal tree species. Many other studies have restricted investigations to taxonomic units such as certain groups of Lepidoptera or Coleoptera (e.g. Wagner 1998, Schulze & Fiedler 2002). I here follow the terminology suggested by Fauth et al. (1996): populations of co-occurring species which are taxonomically and geographically restricted are known as *assemblages*. When populations are further restricted by their utilisation of the same types of resources (e.g. plants), they are correctly known as *ensembles*.

Lepidoptera of the family Geometridae here serve as a model group of herbivorous insects. In a parallel study in the same area, the diversities of pyralid and arctiid moths were investigated (Süßenbach in prep). Lepidoptera are among the most species-rich of phytophagous insects (Scoble 1992), rivalled only by the coleopteran clade Phytophaga (Crowson 1981). Estimates of the numbers of species within Lepidoptera range from 160,000 to 500,000 (Solis & Pogue 1999). Nearly all species feed on plant resources but there are some notable exceptions (Powell et al. 1998 with references therein). The family Geometridae is globally represented and includes about 21,000 named species (Scoble et al. 1995), making it one of the three largest families of Lepidoptera, apart from Noctuidae and Pyralidae. Geometrids are characterised as a monophyletic group by the presence of structurally unique tympanal organs at the base of the abdomen (Cook & Scoble 1992). Usually their larvae can be easily distinguished from those of other families since the number of prolegs on the abdomen is typically reduced to two pairs. The name Geometridae is derived from the “ground-measuring”, looping habit of the walking larvae. Detailed descriptions of the morphological characteristics of Geometridae and subfamilies are given by Minet & Scoble (1998) and Holloway et al. (2001). Most species can be recognised externally by their wing patterns, but species level distinctions have been greatly refined by study of the genitalia (Scoble et al. 1995).

More than 6,400 species (>30% of the global total) of geometrids from the Neotropical region have been described (Scoble et al. 1995). Four subfamilies are most prevalent in the Neotropics compared with other faunal regions (Ennominae, Larentiinae, Sterrhinae, Archiearinae). Species richness in Desmobathrinae, Geometrinae and Oenochrominae is highest in the Indo-Australian region (Gaston et al. 1995, Holloway 1996). In contrast to other similarly large groups of arthropods, the estimated true number of species is by no means like an order of magnitude greater than the number of described species, and probably does not exceed 30,000 (Gaston et al. 1995). Scoble et al. (1995) emphasise that many described species may have to be synonymised in the course of future revisionary work and the total species number may be reduced in that way. This fact is widely ignored in many studies where species numbers are estimated.

Geometrid moth larvae feed on a wide range of plants, although they usually consume the leaves of trees and shrubs (Scoble 1992). Compared with groups such as Noctuidae or Pyralidae, relatively few species have reached pest status. Since Geometridae tend to be a group of forest habitats rather than of open landscapes, most pest species damage forest trees or arboreal crops (d’Araújo e Silva et al. 1968, Swank et al. 1981, McGuffin 1987, Holloway et al. 2001).

Geometrids have frequently served as model organisms for diversity studies in the tropical rainforests of South East Asia (Holloway 1987, Intachat et al. 1997, Chey et al. 1997, 1998, Schulze 2000, Beck et al. 2002). Intachat & Woiwod (1999) describe them as a suitable and practical group for biodiversity studies in tropical forests, yet no detailed ecological studies on geometrids have ever been carried out in the Neotropical region. Although modern revisions are available for only relatively few of the many genera (Scoble et al. 1995), the taxonomy of this group is advanced compared to most other large groups of herbivorous insects in the tropics. This is particularly true for South East Asia, due to Holloway’s investigations (1993, 1996, 1997). A catalogue of all available scientific names of geometrids (Scoble 1999) and generic revisions of Neotropical Geometrinae and Ennominae (Pitkin 1996, 2002) have substantially improved the usefulness of geometrids as model organisms in biodiversity research.

For the first time ever, the diversity of geometrid ensembles of an Andean montane rainforest ecosystem is investigated. Using an elevational gradient as a “natural experiment” (Körner 2000), I explore faunal structure and diversity, as well as relationships between moths and their abiotic and biotic environments.

AIMS OF THE DISSERTATION

I Host-plant relationships and sampling methods

- Which resources are exploited by the larvae of Neotropical geometrids?
- What are the methodological problems of sampling moths?
- How many species can be determined?

II Alpha-diversity (intra-habitat diversity) and structural composition

- Which measures of alpha-diversity are appropriate?
- How diverse are geometrids in an Andean montane rainforest?
- Which environmental factors can best explain the diversity patterns?
- Are montane rainforests richer in endemic species than lowland forests?

III Beta-diversity (inter-habitat diversity) along an altitudinal gradient

- Which ordination methods and similarity measures are appropriate?
- How do ensembles of geometrids change along the gradient?
- Which environmental factors are correlated with beta-diversity of geometrids?

IV Body size patterns

- Do the body sizes of geometrid moths change along the elevational gradient?

2 Host-plant relationships of Neotropical geometrid moths

INTRODUCTION

The available host-plant records of herbivorous insects, such as the species-rich groups Lepidoptera and Coleoptera, are strongly biased towards temperate regions (Heppner 1991, Fiedler 1998a, b, Wagner 1998). This seriously affects the interpretation of evolutionary traits because Holarctic floras are dominated by plant taxa that are underrepresented in tropical regions (Powell et al. 1998). The understanding of host preferences is also an important issue in ecology, because herbivorous insects are the most species-rich guild on earth and play an essential functional role in ecosystems (e.g. Mattson & Addy 1975). In addition, the degree of host-specificity of herbivorous beetles served as a fundamental factor in the estimation of the total global species number (e.g. Erwin 1982, Ødegaard 2000).

In very few groups, such as butterflies, relatively more is known about host-plant preferences of tropical species than in most other insect groups (Ackery 1991, Fiedler 1998a). Knowledge about phytophagous beetles has recently been much increased, but remains scarce due to their enormous number (Basset et al. 1996, Wagner 1998, Basset 2001). The life-cycles and host-plant affiliations of tropical nocturnal Lepidoptera are also unknown in most cases except for some large and conspicuous taxa such as Sphingidae and Saturniidae (see e.g. the database by Janzen & Hallwachs 2001)

This study focuses on the Neotropical members of the family Geometridae, which is one of the three most species-rich groups of Lepidoptera. Geometrid moths occur in every biogeographical region of the world, but with some 6,450 described species, the Neotropical region holds by far the greatest number (Scoble et al. 1995, Scoble 1999). Studies in temperate regions as well as in rainforests of South East Asia revealed that geometrids tend to be more specific to certain habitats than other groups (Scoble 1999), and are sensitive to environmental changes (Intachat et al. 1997, Holloway 1998, Beck et al. 2002). These properties, together with a modern worldwide catalogue of the family, and recent major revisionary works available for Neotropical genera (Scoble 1999, Pitkin 1996, 2002), render geometrid moths a suitable model group to study ecological and evolutionary aspects of a “megadiverse” group of herbivorous insects.

The aims of this chapter are:

- To review and interpret available host-plant records of Neotropical geometrid species from the scattered sources, based on latest systematic concepts, and to compile a first comprehensive source of information that can be used in further studies.
- To contribute new host-plant information concerning species with a previously unknown life-cycle from a montane forest in South Ecuador.

METHODS

COLLECTION AND ARRANGEMENT OF DATA

By far the most data was accessible in the internet: as lists (INBio 1999), or extensive databases (Janzen & Hallwachs 2001, Robinson et al. 2001). The database provided by Janzen & Hallwachs (2001) is comprised of data collected exclusively in the area de conservación Guanacaste in northwestern Costa Rica and gives exact information on date, host, and number of specimens. Robinson et al. (2001) provide information on host-plants on a global scale. Host-plant records in this database are currently biased towards the Nearctic region (Scoble 1999), but information on 61 species from the Neotropical region is available. A. Aiello kindly placed data on 14 species at my disposal (pers. comm.). Host-plant records of agricultural pests are presented by d'Araújo e Silva et al. (1968) and Peña et al. (1998). Comparatively few records are collated in revisionary works (Cook & Scoble 1995, Rindge 1978, 1983, Scoble 1995, Pitkin 1996).

For those geometrid genera that are not restricted to the Neotropical region, host-plant information regarding temperate zone species is often available. Such records frequently show tendencies towards certain preferences of species, and are discussed when appropriate. However, only selected sources from the temperate zone were considered in order to avoid inflating the review: McGuffin (1958, 1987), Ferguson (1985), Skou (1986), and Ebert (2001). Holloway (1993, 1996, 1997) and Holloway et al. (2001) contribute important information from tropical South East Asia.

Records are presented as a species list of subfamilies and tribes, arranged in alphabetical order (Appendix 1). Holloway (1993, 1996, 1997) showed that meaningful interpretations are possible at tribal level, particularly in the large and heterogeneous subfamily Ennominae. A reliable sorting of species to tribes was made possible by recent generic revisions of Neotropical ennomine and geometrine genera (Pitkin 1996, 2002). Most of these tribes, but not all, probably form monophyletic groups. No comprehensive tribal classification is available for the other subfamilies. However, most genera for which host-plant records were available, could be assigned to tribes according to different checklists from other regions (Hodges et al. 1983, Heppner & Inoue 1992, Holloway 1997 for *Eois*). The present compilation of host-plant records is definitely not exhaustive since it includes relatively few sources. Although, those that are available are certainly of particular importance. Species names were checked for correct spelling and replaced in cases of synonymy, according to Pitkin (2002) for Ennominae and Parsons et al. in Scoble (1999) for the remaining geometrid species.

Statistics were performed using the software package Statistica 5.5 (StatSoft 1999).

ORIGINAL RECORDS FROM SOUTH ECUADOR

Larvae were collected in the area of the Estación Científica San Francisco in the province Zamora-Chinchipe in South Ecuador (3°58´S 79°05´W) along an elevational range between 1,800 and 2,300 m above sea level. The area is covered with primary or moderately disturbed montane rainforest. The composition of the vegetation and structure of the area were described by Bussmann (2001) and Paulsch (2002), respectively (see Chapter 4). Larvae were reared in plastic vials at room temperature under the natural day-night photoperiod regime. Fresh leaves or inflorescences were provided at least every other day. For documentation purposes, photographs were taken (Figure 1). Pupae were kept moist until moths hatched. Adults were identified in the Zoologische Staatssammlung, Munich and in the Natural History Museum, London. Host-plants were determined by specialists (J. Homeier, S. Matezki), and by the author in the Herbario Nacional, Quito, Ecuador.

RESULTS AND DISCUSSION

ORIGINAL RECORDS FROM SOUTH ECUADOR

A total of 101 larvae were collected in the field. Thirty-three were reared to adults and belong to 19 species (Table 1). None of these species had ever been reared before, so all records of host-plants and larval morphology are new to science. Twenty-seven additional larvae of these 19 species failed to reach the adult stage, but could be reliably affiliated. The remaining 41 individuals belonged to at most 31 morpho-

Table 1 Species reared in the area of the Estación Científica San Francisco, Zamora-Chinchipe, Ecuador. **n** number of individuals successfully reared, **P** part of plant used: **le**aves, **fl**owers, **ph**otograph available, ***** plants which were accepted in captivity but which were not original host-plants. **on young leaves.

Moth taxon	Plant family	Plant species	n	P	ph
ENNOMINAE					
Boarmiini					
Bryoptera basisignata Warren, 1904	Unknown	Unknown treelet	1	le	+
	Fabaceae*	*Trifolium repens**			
Melanolophia reducta meridiana Rindge, 1964	Asteraceae	*Baccharis latifolia,*	2	le	+
	Podocarpaceae	*Podocarpus oleifolius***			
Physocleora sp.	Euphorbiaceae	*Alchornea* sp.	1	le	
“*Cratoptera*-group”					
Melinodes subapicata Warren, 1904	Asteraceae	*Pentacalia* sp. 1	1	le	+
Nacophorini					
Ischnopteris sp. near *chryses* Druce, 1893	Bignoniaceae	*Tabebuia chryses***	2	le	+
	Grossulariaceae	*Escallonia paniculata*			
Nephodiini					
Bonatea viridilinea Warren, 1904	Urticaceae	*Pilea* sp. herb	1	le	+
	Asteraceae*	Asteraceae treelet*			
Ourapterygini					
Isochromodes fraterna Warren, 1904	Urticaceae	Unknown herb	1	le	+
Isochromodes palumbata Warren, 1904		(found while moulting)	1	-	
	Asteraceae*	Unknown treelet*			
Oxydia agliata Guenée, [1858]	Asteraceae	Unknown treelet	1	le	+
Unplaced genera					
Certima lojanata Dognin, 1892	Asteraceae	*Pentacalia* sp.	1	le	+
Microxydia sp. near *ruficomma* Prout, 1910	Asteraceae	*Baccharis latifolia*	3	le	+
Sabulodes thermidora Thierry-Mieg, 1894	Asteraceae	*Baccharis latifolia*	1	le	+
LARENTIINAE Eupitheciini					
Eupithecia anita Warren, 1906	Asteraceae	*Baccharis latifolia*	5	fl	+
	Amaranthaceae	*Iresine diffusa*	1	fl	
Eupithecia penicilla Dognin, 1901	Asteraceae	*Baccharis latifolia*	1	fl	+
Eupithecia yangana Dognin, 1899	Myricaceae	*Myrica pubescens*	2	le	+
Eupithecia sp. 01	Asteraceae	*Erato polymnioides*	1	fl	+
	Amaranthaceae	*Iresine diffusa*	1	fl	
Eupithecia sp. 02	Asteraceae	*Baccharis latifolia*	1	fl	+
		Piptocoma discolor	1	fl	
		Mikania lanceolata	1	fl	
Eupithecia sp. 03	Asteraceae	*Baccharis macrantha*	1	fl	+
GEOMETRINAE Nemoriini					
Lissochlora cecilia Prout, 1912	Grossulariaceae	*Escallonia paniculata*	2	fl	+

Figure 1 Last instar larvae of geometrid moths collected and successfully reared to adults from the area of the Estación Científica San Francisco, South Ecuador (1,800 - 2,300 m). Bars indicate a length of 10 mm. Identification numbers in brackets. The corresponding host-plants are listed in Table 1.

Bryoptera basisignata (G2)

Melanolophia reducta (young) (G52)

Melinodes subapicata (G32)

Ischnopteris sp. near *chryses* (G19)

Bonatea viridilinea (G9)

Isochromodes fraterna (G5)

Oxydia agliata (G6)

Certima lojanata (G21)

Microxydia sp.near *ruficomma* (G18)

Sabulodes thermidora (G7)

Eupithecia penicilla (G24)

Eupithecia sp. 01 (G47)

Eupithecia sp. 02 (G41)

Eupithecia sp. 02 (G36)

Eupithecia anita (G8)

Eupithecia sp. 03 (G43)

Eupithecia yangana (G57)

Lissochlora cecilia (G27)

species of larvae, but it was impossible to determine these early stages due to the lack of literature.

HOST-PLANT RECORDS OF NEOTROPICAL GEOMETRID MOTHS

Ennominae

Neotropical ennomine moths mainly consume of leaves of trees and shrubs (Pitkin 2002). Host-plant specialisation ranges from extreme polyphagy in some tribes to restriction to a particular plant family in others (Holloway 1993). The records presented here confirm the findings of both of the above named authors, since the majority of larvae were found on trees and shrubs, but not on herbaceous plants. However, host-plant ranges in most Neotropical tribes are still insufficiently documented and many more records are required in order to obtain more reliable patterns. The number of genera that are represented in the Neotropical region is shown in brackets for every tribe, according to Pitkin (2002).

Azelini (2 genera) The tribe is dominated by the large genus *Pero*. According to Poole (1987), species of the North American *honestaria*-complex feed polyphagously on a wide variety of plant species, such as deciduous trees, conifers, and herbs. This is confirmed by Robinson et al. (2001), who list host-plants of twelve North American species. While some were recorded on different deciduous trees, the diet of other species includes conifers or even consists exclusively of them. Janzen & Hallwachs (2001) recorded one Neotropical species on three different plant families. A certain degree of specificity was noted by Poole (1987), who tried to rear species in Venezuela and was not able to find acceptable substitute food in captivity.

Boarmiini (29 genera) Many genera of this tribe are known to be highly polyphagous and sometimes play a role as pests (McGuffin 1987, Holloway et al. 2001). Holloway (1993) also noted a number of species that are narrowly specialised. In Europe, most Boarmiini species tend to be polyphagous on deciduous shrubs and trees, but specialism towards conifers and even lichens occurs (e.g. Skou 1986). The New World genera *Epimecis, Glena* and *Iridopis* were all found on a very wide variety of host-plants in the Neotropics. This is in accordance with patterns known from the Nearctic region (Robinson et al. 2001). *Melanolophia* species also tend to be polyphagous because all records of three species are from different plant families, including a new record from own data from South Ecuador (Table 1). The three North American species of this genus all feed on a wide range of host-plants (Rindge 1964, Robinson et al. 2001), whereas hosts of the related taxa *Pherotesia* and *Melanotesia* are unknown (Rindge 1964). The same applies to most of the other genera of this tribe. In the genus *Melanochroia*, three species were found exclusively on *Phyllanthus* species (Euphorbiaceae). This might reflect a certain specialisation of the genus, although a fourth species was recorded on a Rubiaceae host.

Cassymini (14 genera) In this tribe, only one Neotropical record of the genus *Taeniogramma* is available from a Fabaceae host-plant (Janzen & Hallwachs 2001). This corresponds to a report by Holloway et al. (2001), who stated that Cassymini larvae show some preference for Fabaceae, although they were not found exclusively on that family. Palaearctic representatives of the tribe tend to be more polyphagous (Holloway 1993).

Caberini and Baptini (20 genera) The relationship between the groups could possibly be uncovered by the study of the larval morphologies (Pitkin 2002). Species show specialism towards different plant families. In Malesia, the Caberini show a strong association with Rhamnaceae as larval hosts (Holloway et al. 2001), whereas species of the temperate zone genus *Cabera* feed on Betulaceae and Salicaceae (Skou 1986). Some Neotropical Caberini also use Rhamnaceae as a host plant: larvae of the widespread species *Sphacelodes vulneraria* were recorded exclusively on Rhamnaceae host-plants. Single records of *Erastria* and *Numia* species are also available from this plant family. Two species of *Cyclomia* were also recorded on Rhamnaceae hosts, whereas two other species of the genus were found on Erythroxylaceae. There is only a single record of a *Lomographa* species on a Rosaceae host-plant in Costa Rica. Some Nearctic and Palaearctic *Lomographa* species also show a preference for Rosaceae, but hosts of other families are frequently used as well (Skou 1986, Robinson et al. 2001). Bornean *Lomographa* are often associated with Aquifoliaceae (Holloway 1993). The number of records in other genera is insufficient for reliable interpretation, although the various records for *Paragonia* species suggest that this genus tends towards polyphagy.

Lithinini (12 genera) Neotropical members of this tribe are restricted to temperate austral regions of Chile and Argentina, but until recently their early stages and host-plants were completely unknown (Rindge 1986). In four of the six North American genera of Lithinini the host-plants are ferns, whereas in the other two genera, deciduous trees and conifers serve as hosts (Rindge 1986). The only available record from the Neotropics is of an unknown *Asestra* species, which was found on Sapindaceae (INBio 1999).

Macariini (3 genera) *Digrammia, Macaria* and *Semiothisa* are the only Neotropical genera of the tribe (Scoble & Krüger 2002). Most available records are from Fabaceae host-plants. This corresponds well with Holloway's statement (1993) that tropical representatives show a strong preference for Fabaceae. In contrast, Macariini in temperate regions are specialised to a varying degree towards conifers, deciduous trees and, to a lesser extent, herbs (Ebert 2001, Robinson et al. 2001). I expect that Neotropical Macariini species frequently use Fabaceae as host-plants.

Nacophorini (42 [+5?] genera) Rindge (1983) revised this tribe and described early stages and host-plants of almost any Neotropical species as unknown. According to Rindge, the known North American groups feed on conifers and hard wood trees. Although the life-histories of the vast majority of genera remain unknown, some information is now accessible which shows that many species are likely to be polyphagous. There are no hints towards specialism of any of the six genera for which information is available. Polyphagy can definitely be confirmed for species of *Holochroa*, *Ischnopteris* and *Thyrinteina*. It is also probable for *Cargolia,* which was recorded on two introduced conifer species in Ecuador. *Thyrinteina arnobia* was described as major defoliator of *Eucalyptus* species (Saavedra et al. 1996).

Nephodiini (19 [+4?] genera) Host-plant data are available for a couple of species (belonging to six genera), but there are mostly only one or two records for each. These records cover a wide range of plant families, including conifers. One species of *Fulgurodes* is particularly polyphagous since it was recorded on six different plant families, including two conifer taxa. A Neotropical species of *Patalene* was recorded on three different plant families, whereas a North American member of the genus seems to be specialised towards conifers (Robinson et al. 2001). *Nephodia marginata* was recorded three times on Fabaceae and might be a specialist. However, feeding preferences of the other members of the species-rich genus remain completely unknown.

Ourapterygini (60 [+4?] genera) Larvae of this tribe are known as arboreal defoliators in Malesia and feed on a wide range of plant families (Holloway et al. 2001). Host-plant data are only available for twelve Neotropical genera. Species of the genus *Oxydia* are some of the biggest geometrid moths in the New World and might therefore be better known than other genera of the tribe. Records clearly indicate polyphagy in the species *hispata, nimbata* and *vesulia* and show a wide range of host-plants, including conifers. The genera *Bassania* and *Ira* can be assigned as being polyphagous as well, but the quantitative basis is not very sound. In captivity, one species of *Isochromodes* accepted leaves of an Asteraceae although it had originally been found on an Urticaceae host (Table 1). Some specialism can be noted in two genera. Three independent single records of *Leucula* (of two species) are each from Araliaceae. A *Drymoea* species was recorded on *Croton* (Euphorbiaceae) in two cases.

Palyadini (6 genera) A prominent exception to the polyphagous feeding habits found in many other Ennominae tribes seem to be moths of the small Neotropical tribe Palyadini, which was revised by Scoble (1995). Pitkin (2002) placed the tribe as a subgroup of Caberini and Baptini. Records of eight species belonging to three genera *(Argyrotome, Phrygionis, Opisthoxia*) are from host-plants of the family Myrsinaceae. This is in accordance with data from Scoble (1995) who cited one record for *Phrygionis paradoxata*, found on *Ardisia* (Myrsinaceae). There is only one exception of the use of Myrsinaceae as host-plants by Palyadini. An unknown species in the genus *Ophthalmoblysis* was recorded on *Connarus* (Connaraceae). With records for four out of six genera, Palyadini are currently the best-known group of Neotropical geometrid moths.

"*Cratoptera* group" (9 genera) The only two records available for this group are from the genus *Melinodes*. The larvae have conspicuous "tentacles" which can be erected if they are touched (Figure 1). One species was recorded on a Verbenaceae host-plant (INBio 1999). In South Ecuador, I found a caterpillar of *M. subapicata* on *Mikania* (Asteraceae) (Table 1).

Genera not assigned to tribal level (60+ genera) The remaining Ennominae genera form a heterogeneous and paraphyletic assemblage (Pitkin 2002). Therefore, no clear patterns of host-plant relationships can be expected. A wider range of host-plants was found in the genera *Herbita, Nepheloleuca, Neodora, Pantherodes, Prochoerodes,* and *Sabulodes*. Two records of different plant families were found in species of *Cimicodes, Microxydia, Sericoptera,* and *Sicya*. North American species of *Sabulodes* can be extremely polyphagous, whereas other species are specialised towards deciduous trees or conifers (Rindge 1978, Robinson et al. 2001). Two North American species of *Prochoerodes* are also polyphagous (Robinson et al. 2001), whereas Nearctic *Sicya* species tend towards feeding on deciduous trees (Robinson et al. 2001). *"Acrotomia" mucia* is specialised since it was found exclusively on different species of Rubiaceae.

Larentiinae

The use of herbaceous plants or resources such as flower buds seems to be more widespread in this subfamily compared to Ennominae (e.g. Holloway 1997). However, many species also feed on leaves of deciduous trees and shrubs as well. Larentiinae are an exceptional group since most species live in temperate or montane regions (Holloway 1987, 1997). The documentation of host-plants is particularly poor for tropical representatives in this subfamily (see below). The numbers of genera assigned to tribal level cannot be provided because there is a lack of comprehensive literature on tribal classification in Larentiinae.

Eupitheciini The genus *Eupithecia* is the largest among all geometrids with more than 1,000 valid described species (according to Parsons et al. in Scoble 1999). A wide spectrum of food resources is used, with a few Hawaiian species even predating on small insects (Montgomery 1982). Many species have a tendency towards specialisation on a few taxonomically related host-plants, often on flowers or buds (e.g. McGuffin 1958, Skou 1986, Holloway 1997). Despite the high number of *Eupithecia* species in the region, host-plant data from the Neotropics are extremely sparse: For example, among the 1,092 host-plant records for *Eupithecia* in the database by Robinson et al. (2001), only two are from the Neotropical region (with one of the two species occurring in North America and Mexico). Two other available single records are from Asteraceae and Fabaceae. As a consequence, my own records of six species from South Ecuador already make a significant contribution to the knowledge of *Eupithecia* in the Neotropical region. Five species fed on inflorescences of Asteraceae and / or Amaranthaceae hosts, whereas one species was found feeding on the leaves of a Myrtaceae shrub. *Eupithecia* reach their highest diversity in the Neotropical region in montane Andean rainforests at altitudes above 2,000 m (see chapter 5, Herbulot 2001). I assume that plants of the family Asteraceae play an important role as hosts for the genus. This plant family corresponds with *Eupithecia* in diversity patterns because it reaches its highest species richness (ca. 300 species) at elevations above 2,000 m (Jørgensen & León-Yanez 1999). Asteraceae also play an important role as hosts in temperate regions (McGuffin 1958, Skou 1986). However, many more host-plant records are needed to confirm whether Asteraceae play this suspected important role as hosts.

Holloway (1997) assigned the genus *Eois* to the tribe Eupitheciini. In spite of the high species richness of the genus, there are only very few host-plant records from the Neotropical region. Six out of seven records of three *Eois* species are from Piperaceae hosts. Holloway (1993) noted a species from India (*Eois grataria*) on a Euphorbiaceae host-plant.

Perizomini Host-plant records of two Neotropical *Perizoma* species comprise herbaceous species of the families Basellaceae, Asteraceae and Chenopodiaceae. In temperate regions of the northern hemisphere, *Perizoma* species are specialised feeders on herbaceous plants of families such as Caryophyllaceae and Lamiaceae; many of them feed (like *Eupithecia*) on inflorescences and seed capsules (e.g. Skou 1986). Available data suggests that Perizomini species are specialised on reproductive organs of herbaceous plants, although this needs to be confirmed in the Neotropics by further records.

Euphyiini In the Palaearctic region, *Euphyia* species are known as specialists feeding on herbs, e.g. on those of the family Caryophyllaceae (Ebert 2001), whereas one Nearctic species is more polyphagous (Robinson et al. 2001). The Neotropical *E. repandaria* was reported on host-plants of the families Fabaceae and Solanaceae, which suggests that the species is polyphagous.

Triphosini Although *Triphosa affirmata* was only recorded on Fabaceae hosts in the Neotropics, records from North America show a wider range of plants (Robinson et al. 2001). *Triphosa* species in the Holarctic region show a tendency towards specialisation on Rhamnaceae host-plants (e.g. Skou 1986, Ebert 2001).

Hydriomenini No records of Neotropical representatives of genera such as *Spargania* and *Hydriomena* are available. *Spargania* species from the Holarctic region were recorded on Onagraceae and Ericaceae, whereas *Hydriomena* species are either specialised towards conifers or feed polyphagously on deciduous trees and shrubs of different families (McGuffin 1958, Ebert 2001). Larvae of *Hagnagora* species show a certain preference for Clethraceae host-plants although there is one record from a Boraginaceae host.

Lobophorini The Nearctic species *Dyspteris abortivaria* feeds on Vitaceae and Rosaceae (Robinson et al. 2001), but life-histories of any of the Neotropical species of this tribe are unknown.

Xanthorhoini The cosmopolitan *Orthonama obstipata* feeds on a wide range of plants (Robinson et al. 2001). *O. vittata* has been reported from Menyanthaceae and Rubiaceae. There are no records available for either species or other members of the genus from the Neotropical region.

Geometrinae

Little is also known about the immature stages of Neotropical Geometrinae (Pitkin 1996). Holloway (1996) reported that the larvae of this subfamily feed predominantly on trees or shrubs. According to Holloway, a tendency towards specialisation on reproductive parts or young foliage is common or in two tribes that also occur in the Neotropics (Hemitheini and Nemoriini). The number of genera that occur in the Neotropics is presented in brackets, according to Pitkin (1996).

<u>Dichordophorini</u> (1 genus) Larvae of a North American species of *Dichordophora* were reared on Anacardiaceae (Pitkin 1996).

<u>Hemitheini</u> (6 genera) Most genera of this tribe are distributed in the Old World (Holloway 1996). The majority of New world host records are from North America, e.g. *Chlorochlamys chloroleucaria,* which has been found on a wide range of host-plants (Ferguson 1985). Single records of two species of *Chloropteryx* are both from *Mikania* (Asteraceae). While host-plants of the genus *Chlorissa* are unknown in the Neotropics, species of this tribe (including *Chlorissa* in Europe) are polyphagous on deciduous trees, shrubs and herbaceous plants (Hausmann 2001).

<u>Lophochoristini</u> (5 genera) *Oospila confundaria* is a specialised species which eats the expanding leaves of *Hymenaea courbaril* (Fabaceae) (D.H. Janzen, cited in Cook & Scoble (1995)). The authors state that it is the only one out of 47 species for which host-plant data are available. One other Neotropical record of the tribe is from *Anomphax gnoma* on an Anacardiaceae host-plant (Prout in Ferguson 1985).

<u>Nemoriini</u> (14 genera) From North America, the genus *Nemoria* have been recorded on more than twenty species (Robinson et al. 2001). Most of them feed on a limited range of deciduous trees and shrubs (families Fagaceae and Rosaceae). In contrast, one species (*N. mimosaria*) is highly polyphagous. I could only find two records of an unknown *Nemoria* on two different Lauraceae hosts and a single record of *N. marielosae* on a Fagaceae host-plant in the Neotropical region. Records of other genera are sparse: *Phrudocentra centrifugaria* was reported on the families Myrtaceae and Fabaceae, and on Myricaceae hosts from the Nearctic region (Robinson et al. 2001). There are only single records of other species of *Phrudocentra*. Pitkin (1996) added *P.* (*oubrica*?) on Vochysiaceae. Species of the genus *Lissochlora* species were reared on flowers of a Lauraceae host. I found a caterpillar feeding inflorescences of a Grossulariaceae host-plant (Table 1).

<u>Synchlorini</u> (2 genera) Species of the genus *Synchlora* appear to be rather polyphagous. Most records in North America are from the family Asteraceae

(Robinson et al. 2001). *S. frondaria* and *S. gerularia*, which are distributed in Central and North America, feed on hosts of a wider range of plants.

Sterrhinae

Cosymbiini No clear tendencies can be revealed from the available Neotropical records, although data from temperate regions indicate that the many species are polyphagous. *Cyclophora* species in Europe and North America tend to be specialised on deciduous trees such as *Fagus, Salix, Acer* and *Quercus* (Ebert 2001, Robinson et al. 2001). According to Parsons et al. (in Scoble 1999), Neotropical species formerly placed in the genus were removed from it. *“Cyclophora” nanaria* was recorded on a variety of host-plants from North America through to Chile (however, it is questionable whether this is the same species throughout). The few records of the genera *Tricentrogyna* and *Semaeopus* allow no profund interpretation of host-use patterns. A *Pleuroprucha* species was recorded on hosts of the families Asteraceae and Sapotaceae. It is the only species that was recorded from Graminae. Due to its uniqueness, this observation needs to be confirmed because it appears to be the only geometrid record on this plant family worldwide. *Semaeopus* species have been found on a wide range of host-plants, including conifers (Robinson et al. 2001).

Scopulini No Neotropical record is available for many species-rich genera such as *Scopula*. *Scopula* species are often polyphagous (Robinson et al. 2001), but a degree of specialism towards certain herbaceous plants and shrubs has been noted (Ebert 2001). Holloway (1997) noted some specialism in several genera in Asia.

Sterrhini Some species of this tribe (e.g. *Idaea* species) diverge from the usual herbivorous nutrition and feed on dry foliage or similar substrates (e.g. Sugi 1987, Ebert 2001, Hausmann 2001). The life-cycles of the detrivorous species such as those of *Idaea* are often poorly known/unknown even in the otherwise well sampled Central European fauna. Many of the records listed might not be “real” field data but data from larvae in captivity. *Idaea* also occurs in the Neotropics, but nothing seems to be known about their early stages there.

Sterrhinae not assigned to tribe A species of *Trygodes* was found on Fabaceae and Malvaceae.

Oenochrominae and Desmobathrinae

Plant species of the family Polygonaceae appear to play a role as hosts for several species of the genera *Ametris* and *Ergavia*. A species of the latter genus was also found on a Myrsinaceae host-plant and a species of *Dolichoneura* was recorded on a Sapotaceae host. No further data are currently available from the Neotropics.

BASIC PATTERNS

The total number of Neotropical geometrid species with available host plant data reviewed in this chapter is 245, including new records for 19 species. This corresponds to 3.8% of the 6,400 currently described species of Neotropical geometrid moths (Scoble et al. 1995). The knowledge is poor, particularly if it is compared with the well-known temperate zone faunas (e.g. Ebert 2001). However, the available data is still a valuable source because it is probably better than autecological data on most other species-rich tropical arthropods. This study is only a first step towards the understanding of host-plant relationships of a “mega-diverse” group of herbivorous insects in tropical regions. It must be noted that the data set is biased to some extent. Some properties of the data indicate that it does not represent a random sample of Neotropical geometrid species. However, this does not have a major effect on the conclusions drawn below.

- There is a higher proportion of species (8.8%) that also occur in the relatively well-documented North American fauna than can be expected from a random sample. However, the extent of this bias remains unknown. Heppner (1991) estimated that 75% of the described Lepidoptera species are tropical, whereas only 25% of the available larval food records come from tropical zones. Powell et al. (1998) stated that the true disparity is undoubtedly even greater. Furthermore, most data reviewed in this chapter is from Central America (Costa Rica, Panama), whereas only relatively few records are from South America.
- The subfamily Ennominae is significantly better documented compared with other geometrid moths than the subfamily Larentiinae (χ^2 test statistics: $p<0.001$, $p<0.01$, respectively, Table 2). The reasons for this are as follows: (1) Ennomines dominate in lowland forests which are much better investigated than montane forests, where larentiine moths are the most species-rich group (Holloway 1997, chapter 4). A substantial proportion of the data is from a lowland dry forest in Costa Rica (Janzen & Hallwachs 2001). (2) Ennomines might have been sampled more often because they are larger (Chapter 8) and often have a more conspicuous appearance than larentiines. (3) The taxonomy of ennomines is more advanced than that of larentiines (Pitkin et al. 1996, Pitkin 2002).
- Pest species might also be over-represented. For example, all species listed by d’Araújo e Silva et al. (1968) belong to this category. At least 15% of the reviewed

species were recorded on plants of economic importance. However, the number of geometrid species known as pests is comparatively low compared with other groups of herbivorous insects (A. Aiello, pers. comm.) (see also Saavedra et al. 1996, Peña et al. 1998).

Other problems arise from the fact that for about two thirds of all species only single records are available. This often renders it impossible to state how specialised such a species actually is (see below). Furthermore, some of the records might actually have been derived from larvae in captivity. It is a well-known phenomenon that larvae in captivity frequently accept host-plants on which they never occur in their natural habitats (Ebert & Rennwald 1993). However, narrowly specialised species will usually not accept plants except those belonging to the natural host-plant family or genus. On the other hand, feeding experiments in captivity offer the chance to prove whether species are (potentially) polyphagous or not. An unsolved problem is the question whether some species might be polyphagous at the species level, but are effectively monophagous at the level of local populations (e.g. Michaud 1990).

Table 2 Number of reviewed host-plant records and new own records of Geometridae and four large subfamilies (see Appendix 1). Not shown: Oeonochrominae (three species, two single records) and Desmobathrinae (one species, one single record). Species numbers from the Neotropical region were taken from Scoble et al. (1995). The ratio of species from which host-plant records were available for each subfamily was compared with the ratio of the remaining taxa by performing χ^2 test statistics. Host-plants of Ennominae are significantly better known compared to the rest, whereas host-plants of Larentiinae are less well known. **ns** not significant, ** p<0.01, *** p<0.005, **** p<0.001.

	Geometridae	Ennominae	Larentiinae	Geometrinae	Sterrhinae
Literature records	226	169	20	18	15
Single records	149 (66%)	112 (66%)	12 (60%)	12 (67%	10 (67%)
Species Neotropics	6,433	3,318	1,668	454	902
Proportion covered	3.5%	5.1%	1.2%	4.0%	1.7%
χ^2 (df = 1)	-	12.5 ****	10.01 ***	0.07 ns	2.61 ns
New records	19	12	6	1	0
New proportion covered	3.8%	5.5%	1.6%	4.2%	-
χ^2 (df = 1)	-	11.41 ****	7.46 **	0.07 ns	-

As mentioned above, the data set contains many species that were recorded only once. This data can only be interpreted in a meaningful way if it is regarded in a phylogenetical context. For example, four species of the Ennomine tribe Palyadini were recorded only once or twice on a Myrsinaceae host-plant. While nothing could be stated on the basis of the information from one species, the picture alters if all four species and additionally other members of the tribe are regarded. In this case a clear tendency towards monophagy on Myrsinaceae host-plants becomes evident. This example shows that even single records can contribute to the synoptical understanding of larger patterns (see also Fiedler 1995, 1998a). Basset (1992) pointed out that rare species often tend to appear to be more specialised than they really are. Five or more independent records could be obtained from only 20 (8.2%) of 245 species reviewed and collected. Among these, only five species are restricted to one plant family, whereas seven species were recorded on two or three families, and eight species were recorded on four or more plant families. These numbers indicate that many geometrid species tend to be polyphagous (see further discussion below).

In accordance to Scoble (1992), arboreal plants are used more frequently by geometrids than herbaceous plants. The feeding on leaves appears to be prevalent, particularly in Ennominae. The importance of young leaves as nutrient-rich resources in rainforests has been emphasised by several authors (Coley 1983, van Schaik et al. 1993, Basset 1994, Coley & Barone 1996). Most species found in South Ecuador were feeding on young leaves, herbs, or gap colonisers (see Coley 1983). No geometrid caterpillar was recorded on the long-lived tough leaves of shade-tolerant tree species in the forest. Inflorescences were used by five out of six species of *Eupithecia* (Larentiinae); the usage of this resource is also known in species of the subfamily Geometrinae.

So far, there are no records of ferns, mosses and lichens as hosts of Neotropical geometrids, although some species of the ennomine tribe Lithinini can be expected to feed on ferns (see above). Lichens are used by a few exceptional specialist species in the ennomine tribe Boarmiini (for example, Hausmann 2001 lists three species in Europe), but no records are available from the Neotropical region. Only one record of a species that has been found on monocotyledons is available (Sterrhinae: polyphagous *Pleuroprucha asthenaria* on a Gramineae host, among various dicot hosts). Since geometrid moths do not appear to exploit monocot resources, the very high diversity of this moth family in Andean montane rainforests cannot be explained by the high diversity of e.g. orchids and bromeliads in these habitats (Chapter 5). Up to 80% of all epiphytic vascular plants in Neotropical rainforests are monocotyledons (Gentry & Dodson 1987, Rauer & Rudolph 2001, Werner 2002). Some Sterrhinae feed on detritus in other regions in the world, but this has not yet been shown in the Neotropics.

HOST-PLANT SPECIFICITY AND FUTURE INVESTIGATIONS

There is still little knowledge about the host specificity of rainforest herbivores (Basset 1992, Ødegaard et al. 2000). Theory suggests that species in the tropics should be highly specialised ecologically towards a narrow range of hosts (Futuyma 1976, Michaud 1990, Coley & Barone 1996). Estimates on the global species number assumed a ratio of 20% of host-specific herbivorous insects (Erwin 1982). However, more recent studies suggest that the host-specificity in tropical rainforests has been overestimated. There is growing evidence that only a few groups are more specialised at low latitudes compared with high latitudes. Basset (1992) listed the butterfly families Ithomiinae, Satyrinae, and Heliconiinae, which utilise mostly herbs and vines as hosts. However, Fiedler (1998a) showed that no such differences were detectable in the latter two families. The selection pressure towards specialism is higher when host plants that are protected by toxic substances such as alkaloids are used (qualitative defence, Coley & Barone 1996). Most rainforest trees differ in their chemical defence from herbs and vines because they are often protected by dose-dependent, quantitative defences (Waterman & McKey 1989).

Basset (1992) and Basset et al. (1996) recorded a proportion of monophagous species of herbivorous insects on tropical rainforest trees in Papua New Guinea of only 11% and 4%, respectively. A low host-specificity of herbivorous insects in rainforests was confirmed by Mawdsley & Stork (1997), Kitching et al. (1997), and Wagner (1998). Fiedler (1998b) found that the proportion of polyphagous lycaenid butterflies increases towards the equator. Host specificity in other guilds was also found to be lower in tropical forests than in temperate forests (ambrosia and bark beetles, Beaver (1979)).

The patterns of utilised host plants indicate a rather low degree of specialism in Neotropical geometrids. At most, approximately 25% of the species can be regarded as being monophagous on the host-plant family level (see above). This figure is a very rough estimate since the database is small. More field data, combined with feeding trials will be required to substantiate the result. Another field of further research is to investigate possible differences in the proportion of polyphagous species along environmental gradients. Polyphagy may be a widespread strategy, particularly on nutrient-poor rainforest trees (Mattson & Scriber 1987, Basset 1992).

Furthermore, there is growing evidence that differences in chemical defences and nutrient levels also exist between different types of rainforest and that this might influence the feeding strategy of herbivorous insects. Another aspect was investigated by Dyer (1995) who found that specialist caterpillars were better protected than generalists, and that predation could be a substantial selective force in the evolution of a narrow diet breadth. Since predation pressure on geometrid moths might decrease as altitude increases (see Chapter 5), a higher degree of specialism may be expected at lower altitudes than in montane habitats.

CONCLUSIONS

Polyphagy appears to be rather widespread in Neotropical geometrid moths. The results presented here are a first step towards understanding the host-plant relationships of a highly diverse group of tropical herbivores. Geometrid moths appear to be a very suitable group that should be the target of more thorough investigations. Basset (2001) suggested the mass rearing of live insects obtained from various rainforest habitats as a very promising approach. Collecting and rearing a larger number of species could substantially improve the knowledge about the host-specificity of herbivorous insects. The present study has shown that this is manageable for geometrid moths within a reasonable time period. Collecting and rearing should be combined with additional feeding trials to explore the physiological limits of acceptable food-plant ranges for a larger number of species.

3 Sampling and processing species-rich tropical moth ensembles

INTRODUCTION

The analysis of the diversity of extremely species-rich arthropod communities from tropical regions poses considerable methodological challenges. Samples typically contain a large number of rare species that cause statistical problems (Novotný & Basset 2000), and are incomplete. Apart from these analytical issues, which are discussed in Chapter 5, a number of other problems are addressed in this chapter. The following questions will be briefly reviewed and, where available, illustrated with own field data:

- Do light-trap samples provide appropriate information about the occurrence and abundance of species in a habitat?
- Does the type of trap and its position have an effect?
- How do weather, moonlight and habitat structure affect the results?
- How can specimens be processed effectively?
- How many species can reliably be identified?
- What impact might constraints on the time effort as well as seasonality have on the samples?

METHODS

Geometrid moths have frequently been described as a suitable and practical group for biodiversity studies in tropical forests (Intachat & Woiwod 1999, see Chapter 5). Ensembles (Fauth et al. 1996) of the group were investigated at 22 sites situated along an altitudinal gradient between 1,040 and 2,677 m above sea level in a montane rainforest in South Ecuador. The study area is described in more detail in Chapter 4. Moths were attracted to light, and between two and four catches were performed at each site using two 15 W tubes (Sylvania blacklight-blue, F 15 W / BLB-TB and Phillips TLD 15 W 05). All catches were carried out in co-operation with D. Süßenbach, who investigated the diversity of pyralid and arctiid moths in the same area (Süßenbach in prep.). The accumulator-driven tubes were put in a white gauze cylinder (diameter 0.80 m, height 1.60 m, “light tower”, Firma Weber, Stuttgart, see Figure 1), and placed at ground level. Sites with very dense vegetation were avoided (see below). The traps were operated between 6.30 and 9.30 p.m. local time, and the catches were separated into six intervals of 30 minutes duration (Figure 3). Catches were restricted to periods from three days after full moon until five days before full moon. Specimens were sampled manually using standard cyanide jars, subsequently put into paper bags, and eventually frozen until they were spread. Specimens were sorted to morphospecies level and were identified as far as possible in the Zoologische Staatssammlung, Munich, and the Natural History Museum, London. Appendix 2 provides a list of all taxa sampled. Each specimen was labelled with information on locality, GPS-derived geographical coordinate and altitude data (Garmin GPS III), data and time of catch, and collector. This data, taxonomical information and sex of the specimen were entered into the database Microsoft Access 97. Standard statistical analyses were performed with the program Statistica 5.5 (StatSoft 1999).

Figure 1 A "light tower" was used to sample moths in South Ecuador. The cylinder has a diameter of 0.80 m and is 1.60 m high. Moths were attracted by two 15 W tubes which were run by accumulators. High numbers of moths were attracted at site 1b at 1,040 m, on 5th December 1999 (geographical coordinates see Chapter 4).

RESULTS AND DISCUSSION

GENERAL AND ETHICAL CONSIDERATIONS

Any suitable field data has to fulfil the criteria of validity and comprehensibility. Apart from these basic demands, methods are also affected by certain economic constraints with regard to the amount of time and money that can be spent. Ethic questions come into play if organisms have to be killed for scientific purposes. The investigation of arthropod communities usually requires the killing of specimens in order to reliably identify specimens. This is particularly the case in tropical communities where there is often a high degree of specimens that are unknown to science (e.g. Wagner 1998). There is a general consensus that “reasonable” sampling is unlikely to have any adverse impact on arthropod species (Holloway et al. 2001). Field guides are only available for a small minority of arthropods, mostly from temperate regions, and do not usually provide any serious alternative to the collection of insects. Specimens from museum collections cannot replace field data in ecological studies. Such collections are neither comprehensive nor are they random samples (Scoble et al. 1995). Since the public is often concerned about the necessity of killing animals, and there is growing objection to the collection of insects in many countries, the number of killed specimens should always be kept to a reasonable number, as suggested by Holloway et al. (2001). In cases of tropical arthropod communities, such numbers can easily reach the magnitude of several 10,000. It is easier to justify research if specimens are made available for further investigations, e.g. taxonomical research in natural history museums. However, it should always be kept in mind that the killing of insects for scientific purposes has virtually no impact on insect populations, in comparison to the massive destruction of natural habitats and other factors such as traffic or street lighting. For example, McKenna et al. (2001) estimated that the number of Lepidoptera killed in the state Illinois alone might be as many as 20 million specimens per week. In contrast, samples for scientific purposes contain considerably fewer specimens, and the results often contribute to the long-term preservation of habitats. Therefore, such collecting efforts are also acceptable on the grounds of ethical considerations.

THE USE OF LIGHT-TRAPS

Lepidoptera have frequently been used as model organisms in ecological studies in temperate as well as in tropical regions (Thomas & Thomas 1994, Holloway et al. 2001). While the mostly diurnal butterflies can often be observed with ease, nocturnal

Lepidoptera usually behave more secretively. However, many species can easily be attracted to artificial light sources (Canaday 1987, Muirhead-Thomson 1991). This renders moths a very attractive group to study, particularly if large data sets are required for statistical analyses. Although the underlying physiological and behavioural mechanisms of the attraction to light are still not fully understood (e.g. Bowden 1982), light-traps have become an important tool for taking an inventory of insects in a wide range of studies. No other trapping method has proved so consistently successful in capturing large numbers or such a great variety of species (Muirhead-Thomson 1991). Moreover, light traps have been used for monitoring for more than 50 years (Leinonen et al. 1998). There is extensive literature detailing advantages and disadvantages of light-trapping and factors that might influence the results of this technique (Holloway et al. 2001). Three specific criticisms on the method were formulated by Schulze & Fiedler (2002): (1) Light traps sample selectively rather than randomly, (2) moths are attracted from a distance, i.e. from other habitats than those targeted, and (3) the effective attraction radius may depend on the visibility of the trap and hence be influenced by vegetation structure. Besides these issues, there are problems regarding the trap type, the site, and the influence of weather and the moon on the catches. In the following, I refer to light-traps, although not exclusively to automatic traps, but also to light sources which are used to sample attracted insects manually.

DO LIGHT TRAPS SAMPLE SELECTIVELY?

Relative abundances of species in trap collections do not necessarily reflect relative abundances of species in a particular habitat but rather their activities (Wolda 1992, Simon & Linsenmair 2001). Furthermore, not all insect groups and species are attracted to light traps to the same extent (Bowden 1982, Butler et al. 1999). Therefore, samples cannot perfectly represent all flying insects in a habitat. Even if they would, flying specimens do not inevitably represent the actual populations (Schowalter 1995, but see Lepš et al. 1998). This problem is illustrated by the proportion of females that were collected in South Ecuador. Only 12.6% of all analysed specimens are females. For the larger subfamilies, the proportions range between 11.0% for Geometrinae and 18.7% for Sterrhinae (Table 1 shows proportions and χ^2 test statistics). In contrast, rearing of Lepidoptera species ex ovo usually results in a roughly 1:1 ratio between the sexes (e.g. Fischer & Fiedler 2001). The higher proportion of males in trap catches probably reflects their higher activity when they are searching for mates. Sex biases are common in Lepidoptera samples

(Pollard & Yates 1993, Fischer & Fiedler 2000, Holloway et al. 2001) and their interpretation does not present any difficulties.

Generally, light trap samples represent a certain unknown “distortion” of the real situation. Some species might actually be more abundant than the light trap samples suggest. On the contrary, species that were found to be very abundant in samples must also be abundant in a habitat. Statistical analyses have to consider these methodological constraints. For example, light-traps do not usually allow the estimation of population sizes (Bowden 1982). On the contrary, many measures of alpha- and beta-diversity remain largely unaffected by “distorted” communities. For example, the calculation of the measure Fisher’s alpha (Fisher et al. 1943, Chapter 5) requires only the sums of species and individuals from a sample. Therefore, the measure will not be seriously affected by differences in the abundance of single species. Furthermore, the comparison of beta-diversity of ensembles (Chapters 6 and 7) does not pose any significant problems, because the “distortion” is expected to be dependent on the physiology of the species rather than on different habitats.

Table 1 Species numbers, proportions of females, and numbers of species assigned to species level of Geometridae and four subfamilies. Not included are the subfamilies Oenochrominae (three species) and Desmobathrinae (one species). The subfamilies Ennominae and Sterrhinae have a significantly higher proportion of females than found in the remaining geometrids, whereas the ratio is significantly lower in larentiine moths. Ennomine and geometrine moths could be significantly better assigned to species level, whereas the identification in Larentiinae proved to be more difficult. Expected numbers for χ^2 test statistics for each of the subfamilies were calculated on the basis of the data from the respective remaining subfamilies. ** p<0.01, **** p<0.001, **ns** not significant.

	Geometridae	Ennominae	Larentiinae	Geometrinae	Sterrhinae
Species number	1,010	500	391	57	58
Proportion of females	12.6%	13.2%	11.2%	11.0%	18.7%
Observed / expected	-	879 / 793	640 / 796	79 / 92	157 / 95
χ^2 (df = 1)	-	10.56 **	35.54 ****	2.19 ns	45.83 ****
Assigned to species level	51.7%	56.9%	41.0%	78.9%	50.0%
Observed / expected	-	285 / 234	161 / 235	45 / 29	29 / 30
χ^2 (df = 1)	-	20.86 ****	57.96 ****	17.97 ****	0.07 ns

It is well known that geometrid moths are attracted to light (e.g. Holloway et al. 2001). Eighty-seven percent of the geometrid moths in Northern Europe listed by Skou (1986) can be assessed using light traps. There are no reasons why there should be any basic differences between the behaviour of Neotropical geometrids at light sources and those from Europe. Additional sampling with other methods, such as the collection of larvae, might reveal potential biases. All 19 species of geometrids collected as larvae in the study area in South Ecuador (Chapter 2) were also represented in the light trap samples. Hence, light-trap sampling produces a distorted picture, but the problem is manageable. Moreover, any other comparable sampling method poses similar constraints (Schulze & Fiedler 2002, Southwood & Henderson 2000).

ARE MOTHS ATTRACTED FROM A DISTANCE ?

A potential problem with the use of light traps is the attraction of insects from a distance. This is particularly the case in mosaic habitats, whereas large and more homogenous habitats are less affected. Electroretinographic studies showed that moths can indeed perceive light from long distances, but they are actually only attracted from much shorter distances (Baker & Sadovy 1978). Data provided in the literature on responding distances varies considerably from 3 m to more than 250 m (Baker & Sadovy 1978, Bowden 1982). Muirhead-Thomson (1991) estimated the effective radius of light traps (125 W bulbs) to be less than 25 m. The effective trapping region varies from species to species (Bowden (1982), see previous section) and between different trap types.

Field data obtained from blacklight samples support the view of a rather small effective radius of weak light sources. Schulze & Fiedler (2002) sampled pyralid moth ensembles from different strata of a lowland rainforest in Borneo using a single 15 W tube. Ensembles from sites in close proximity were significantly distinct (measured with the NESS index of similarity, see Chapter 6). The same was found with geometrids in two habitat gradients and two forest strata in Borneo (Beck et al. 2002). Schulze & Fiedler reason that traps with a wide attraction radius would have sampled a more homogeneous fauna. In another study in a forest in Central Europe, two light traps (15 W blacklight) were operated at 45 m distance from one another (Hausmann 1990). Depending on the measure of similarity applied to Hausmann’s data set (not shown), his Macrolepidoptera samples were similar but certainly not identical. Hence, relatively weak light sources such as those used in South Ecuador are expected to only attract moths from relatively short distances.

DOES THE ATTRACTION RADIUS DEPEND ON THE VEGETATION STRUCTURE?

The density of the vegetation around a light trap might be assumed to have an impact on the number of individuals and species caught. Although this assumption is plausible to a certain extent, evidence for such an impact is lacking and needs to be tested explicitly. As shown above, the effective radius of a light trap is rather small. Hence, differences in the attraction of insects can only be expected if the vegetation differs between sites within a narrow radius around the trap. In any case, dense stands of vegetation should be avoided. Schulze & Fiedler (2002) found little influence of vegetation density on light trap samples. They argued that if this were the case, light sources in the upper open canopy would have attracted more moths than traps placed in the rather dense understorey vegetation. However, no such effects were apparent (see also Beck et al. 2002).

INFLUENCE OF WEATHER AND MOON

There is extensive literature concerning the influence of weather factors and the phase of the moon on light-trap catches (e.g. Persson 1976, Muirhead-Thompson 1991, Yela & Holyoak 1997, Holloway et al. 2001, Intachat et al. 2001). It can be reviewed only briefly here. Catches in South Ecuador were usually carried out without regard to the weather. Geometrid moths were apparently unaffected even by heavy rainfalls and came towards the light source in high abundance. The beginning of light rain during a catch often corresponded with an increased activity of the moths, but this has not been quantified. Sample size is generally known to be influenced by weather conditions such as temperature, wind and humidity (Holloway et al. 2001). For example, Persson (1976) and Yela & Holyoak (1997) found that light-trap catches decreased with mean wind speed. An increased mean temperature can be associated with an increased catch in some Lepidoptera groups (McGeachie 1989).

In the study area in South Ecuador, the temperature declined at an average of 1.26 K (± 0.36) during the three-hour period of moth catching. Figure 2 shows the linear decrease of the temperature along the elevational gradient. Braun (2002) provided very similar data on temperature changes along the gradient. One question that arises is whether temperature had a systematic effect on the activity of ensembles along the altitudinal gradient. I expected that the flight period of species that occur at high altitudes is restricted to the relatively warm period of time that follows immediately after dusk. On the contrary, species at lower altitudes should be less dependent on the time of the night and will not show a similarly strong decrease in activity. Therefore, I calculated the proportions of specimen numbers of six time intervals (only autumn data) between 6.30 and 9.30 p.m. local time for all sites except those where no data from autumn were available (7a, 8b, 9b, see Chapter 4). Samples from spring 1999 were not included because of a time shift due to differences in the beginning of dusk (Figure 3, see below). I subsequently plotted the proportions of the total number of specimens caught within each of the six intervals against altitude. While there were no significant correlations in the first five time intervals, the proportion of specimens significantly decreased in the 6th time interval as altitude increased (Spearman's r = -0.59, p<0.01, sequential Bonferroni correction according to Hochberg (1988)). Figure 4 shows the non-linear decrease. Hence, this results supports the theory that the flight period is subject to a certain temperature effect with regard to the length of the nightly flight period. However, the correlation is not strong. A prolonged sampling effort could substantiate the results and show possible differences in the flight activities at different altitudes more clearly.

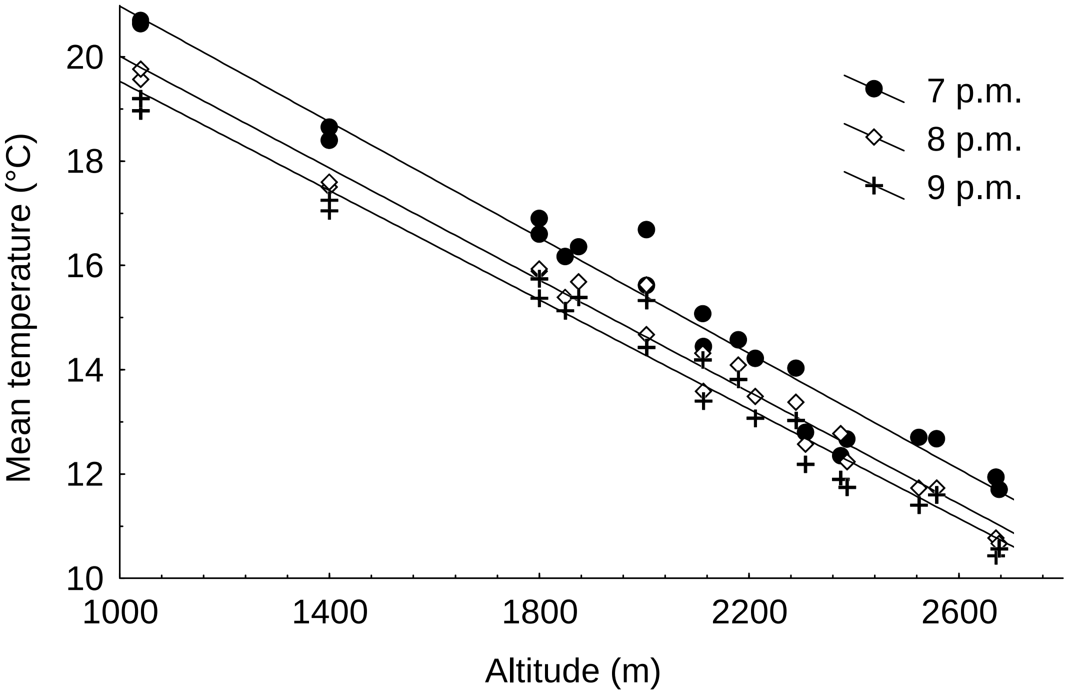


Figure 2 Average temperature measured at 7, 8 and 9 p.m. local time during the catches. The temperature declines linearly as altitude increases. Pearson correlations (all p<0.001): **7 p.m.** r =-0.98, **8 p.m.** r = -0.99, **9 p.m.** r = -0.99

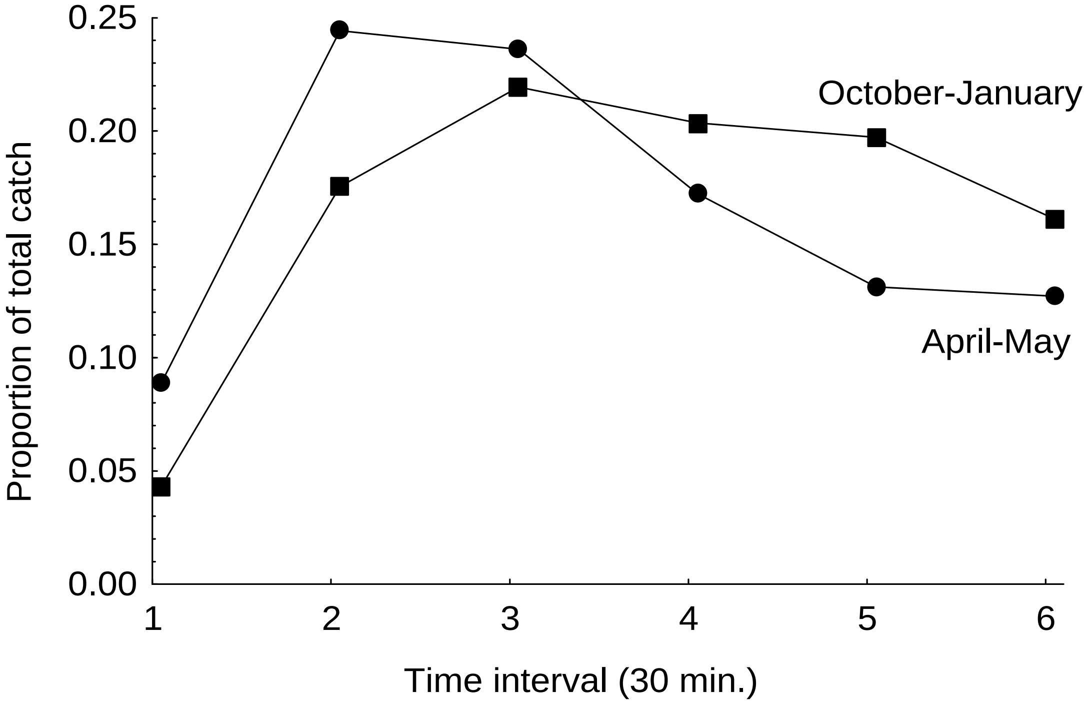


Figure 3 Average proportions of specimens collected during a period of three hours from 6.30 to 9.30 p.m. local time (six time intervals). Catches performed in April to May 1999 peak in the second time interval, whereas catches performed in December 1999 to January 2000, and October to November 2000, peak in the third interval.

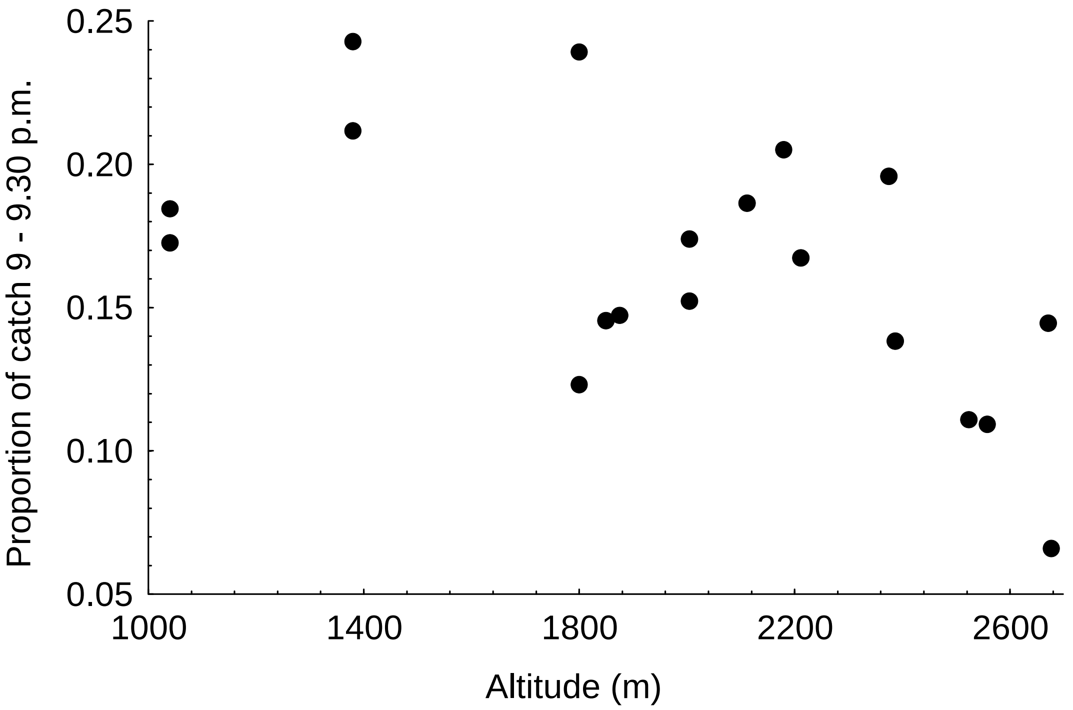


Figure 4 Correlation between the proportion of activity in the time period from 9 to 9.30 p.m. and altitude at 19 sites. Among all six time intervals analysed, the activity significantly decreases with altitude only in this last 30 min. interval (Spearman's r = -0.59, p<0.01). The result remains significant after sequential Bonferroni correction according to Hochberg (1988).

The phase of the moon has an important impact on the efficiency of light traps. For example, Rothampstead trap catches were at their lowest around the period of full moon and at their highest during periods when there was a new moon or there was no moon apparent (Muirhead-Thomson 1991). McGeachie (1989) and Yela & Holyoak (1997) found similar patterns. Catches near full moon in Ecuador yielded very low numbers of specimens. For "economical" reasons, catches were subsequently restricted to phases between three days after full moon until five days before full moon. The background illumination of the full moon makes artificial light sources practically "invisible" for insects. This effect is particularly strong in the tropics when the moon is at its zenith. There are considerable differences between illumination on nights where there is no moon and those where there is full moonlight; for example, the full moon gives about ten times more light than the half-moon (Bowden 1973).

EFFECTS OF THE TYPE OF TRAP

Worldwide, many different types of light traps are used (see Muirhead-Thomson 1991). Although it would ideally be desirable to use one standard method, there are practical reasons why trap designs have to be adjusted to different environments. For example, Leinonen et al. (1998) stressed the importance of background illumination at high latitudes in summer months, which required a certain type of trap. Areas exposed to wind may also require a different design than sheltered areas in forests, and tropical rainforests pose different problems than temperate habitats. Leinonen et al. (1998) calibrated several trap designs in Northern Europe, but cross calibration, as suggested by Holloway et al. (2001), has rarely been performed in tropical regions (but see Intachat & Woiwod 1999).

In Borneo, Schulze & Fiedler (2002) and Beck et al. (2002) used a single actinic tube that was powered by batteries. They caught a sufficiently large number of specimens, which allowed an analysis of single catches of pyralid moths. A major advantage of this type of trap is that it can be transported to remote places in a backpack by one person, which is usually not feasible with a generator-run light trap. Stronger light sources often lead to a larger number of specimens responding to the trap (Bowden 1982). However, particularly small moths such as Pyralidae and most Geometridae tend to avoid very strong light sources and hide in nearby vegetation. Hsiao (1972) discussed this as a "dazzle and escape" behaviour. On the other hand, larger moths can be more effectively sampled with stronger mercury vapour lamps (W. Nässig pers. comm.).

Particularly small and delicate moths will usually be left in a much better condition if specimens are collected manually, compared with those specimens which are obtained from automatic traps (Robinson et al. 1995, Holloway et al. 2001). In a few nights in South Ecuador an upper limit of manual collecting capacity was reached when more than 800 individuals responded to the trap within three hours. If automatic traps had been used, such a large number of specimens would have led to a lot of damage to the specimens themselves, and many specimens would have escaped. In montane forests at Mount Kilimanjaro, J. Axmacher (pers. comm.) compared the performance of an automatic trap and a light tower (hand sampling) as described above (Figure 1). Although the automatic traps were run 250 times during the whole night, fewer species were caught than with the light tower, which was operated 46 times for three hours per night. However, automatic traps are advantageous with regard to the time effort required, particularly in habitats with low species abundances and for all-night sampling.

SITE OF LIGHT-TRAP: GROUND OR CANOPY?

Tropical tree canopies often contain a very diverse selection of arthropods (review in Basset 2001). This raises questions as to whether a significant proportion of moths are restricted to canopies and whether light-traps have to be operated not only at ground level but also at upper strata in order to completely sample ensembles. Schulze (2000) and Schulze et al. (2001) did indeed find significant differences between ensembles at different strata in pyralid and sphingid moths in a Bornean lowland rainforest. However, light-trapping in canopies poses considerable logistical problems and cannot be carried out in forests with weak crown architecture such as in upper montane forests. The ECSF area is also very steep and trees in ridge stands are relatively small (heights <20 m, declining with altitude (Paulsch 2002)). Under these circumstances, no distinct canopy moth faunas can be expected. The situation might be different at the lowest sites of the study area (at 1,040 m) where trees are larger (ca. 25 m height, D. Piechowski pers. comm.), and the area is not very steep. If a certain proportion of the fauna was restricted to canopies, this could lead to a potential underestimation of diversity. However, in a study of geometrids in Borneo, Beck et al. (2002) showed that neither diversity nor abundance were higher in the canopy than at the ground. Although samples were distinctly different between the canopy and understorey, the observed patterns were largely due to differences in abundance of species rather than different species compositions. Furthermore, Beck et al. (2002) found that combined understorey and canopy geometrid samples never exceeded diversity scores for understorey ensembles alone. Hence, the restriction of sampling to ground level appears to be justified, in particular in montane forests.

SEASONALITY AND TIME EFFORT CONSTRAINTS

Samples from three field periods were analysed in this study (April to May 1999, December 1999 to early January 2000, and October to November 2000). Temporal variation occurs in insect communities in tropical regions with regard to the number of species and specimens. Regions where there are marked seasonal changes between wet and dry periods are particularly affected (Wolda 1978a, b, Novotný & Basset 1998, Wagner 2001). In contrast, Hebert (1980) showed that Lepidoptera ensembles were apparently aseasonal in climates with constant rainfall levels (see also Barlow & Woiwod 1989, Schulze & Fiedler 2002). A similar pattern is expected in the study area in Ecuador because it receives rainfall throughout the year without a marked dry season. However, a short drier period (“veranillo”) occurs between October and February with precipitation rates around 75 to 150 mm per month at 1,950 m above sea level (ca. 2,000 mm per annum, Emck (in prep.)). The database is not sufficient to state whether or not any seasonal (i.e. regularly re-occurring) effects appear. However, even in nearly constant environments, fluctuations in the abundance of species must always be expected. This phenomenon has to be considered, e.g. in the choice of the analytical instruments (Chapters 5 and 6). For example, similarity indices should not over-emphasise the most abundant species since changes in their population sizes would greatly affect the results (Chapter 6).

We restricted and standardised the time effort of nightly catches to three hours from the start of dusk. Sampling in this period has proven to be most effective because the flight activity of many species reaches a maximum in this time and then declines slowly (Thomas 1996, Schulze 2000). Many moth species commence activity around the end of twilight (Dreisig 1980). Figure 3 shows activity patterns of geometrid moths in South Ecuador. The activity peaks soon after dusk and eventually declines gradually. The peak occurs slightly earlier in April – May than in October – January because of a later sunset in the latter period. Certain species which are active exclusively late at night might have been missed (see Schulze & Fiedler 2002). However, unlike other groups such as Arctiidae, geometrids generally show no tendency towards late-night activity (R. Trusch, pers. comm.) In a study of Macrolepidoptera in an East Canadian forest, Thomas & Thomas (1994) compared one-hour samples with eight-hour samples and found that diversity values of the alpha-parameter of the log-series (Fisher et al. 1943) were very similar. They concluded that the short sampling period was sufficient for the comparison between sites.

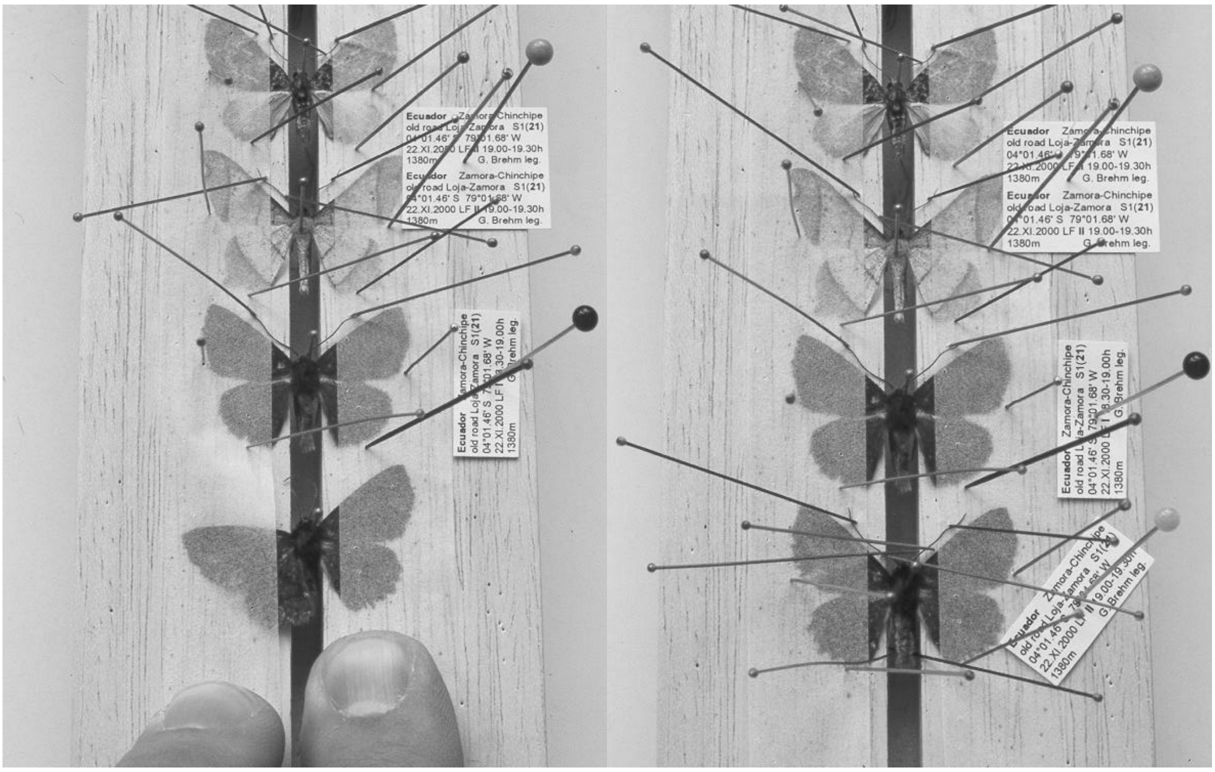


Figure 5 Spreading of moths on a spreading board. Insect pins are utilised in order to minimise damage of the board. The number of pins is kept to a minimum. If the pins that fix the antennae are removed after approximately one hour, the breaking of the antennae can be avoided because they are fixed but still flexible. The paper must be kept tight in order to fix the wings in a horizontal position. Labels provide information of date, time and place of catch. In order to ease later sorting, each specimen is provided with an extra label with the individual identity database number (e.g. ID# 1234).

PROCESSING OF SPECIMENS

The time required to process specimens becomes an increasingly important factor as sample size increases (e.g. Holloway 1984). For example, a difference of one minute of work per moth adds up to more than 16 working-hours per 1,000 specimens. As a consequence, even little improvements in the flow of work can result in considerable time saving. Therefore, every step of processing should be evaluated in terms of efficiency. For example, moth specimens that have been frozen for storage can often be spread more easily and faster (and are of better quality) than dried specimens (D. Bartsch pers. comm.). Some authors have recommended drying the material in order to avoid the specimens going mouldy (Holloway et al. 2001). However, freezing should be considered as an alternative method, provided that a freezer is available, provision of electricity is safe, and transportation requires a relatively short period of time. Some Thymol might be added to the material as an anti-mould agent (Holloway et al*.* 2001).

Proper spreading of all specimens from a sample is recommended since this optimises rapid and reliable identification. However, if it is possible to identify specimens "on the hand", it might suffice to put the specimens onto a pin without spreading them. Spreading boards made of soft wood such as Samba (e.g. Firma Meier, Munich) are most appropriate. The technique of spreading has been described in various sources, e.g. by Koch (1982) and Reid (1983). If moths are arranged close to each other and the fixing paper is kept tight, a minimum of four pins per specimen has proven to be sufficient to fix the wings (see Figure 5). When insect pins are used instead of normal pins, damage to the spreading boards is minimised. The boards should be stored in a dry and dark place for at least two weeks before moths can be removed. The process can also be accelerated when boards are put into an oven at moderate temperatures (ca. 50°C) for two days (Holloway et al. 2001, W. Nässig pers. comm.). The correct labelling is crucial for the scientific value of specimens (Holloway et al. 2001). The use of unique individual identification numbers (= database numbers) allows a quick identification of specimens and the resorting and reanalysing of the material.

IDENTIFICATION

No comprehensive literature is currently available that allows the identification of Neotropical geometrids, but several taxonomical revisions allow a determination of species in a number of genera, predominantly in the subfamilies Ennominae and Geometrinae (Cook & Scoble 1995, Pitkin 1996, 2002, Pitkin et al. 1996, Rindge 1964, 1967, 1973, 1978, 1983, 1986, 1990, Scoble 1995, Scoble & Krüger 2002). Furthermore, a systematic catalogue is available (Scoble 1999), and there are some encouraging attempts towards a systematic work on the Lepidoptera of Ecuador (Piñas Rubio & Pesántez 1997, Piñas Rubio et al. 2000, Bollino & Onore 2001). Despite this lack of reliable identification literature in most taxa, a high proportion of geometrid taxa could be determined in the Zoologische Staatssammlung, Munich, and the Natural History Museum, London. So far, 51.7% of the morphospecies of the whole family Geometridae were assigned to species level, 12.8% were placed near a known species (but were apparently different from it), 33.5% were assigned to genus and 2% to subfamily level. The determination success is not identical between the subfamilies (Figure 6). In Ennominae and Geometrinae a significantly higher proportion was assigned to species level than in the respective remaining

Geometridae. The proportion of Larentiinae is significantly lower and no deviations occur in Sterrhinae. Table 1 (p. 45) shows the χ^2-values. The total numbers of species are shown in Chapter 5. The patterns can be explained by the relatively high “attractiveness” of the larger-sized Ennominae and the colourful Geometrinae to taxonomists. It is well known that larger and more conspicuous animals have generally attracted more attention by taxonomists than small and inconspicuous ones (e.g. Scoble et al. 1995). The total proportion of taxa that could be assigned to species-level is remarkably high, but still underestimated. The true proportion of species in the sample that are new to science is very difficult to assess. All relevant museum collections would have to be checked because no comprehensive literature exists which allows the identification of Neotropical geometrids (see above). The proportion of specimens that could be identified to species level (66.5%) is considerably higher than the proportion of morphospecies (51.7%) identified to this level. The reason for this difference might be that the probability of collecting the more common species is higher, and that subsequently, these were more often described by taxonomists.

All sorting was based on the differentiation of wing patterns. Four hundred and ten specimens (2.9% of the total catch of 14,348) could not be reliably identified because they were too worn, and had to be discarded before further analyses were carried out. The study of the genitalia structures offered a potential alternative approach (e.g. Fernández-Rubio 1986 and Holloway 2001 with references therein). However, if properly performed, the method is very time-consuming and was therefore only applied to a selected set of 47 taxa of “doubtful cases” (one to three specimens each). Durable slides were made and the structures of male genitalia were carefully examined by R. Trusch (unpubl. data). In 27 cases, the sorting was maintained, in ten cases one externally defined morphospecies was split into two species, and in five cases, supposed species-pairs were fused to one species. In total the change in the number of taxa was modest (from 47 to 52). This examination shows that the species number even in a subset of doubtfully sorted taxa (“worst case scenario”) remains at the same level of magnitude.

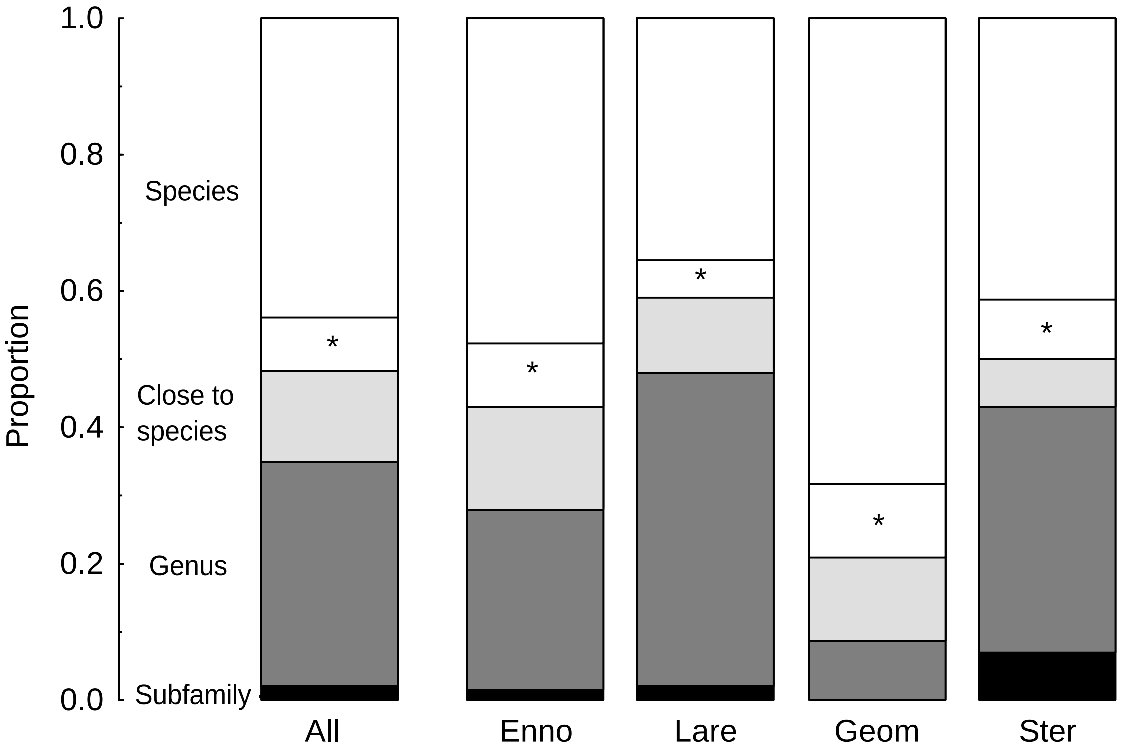


Figure 6 Identification success in Geometridae and four subfamilies. **Enno**minae, **Lare**ntiinae, **Geom**etrinae, **Ster**rhinae. ***** not fully certain. 51.7% of the whole family Geometridae could be assigned to species level. Identification was comparatively easier in Ennominae and Geometrinae, whereas a smaller proportion could be assigned to species level in Larentiinae and Sterrhinae.

Conclusions

Collecting with light-traps is the only method that enables a wide array of taxonomic groups to be sampled quantitatively in large numbers (Holloway et al. 2001). Methodological constraints that result in a somehow “distorted” picture of moth assemblages must be considered. The application of additional collecting techniques would be required if a complete inventory is to be achieved since some species are exclusively diurnal (Appendix 4). Species that are not attracted to light have to be sampled by hand-netting, bait-traps or by collection of larvae. However, as with geometrid ensembles worldwide, the proportion of such species is expected to be rather low (see also Chapter 5). The overall influence of seasonal effects as well as site of the trap are also expected to be low. Analytical instruments have to take distortions into account. As will be shown in the following chapters, results from light-trap samples are all readily interpretable and ecologically meaningful.

4 Faunal composition and endemism of geometrid moths in an Ecuadorian montane rainforest

INTRODUCTION

It is well known that animal species, and higher taxa such as families, are not evenly distributed throughout the earth, and that their diversity often changes along environmental gradients. For example, most groups of insects such as ants, termites, butterflies and beetles are most species-rich at low latitudes. Relatively few insect groups, e.g. aphids, sawflies, syrphids, psyllids, ichneumonids, braconids and bees, reach their highest species numbers at higher latitudes (Gauld 1987, Holloway 1987, Gaston 2000 with references therein, but see Horstmann 1999). There is an intense debate about the possible underlying mechanisms of latitudinal patterns of species richness (Chown & Gaston 2000). However, altitudinal gradients have often been neglected despite their potential as powerful natural experimental systems (Körner 2000, Lomolino 2001). Altitudinal gradients offer very different climates and habitat types in close proximity to each other. The role of historical factors such as long-lasting isolation is much less pronounced than in latitudinal gradients, and the regional species pool is virtually identical at all study sites. Hence, actual distributions of species are mainly influenced by ecological factors. However, studies on insect diversity along altitudinal gradients are relatively scarce, in particular for tropical mountain areas (but see e.g. McCoy 1990 with a review, Olson 1994, Brühl et al. 1999, Schulze 2000, Holloway et al. 2001).

The species-rich family Geometridae was investigated along an altitudinal gradient in a montane rainforest in southern Ecuador. Geometrids are a relatively habitat-specific group of herbivorous insects and thus very suitable for ecological studies (for tropical geometrids: Intachat et al. (1997), Kitching et al. (2000), Beck et al. (2002)). Changes of diversity along gradients can be documented in various complementary ways. Alpha-diversity (intra-habitat diversity) is compared in Chapter 5, while in Chapters 6 and 7 beta-diversity (inter-habitat diversity) along the altitudinal gradient is discussed. In this chapter, I will compare community structures on a higher taxonomic level and assess the relative contributions of subfamilies, tribes and genera within the Geometridae.

Geometrid moths occur in every biogeographical region (Scoble et al. 1995 give detailed lists). Worldwide the family contains approximately 21,000 described species and is currently divided into nine subfamilies (Holloway et al. 2001).

Fauna and flora can often be characterised by the relative proportions of their components (e.g. Gentry 1988, Hayek & Buzas 1997). Proportions (= ratios) of certain taxa compared with other taxa are frequently used for the estimation of species numbers (reviewed in Colwell & Coddington 1994), but for this purpose the relevant ratios have to be approximately constant throughout the entities compared. The calculation does not require complete inventories and allows for comparison of samples taken from areas of different size. Thus, investigation of the composition of communities along environmental gradients can reveal important patterns which complement absolute measures of diversity.

So far, the relative proportions of geometrid moth subfamilies have only been investigated and quantified thoroughly in the Indo-Pacific region (Holloway 1987, Beck 1998, Kitching et al. 2000). Holloway showed that the subfamily Larentiinae increases in proportion with altitude and isolation of island habitats, whereas other subfamilies such as the species-rich Ennominae, as well as Geometrinae and Sterrhinae, decrease. Hausmann (2001) reported a strong proportional decline of Sterrhinae in southern Italy from 47% of geometrid species in lowland regions to 9% at higher elevations while Larentiinae concomitantly increased to ratios of up to 61%. Notably, a similar increase of Larentiinae towards higher latitudes has been reported (e.g. Holloway 1987), but has never been explicitly documented and tested for significance.

The number of endemic species in an area is an important criterion for conservation priorities (Gentry 1986, Pressey et al. 1993, Kessler 2001). For example, Andean montane cloud forests have been shown to be richer in endemic vertebrate species than Amazonian lowland rainforests (Leo 1995, Myers et al. 2000). The highest ratios of endemic species of vascular plants world-wide are found in the Northern Andes (Myers et al. 2000). In this chapter, the general term endemism refers to any localised distributions (according to Gentry 1986). The conservation of endemic tropical insect species has also become an issue in recent years (Lewis et al. 1988, Morrone 1999, Anderson & Ashe 2000, Fermon et al. 2000). However, little is known about the degree of endemism of invertebrates in tropical regions, because detailed information on their distribution is not usually available. Since this also applies to Neotropical geometrid moths I utilised type localities of species as a coarse surrogate for endemism. Data of type localities is easily accessible in a modern catalogue of the geometrid moths of the world (Parsons et al. in Scoble 1999). By using this data, it was possible to test if a higher ratio of species was originally obtained from high-altitude samples, compared with low-altitude samples in Andean countries such as Ecuador and Peru. I expected to find a higher ratio of endemic species from sites at high altitudes: species which are adapted to the colder climates in such habitats are probably geographically much more restricted than those which are adapted to the warmer environments of the Amazonian lowlands. As a corollary, I expected to find a higher proportion of widespread species at the lower sites, indicated by type localities in non-Andean countries such as Brazil or Panama.

In addition to investigating the ratios of taxa and endemic species, I examined the dominance structure within geometrid ensembles (terminology according to Fauth et al. 1996) along the altitudinal gradient. Vegetation structure and diversity in high-altitude habitats is less complex and diverse compared with low-altitude sites (Paulsch 2002, Homeier in prep., Matezki in prep.). In particular, one tree species tends to dominate the vegetation at higher altitudes in the study area (Cyrillaceae: *Purdiaea nutans*). Hence, high-altitude habitats were expected to support fewer species and to exhibit a higher dominance of adapted geometrids. However, Chapter 5 shows that the diversity in fact remains consistently high throughout the gradient. Whether or not there are changes in terms of dominance of single moth species will be discussed here.

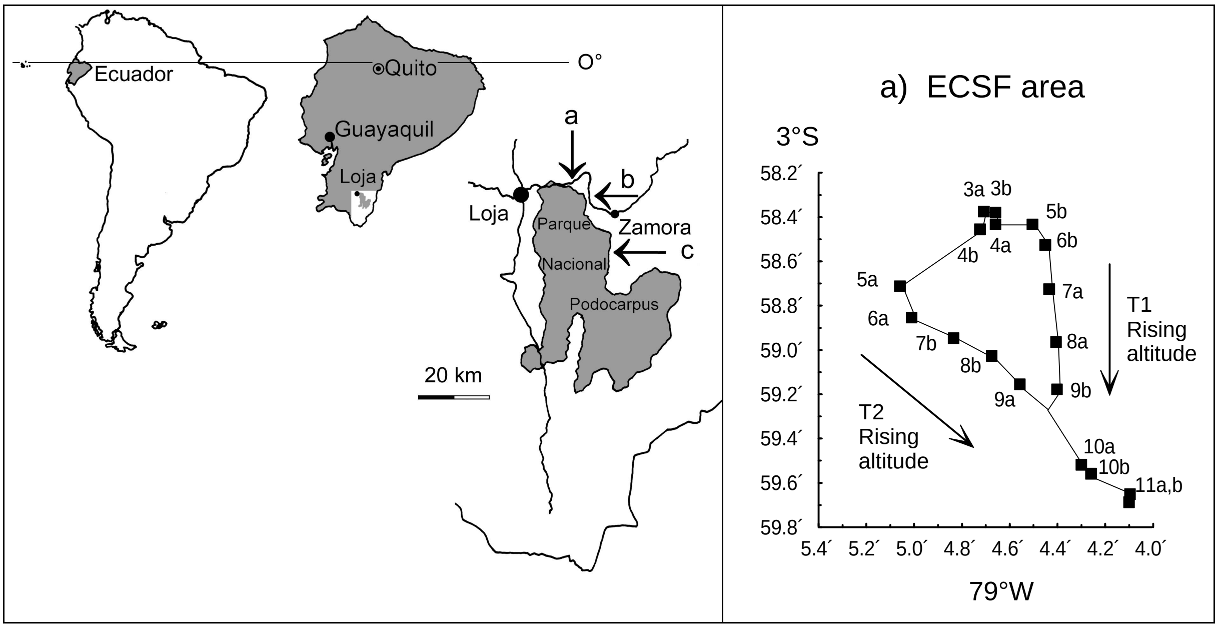


Figure 1 Geographical positions of the 22 sampling sites in South America and Ecuador at the northern border of the Podocarpus National Park, province Zamora-Chinchipe. Left: overview, right: sites in the area of the Estación Científica San Francisco (ECSF), covering ca. 2.56 x 2.92 km (7.46 km^2). **(a)** Eighteen sites are situated within the area of the ECSF and range between 1,800 m above sea level (sites 3a and 3b) and 2,677 m (site 11b). **(b)** Two sites (2a and 2b) are situated close to the old road Loja-Zamora (4°1.11´S, 79°0.95´W) at 1,400 m **(c)** Two sites are situated south of Zamora at Bombuscaro (4°6.87´S, 78°58.31´W and 4°6.99´S, 78°58.89´W) at 1,040 m (1a and 1b). Table 1 provides a complete list of all altitudes and coordinates.

METHODS

STUDY AREA

The study area in southern Ecuador is situated within the Eastern Cordillera of the Andes and belongs politically to the province of Zamora-Chinchipe (Figure 1). It lies at the northern border of the Podocarpus National Park which comprises 146,280 ha of mostly undisturbed vegetation at elevations ranging between 1,000 and 3,600 m above sea level (Madsen & Øllgard 1994).

Table 1 List of sampling sites (sorted by altitude), geographical positions and dates of collection. Coordinates were measured using a Global Positioning System (Garmin GPS III). Localities: **B** Bombuscaro, **S** Road between Loja and Zamora, **T1**, **T2** transect paths in the area of the ECSF. Each site was sampled between two and four times. Dates of collection: day, month (**Apr**il, **Oct**ober, **Nov**ember, **Dec**ember, **Jan**uary), year (19**99**, 20**00**). Further data on vegetation structure is provided in Appendix 5.

Site	Locality	Latitude (S)	Longitude (W)	Altitude (m)	Dates of collection
1a	B	4° 06´ 870	78° 58´ 031	1,040	05Dec99, 27Oct00
1b	B	4° 06´ 985	78° 58´ 089	1,040	05Dec99, 27Oct00
2a	S	4° 01´ 109	79° 00´ 948	1,380	30Oct00, 22Nov00
2b	S	4° 01´ 109	79° 00´ 948	1,380	30Oct00, 22Nov00
3a	T1	3° 58´ 454	79° 04´ 726	1,800	13Apr99, 06May99, 23May99, 26Dec99
3b	T2	3° 58´ 375	79° 04´ 710	1,800	19Apr99, 07May99, 17May99, 26Dec99
4a	T2	3° 58´ 379	79° 04´ 661	1,850	12Apr99, 26Apr99, 16May99, 28Dec99
4b	T1	3° 58´ 431	79° 04´ 661	1,875	11Apr99, 25Apr99, 11May99, 28Dec99
5a	T1	3° 58´ 710	79° 05´ 063	2,005	20Apr99, 11May99, 18May99, 30Dec99
5b	T2	3° 58´ 429	79° 04´ 507	2,005	21Apr99, 03May99, 13May99, 30Dec99
6a	T1	3° 58´ 853	79° 05´ 011	2,112	24Apr99, 10May99, 18May99
6b	T2	3° 58´ 522	79° 04´ 455	2,113	16Apr99, 03May99, 13May99
7a	T2	3° 58´ 724	79° 04´ 435	2,180	14Apr99, 05May99, 12May99, 29Dec99
7b	T1	3° 58´ 944	79° 04´ 837	2,212	27Apr99, 07May99, 17May99, 02Jan00
8a	T2	3° 58´ 962	79° 04´ 409	2,290	17Apr99, 05May99, 12May99
8b	T1	3° 59´ 025	79° 04´ 679	2,308	25Apr99, 09May99, 21May99, 03Jan00
9a	T1	3° 59´ 153	79° 04´ 560	2,375	26Apr99, 09May99, 21May99, 03Jan00
9b	T2	3° 59´ 173	79° 04´ 403	2,387	21Apr99, 06May99, 10May99, 01Jan00
10a	T1	3° 59´ 516	79° 04´ 300	2,524	16Dec99, 18Oct99
10b	T1	3° 59´ 558	79° 04´ 262	2,558	16Dec99, 18Oct99
11a	T1	3° 59´ 648	79° 04´ 096	2,671	21Oct00, 20Nov00
11b	T1	3° 59´ 684	79° 04´ 103	2,677	21Oct00, 20Nov00

A total of 22 sites were chosen at altitudes between 1,040 m and 2,677 m, two replicates at each level of altitude. Eighteen plots lay within the area around the Estación Científica San Francisco (ECSF, 3°58´ S, 79°5´ W) and four were situated outside at lower elevations. Table 1 shows the altitude and geographical coordinates of the sites measured using a Global Positioning System (Garmin GPS III). Annual precipitation ranges between some 2,000 mm at the lower elevations and reaches approximately 5,500 mm at the highest sites, depending on aspect and altitude (Emck in prep.). The mean monthly temperature is 20 – 22°C at 970 m (Zamora) and 10 – 12°C at 2,670 m (ECSF area). A detailed description of the climate of the area will be provided by Emck (in prep.). The potential influence of climatic factors on the diversity of geometrid moths is discussed in Chapters 5 and 7. According to Sierra's vegetation classification system (1999), the study sites are situated in three different types of forest (as translated from Spanish): evergreen forest of foothills (800 – 1,300 m), evergreen lower montane forest (1,300 – 1,800 m) and montane cloud forest (1,800 – 2,800 m). Bussmann (2001) provided a more finely scaled approach for the area of the ECSF, and split the latter category into montane broadleaved forest (1,850 – 2,100 m), upper montane forest (2,100 – 2,750 m), and subalpine elfin forest (from 2,450 m upwards). Another approach has been pursued by Paulsch (2002) who classified the forest by the characteristics of the vegetation structure. Appendix 5 provides additional information on the forest types of the sampling sites according to his classification.

SAMPLING AT LIGHT AND IDENTIFICATION

Chapter 3 discusses in-depth applied methods of sampling and potential problems. They are only briefly described here. Two 15 W tubes in a white gauze cylinder were operated at ground level between 6.30 and 9.30 p.m. local time. Specimens were collected manually during three field periods (April to May 1999, October 1999 to January 2000, and October to November 2000, Table 1). The sites at medium to high elevations were sampled during the first two periods whereas the lowest and highest sites were sampled during the two last periods. Between two and four nightly catches were analysed from each site (Table 1). Specimens were first sorted to morphospecies and later identified in the Zoologische Staatssammlung, Munich and the Natural History Museum, London. Fifty-two percent of species could be assigned to species level (Chapter 3).

RELATIVE PROPORTIONS OF TAXA

Proportions were calculated from species numbers as well as from specimen numbers. Within Geometridae, the four largest subfamilies (Ennominae, Larentiinae, Geometrinae and Sterrhinae) were compared. The remaining subfamilies Oenochrominae and Desmobathrinae were ignored because of their minimal numbers (three and one species, respectively). The two largest subfamilies Ennominae and Larentiinae had sufficiently high numbers of species to allow further analyses. Due to the availability of a modern revision of Neotropical genera (Pitkin 2002), it was possible to analyse ennomines at tribal level. In Larentiinae, reliable sorting of all species at tribal level was not possible. However, analysis of the patterns of the three largest genera offered a suitable alternative, since the genera *Eois, Eupithecia* and *Psaliodes* account for more than 70% of the species and more than 60% of the specimens in all samples.

STATISTICS

The Spearman rank correlation coefficient was used since this is recommended when proportions are measured (Fowler et al. 1998). In order to compare relationships between subfamilies, χ^2 test statistics were applied. Observed values of one subfamily were compared with the values calculated from the total of the respective remaining subfamilies. All analyses were performed with the program Statistica 5.5 (StatSoft 1999). Multiple tests of significance on inter-related data sets were Bonferroni-corrected according to Hochberg (1988).

ENDEMISM AND DOMINANCE STRUCTURE

Type localities of species were taken from the catalogue of geometrid moths of the world (Parsons et al. in Scoble 1999). The following regions were categorised for analysis: (1) Ecuador and Peru, (2) the remaining tropical Andean countries, Bolivia, Colombia and Venezuela, (3) the remaining Neotropical countries (including Mexico), and (4) imprecise, unknown or incorrect localities (e.g. “South America” or “Bengale”), as well as series of syntypes described from two different categories of (1) to (3). Ecuador and Peru were combined into one data point since the study area is situated near the border of these two countries. The Berger-Parker dominance index is defined as the ratio of the most common species in an assemblage (Magurran 1988, Lepš et al. 2001). It was calculated with the software package by Henderson & Seaby (1998).

RESULTS

PROPORTIONS OF SUBFAMILIES WITHIN GEOMETRIDAE

Figure 2 shows the proportions of the subfamilies, based on the species number. Species of the subfamily Ennominae clearly dominate at low elevational levels, whereas the ratio of Larentiinae increases towards high altitudes. While proportions of Ennominae, Geometrinae and Sterrhinae steadily decrease, the proportion of Larentiinae increases. Species proportions and altitude are all highly significantly correlated (Table 2). Very similar patterns occur when numbers of specimens are analysed (not shown in a figure, but see Table 2), although changes in the smaller subfamilies Geometrinae and Sterrhinae are only of modest significance, probably due to stochastic effects.

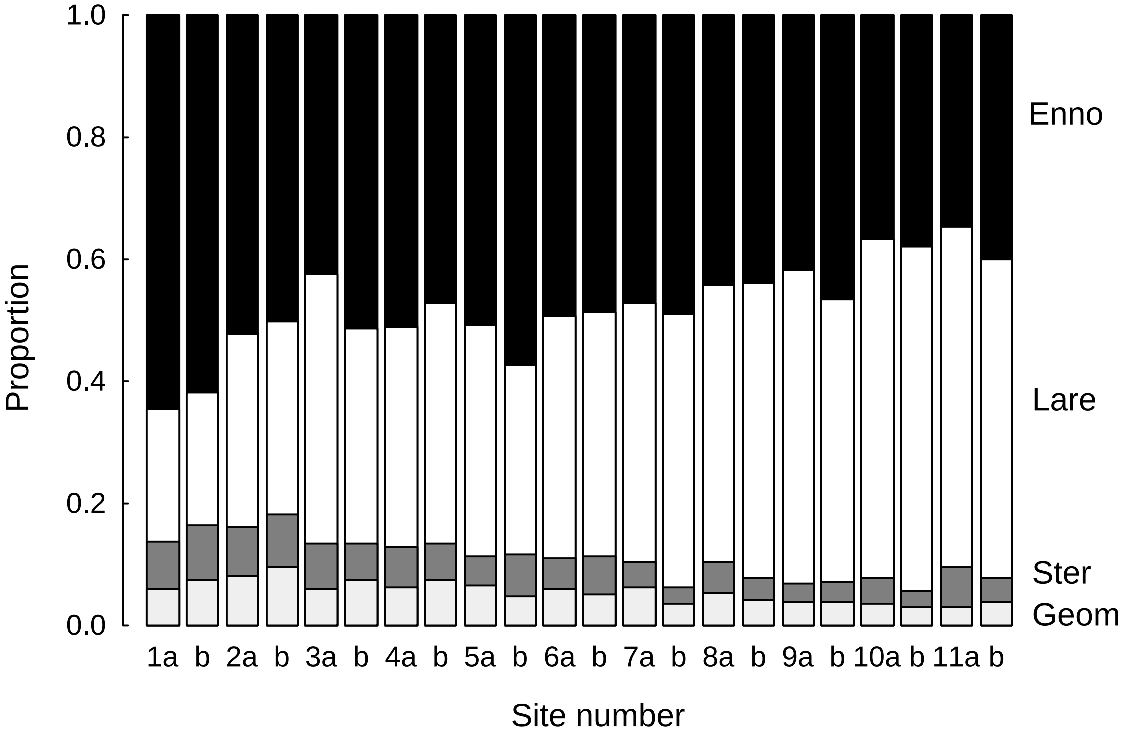


Figure 2 Proportions of subfamilies, based on species numbers, see Table 2 for correlation coefficients. Sites are sorted by altitude. Geographical positions of all sites are provided in Table 1. **Enno**minae, **Lare**ntiinae, **Ster**rhinae, **Geom**etrinae.

Table 2 Spearman rank correlation coefficients between proportions of four subfamilies within Geometridae and altitude. * p<0.05, **** p<0.001. All results remain significant after sequential Bonferroni correction.

	Ennominae	Larentiinae	Geometrinae	Sterrhinae
Species number	-0.84 ****	0.92 ****	-0.79 ****	-0.84 ****
Specimen number	-0.84 ****	0.89 ****	-0.45 *	-0.52 *

PROPORTIONS OF TRIBES WITHIN ENNOMINAE

The picture of proportions within Ennominae is more complex because of the high number of analysed taxa (ten tribes and rest, Figure 3). Three smaller tribes are restricted to a few lower sites (Cassymini) or vanish at the highest altitudes (Macariini and Palyadini). The remaining groups occur throughout the whole gradient. Only one of them, the Boarmiini, significantly decreases in species proportion. The other tribes all increase in their ratios, but this is only at a significant level in the Caberini and the "*Cratoptera* group" The patterns of specimen proportions are similar in most tribes (Table 3), with two exceptions: Caberini (no significant relationship) and Nacophorini (a strong positive correlation between altitude and number of specimens).

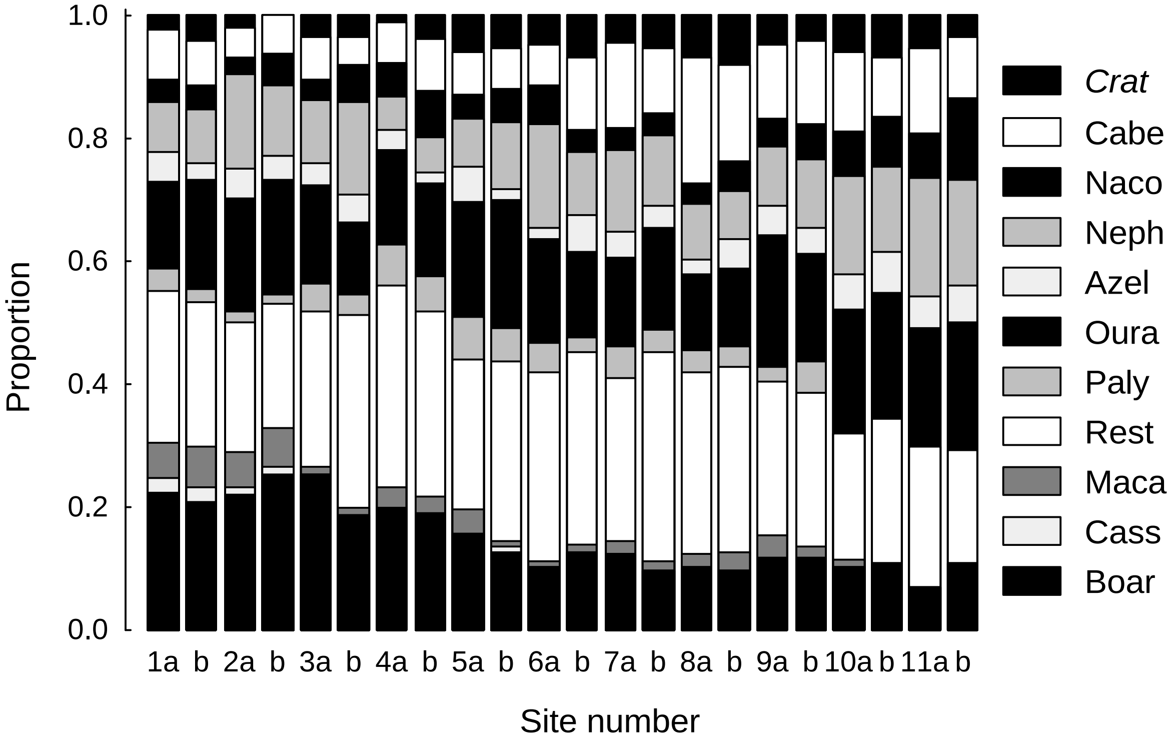


Figure 3 Proportional contribution, based on species numbers, of ten tribes and the remainder within Ennominae. **Azel**ini, **Boar**miini, **Cabe**rini, **Cass**ymini, "***Crat**optera* group", **Maca**riini, **Naco**phorini, **Neph**odiini, **Oura**pterygini, **Paly**adini, **Rest**: Ennominae not assigned to tribe. Sites are sorted by altitude. Geographical positions of all sites are provided in Table 1.

Table 3 Spearman rank correlation coefficients between proportions of species of ten tribes within Ennominae versus altitude. **ns** not significant, * p<0.05, *** p<0.005, **** p<0.001. Ennominae species not assigned to tribe r = -0.16, ns; Ennominae specimens not assigned to tribe: r = 0.34, ns. Printed in **bold** are results that remain significant after sequential Bonferroni correction.

	Azelini	Boarmiini	Caberini	Cassymini	"*Cratoptera* group"
Species number	0.45 *	**-0.86 ******	**0.71 ******	**-0.67 ******	**0.61 *****
Specimen number	0.38 ns	**-0.79 ******	0.25 ns	**-0.67 ******	**0.81 ******

	Macariini	Nacophorini	Nephodiini	Ourapterygini	Palyadini
Species number	**-0.61 ******	0.49 *	0.41 ns	0.35 ns	-0.35 ns
Specimen number	**-0.67 ******	**0.75 ******	0.44 *	0.46 *	-0.32 ns

PROPORTIONS OF GENERA WITHIN LARENTIINAE

Clear patterns along the altitudinal gradient are also visible in this second large subfamily. Three large genera account for at least 70% of the species in this taxon (Figure 4). The proportion of the genus *Eupithecia* increases highly significantly with altitude, whereas it decreases in the genus *Eois.* The genus *Psaliodes* shows no or only a modest correlation and the remaining species show a significant decrease only in specimen numbers.

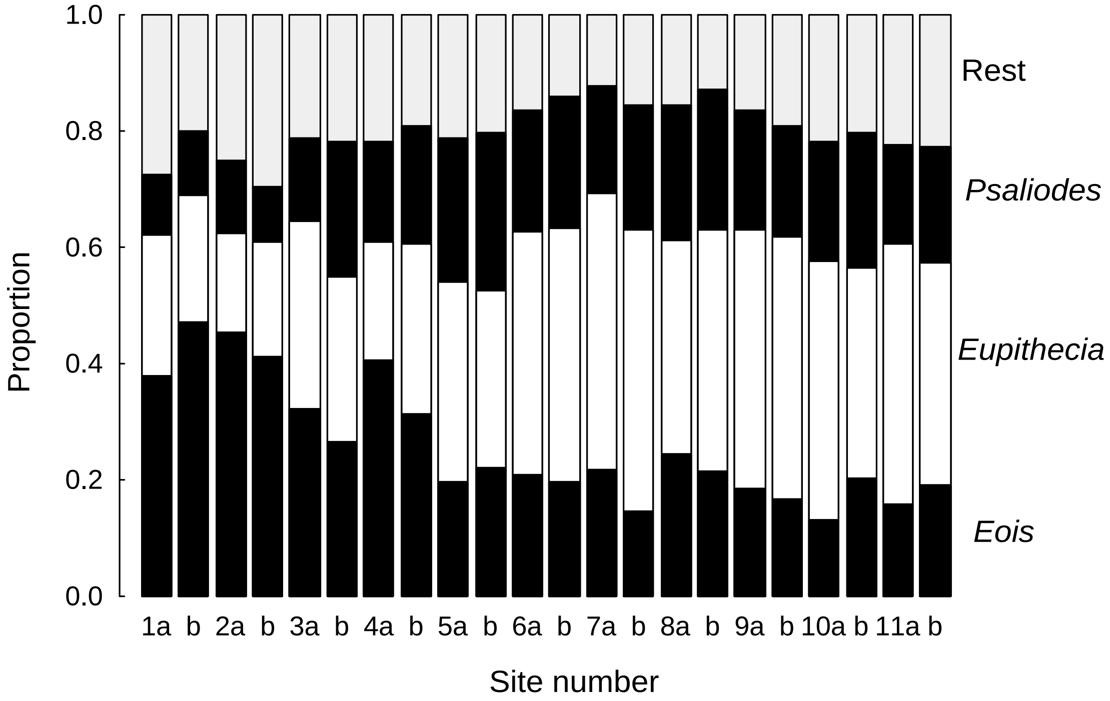


Figure 4 Proportions of three large genera, based on species numbers, within the subfamily Larentiinae. Sites are sorted by altitude. See Table 1 for geographical positions of all sites.

Table 4 Spearman rank correlation coefficients between proportions of three genera and rest within Larentiinae versus altitude. **ns** not significant, ***** p<0.05, *** p<0.005, **** p<0.001. All results remain significant after sequential Bonferroni correction.

	Eupithecia	*Psaliodes*	*Eois*	Rest
Species number	0.77 ****	0.39 ns	-0.85 ****	-0.28 ns
Specimen number	0.78 ****	0.53 *	-0.65 ***	-0.58 ***

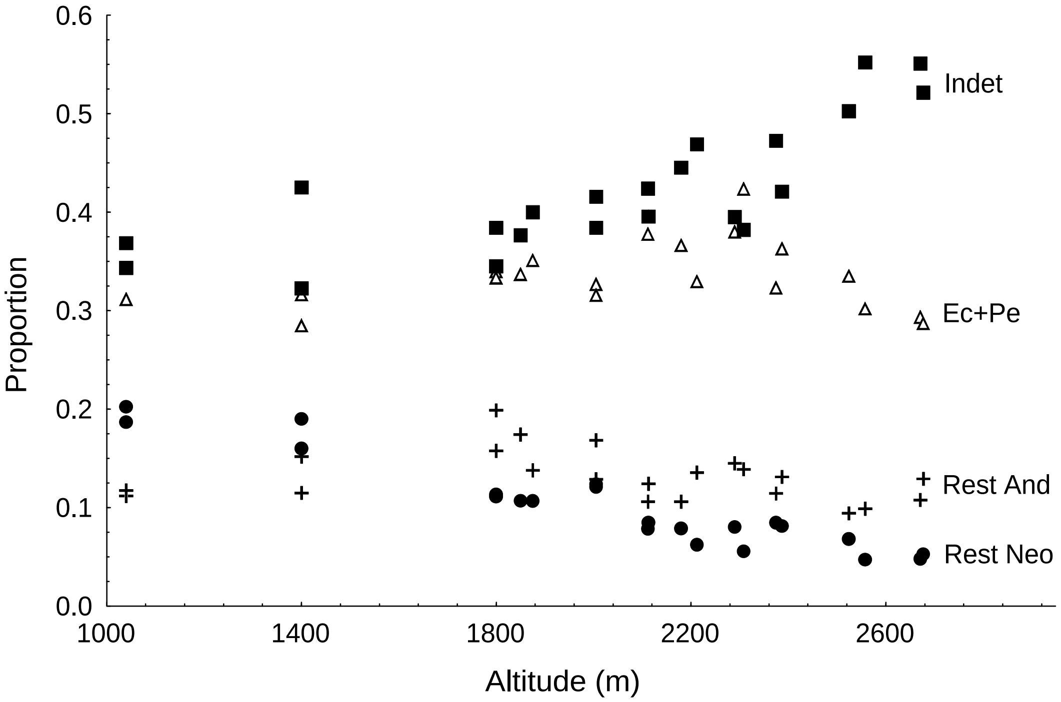


Figure 5 Proportions of different categories of type localities of Geometridae along the altitudinal gradient, undetermined species are included. **Indet** not determined to species level; **Ec + Pe** Ecuador and Peru; **Rest And** Bolivia, Colombia, Venezuela; **Rest Neo** All remaining Neotropical countries except the formerly listed.

ENDEMISM

Type localities of the majority of determined species are situated in Ecuador and Peru (55.4%), 21.2% in Bolivia, Columbia and Venezuela, 21.4% in the remaining Neotropical countries, and in only 1.7% no type locality is available. More than 75% of the securely identified species were thus originally described from tropical Andean countries. This clearly indicates a high total degree of endemism of the sampled geometrid moths. Along the altitudinal gradient, two strong correlations can be recognised (Figure 5, Table 5). First, the ratio of taxa that can be determined to species level significantly decreases along the altitudinal gradient. Second, the proportion of species with type localities in Neotropical countries other than the

Andean nations significantly decreases from around 20% at 1,040 m to ca. 5% at 2,677 m. If undetermined species are excluded from the analysis, the proportion of species described from Ecuador and Peru significantly increases (Table 5).

Table 5 Spearman rank correlation coefficients of proportions of type localities of Geometridae versus altitude. (a) undetermined species included, (b) undetermined species excluded. **** p<0.001, **ns** not significant. All results remain significant after sequential Bonferroni correction.

	Not determined	Ecuador + Peru	Rest Andean	Rest Neotropics
(a)	0.78 ****	-0.01 ns	-0.38 ns	-0.90 ****
(b)	-	0.81 ****	0.15 ns	-0.88 ****

It has been shown that the ratios of subfamilies change significantly along the gradient (Figure 2). Since differences in the distribution of type localities between subfamilies could potentially be responsible for the patterns described here, such differences were tested with χ^2 statistics. It had to be shown that patterns in single subfamilies did not differ from those of the remaining geometrids. As presented in Table 6, subfamilies do not differ significantly in their type-locality composition. Hence, this indicates there is a “true” increase in endemic species with altitude.

Table 6 Total number of species, number of taxa identified at species level, and proportions of type localities for all samples pooled for Geometridae, and the four major subfamilies. The proportions of type localities were tested for differences between the subfamilies. Expected numbers (not shown) were calculated from the respective remaining subfamilies. **ns** not significant.

	Geometridae	Ennominae	Larentiinae	Sterrhinae	Geometrinae
Total number of species	1,010	500	391	57	58
Identified at species level	518	281	159	29	45
(1) Ecuador + Peru	0.56	0.58	0.53	0.48	0.58
(2) Other Andean countries	0.21	0.21	0.23	0.28	0.09
(3) Rest South America	0.21	0.20	0.21	0.24	0.31
(4) Unknown etc.	0.02	0.01	0.03	0.00	0.02
χ^2 (df = 3), p	-	2.99 ns	2.42 ns	0.93 ns	6.25 ns

DOMINANCE STRUCTURE

The dominance of the most abundant species is generally very low in Geometridae (Table 7). In the smaller systematic entities, dominance increases with elevation. Sterrhinae and Geometrinae are dominated by species of *Idaea* and *Lissochlora*, respectively. However, sampling effects become particularly pronounced in these small subsamples (5-22 species, 8-90 specimens per site). In Ennominae, dominance significantly decreases along the altitudinal gradient whereas in the other subfamilies no or only very weak correlations occur.

Table 7 Proportions of the most abundant species (Berger-Parker index) in Geometridae and four subfamilies, and Spearman rank correlations between the proportions and altitude. **ns** not significant, * p<0.05, *** p<0.005. Printed in **bold** is the result that remains significant after sequential Bonferroni correction.

	Geometridae	Ennominae	Larentiinae	Sterrhinae	Geometrinae
Berger-Parker ± SD	0.08 ± 0.04	0.12 ± 0.07	0.10 ± 0.04	0.48 ± 0.24	0.37 ± 0.16
r, p	-0.50 *	**-0.64 *****	-0.17 ns	0.39 ns	0.50 *

DISCUSSION

PATTERNS ALONG ALTITUDINAL AND LATITUDINAL GRADIENTS

Altitudinal and latitudinal gradients are similar in many ways (e.g. declining temperature), but differ fundamentally in others (e.g. increase of seasonality at high latitudes and much greater distances between sampling sites). Chown and Gaston (2000) stressed the importance of latitudinal gradients in the understanding of macroecological patterns, whereas Körner (2000) emphasised the advantages of investigating altitudinal gradients. Since data sources are available that allow an interpretation of latitudinal gradients, I aimed to compare latitudinal with altitudinal gradients. Unfortunately, no suitable data source currently exists in the New World. However, the use of a recent checklist of geometrid moths of all European countries (Müller 1996) seemed to be appropriate, because it offers reliable and detailed faunal information on a regional scale. Countries and islands were sorted by their median latitude. Iceland and Malta were excluded because of their low total number of species, while data for Turkey are incomplete. The proportions of subfamilies are shown in Figure 6. Qualitatively the patterns resemble those found along the altitudinal gradient in Ecuador (Figure 2). The subfamilies follow the very same tendencies: all groups significantly decline, except for Larentiinae which increases in proportion towards high latitudes (Table 8). Some substantial differences exist in the relatively low proportion of Ennominae and the high proportion of Sterrhinae in Europe, compared with Ecuador. The occurrence of *Idaea* species (Sterrhinae) in dry habitats can be explained by their ability to use leaf litter and detritus as food (Hausmann 2001). Sterrhinae are important in the Mediterranean, but strongly decline towards higher latitudes in Europe. Since strong wet-dry gradients exist in the Andes, it would be very interesting to test whether the occurrence of Sterrhinae might reflect such gradients there. Ennomines are overall much less prevalent in Europe and have a very different tribal composition than in South America. Differences in their total ratio are thus difficult to interpret.

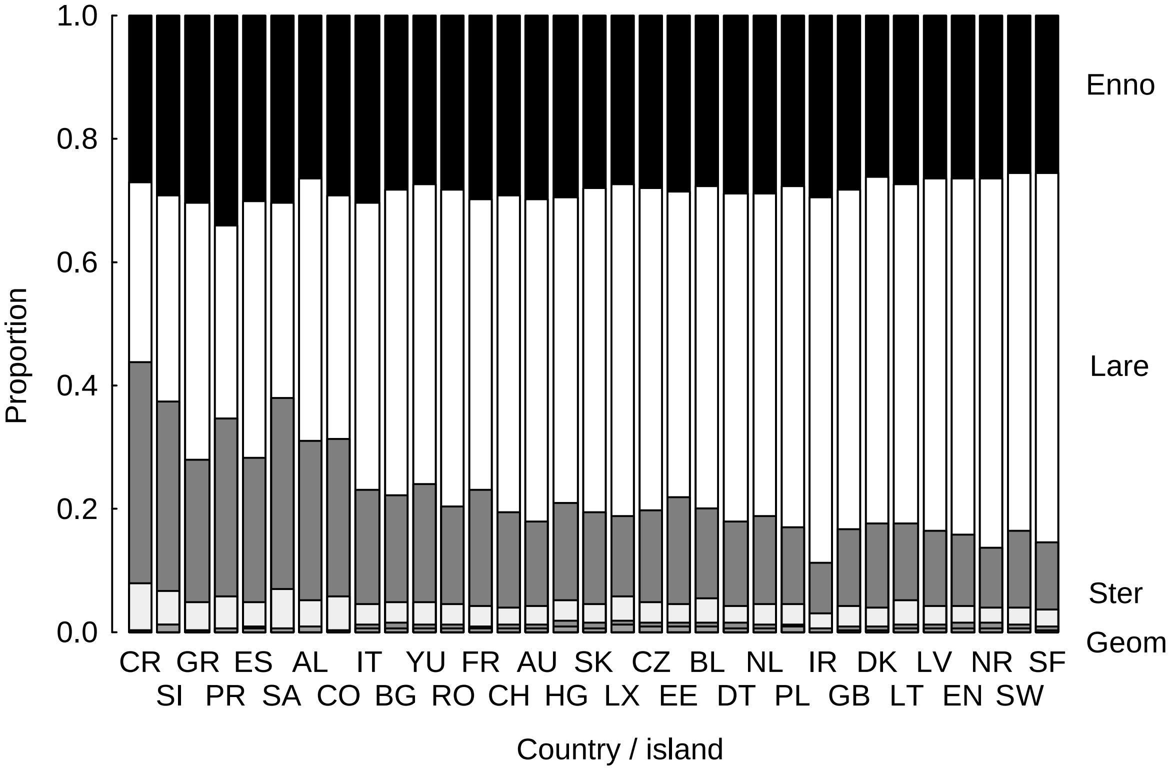


Figure 6 Proportions of subfamilies of European Geometridae. Data is from Müller (1996). Locations are sorted by their median latitude. Abbreviations: SI Sicily, CR Crete, GR Greece, PR Portugal, ES Spain, SA Sardinia, AL Albania, CO Corse, IT Italy, BG Bulgaria, YU (former) Yugoslavia, RO Romania, FR France, CH Switzerland, AU Austria, HG Hungary, SK Slovakia, LX Luxembourg, CZ Czech Republic, EE Eastern Europe, BL Belgium, DT Germany, NL Netherlands, PL Poland, IR Ireland, GB Great Britain, DK Denmark, LT Lithuania, LV Latvia, EN Estonia, NR Norway, SW Sweden, SF Finland. Iceland, Malta (small faunas) and Turkey (incompletely covered fauna) were excluded from the analysis. **Enno**minae, **Lare**ntiinae, **Ster**rhinae, **Geom**etrinae.

Table 8 Spearman rank correlation coefficients between proportions of species of four subfamilies within European Geometridae and the median latitude of European countries and islands. **** p<0.001. All results remain significant after sequential Bonferroni correction.

Ennominae	Larentiinae	Geometrinae	Sterrhinae
-0.85 ****	0.93 ****	-0.80 ****	-0.79 ****

Both the more local analysis along an altitudinal gradient in Ecuador and the large-scale comparison along a latitudinal gradient in Europe reveal that Larentiinae increase significantly towards cooler environmental conditions. This strongly suggests a common underlying mechanism. Larentiinae are obviously better adapted to cold and wet conditions than are other groups. Their montane characteristics have already been emphasised by Holloway (1997). The “strength” of temperate-zone Larentiinae moths might be their ability to cope with frost, but this does not apply to most of the tropical species. Some species, such as *Operophtera brumata*, show a remarkable flight physiology during winter months in temperate regions. A particular physiological adaptation of larentiines seems to be their ability to develop and fly in unfavourable climatic conditions such as prevail at the upper end of the investigated elevational gradient. The annual precipitation is ca. 5,500 mm, and the average monthly temperature ranges between 10 – 12°C (Emck in prep.). Similarly unfavourable conditions are also found at high latitudes, e.g. in Iceland, where 16 out of 17 geometrid moth species are larentiines (Müller 1996). Larentiine species appear to be relatively weak flyers and might profit disproportionately from a nearly enemy-free space with regard to insectivorous bats.

RATIO CHANGES WITHIN ENNOMINAE AND LARENTIINAE

The patterns in Ennominae can partly be explained by the different host-plant preferences of the tribes. The available information on host-plant relationships has been reviewed in Chapter 2. While tribes comprised of host-specialists tend to decline with altitude, the more polyphagous groups exhibit different patterns.

Three small tribes vanish completely at higher altitudes. It is notable that the species in these tribes tend to be specialised towards Fabaceae (Cassymini, Macariini), or Myrsinaceae (Palyadini). In Ecuador, Fabaceae are mainly distributed in lowland rainforests and decrease towards higher altitudes (Gentry 1988, Jørgensen & León-Yanez 1999, in the study area: Homeier in prep.). The distribution of specialised herbivores depends on that of their host-plants. In contrast, potential host-plants of Palyadini do occur at high altitude habitats (Myrsinaceae: *Myrsine* *andina*) (Bussmann 2001). Either there are physiological constraints that do not allow Palyadini to exceed altitudes of 2,400 m, or species such as *M. andina* are not suitable as hosts.

Polyphagous groups such as Nacophorini and Ourapterygini do not change or even increase in ratio as altitude increases. On this higher taxonomical level, host-plants appear not to be a limiting factor, and the habitats seem to be structurally rich enough to support a high diversity of species. However, the same would be expected for all other tribes with mainly polyphagous larvae. Most species of the tribe Boarmiini are also expected to be rather polyphagous (Chapter 2), but Boarmiini decline in relation to all other Ennominae. Boarmiini species are possibly less cold-adapted than species of the other tribes, but this hypothesis needs to be further supported.

The changes in species composition in Larentiinae are remarkable, but even more difficult to interpret than in Ennominae, since the host-plant relationships of Neotropical Larentiinae are particularly poorly documented (Chapter 2). In the genus *Eois* some preference for Piperaceae has been shown. *Eois* species dominate the Larentiinae ensembles at low altitudes where plants of the family Piperaceae are more abundant than at higher altitudes (Homeier in prep.). It is possible that the increase of the genus *Eupithecia* is related to the higher availability of the potential hosts (e.g. inflorescences of Asteraceae, see Chapters 2 and 5). Nothing is known about the hosts of the genus *Psaliodes*.

ENDEMISM AND CONSERVATION PRIORITIES

Can type localities reflect endemism? They are often inexact, do not necessarily represent the centre of distribution of a species, and are potentially biased towards certain preferred collecting places. However, in large samples such effects will not play a major role. Furthermore, the present study focussed on relative changes. Absolute numbers of different type localities are not crucial, but changes of their relative representation along the altitudinal gradient are. Given considerable time more data on distribution could be extracted from museum specimens, but even such data would not be comprehensive nor would it represent random samples (Scoble et al. 1995). Hence, at least for a first tentative approach, type localities appear to be suitable surrogates for the location of distributional ranges.

The increasing number of taxa along the altitudinal gradient which cannot be determined to species level, can be explained by the increasing species number of Larentiinae whose members are more difficult to identify (Chapter 3). In this subfamily in particular, many of the still undescribed species will be restricted to montane regions. Furthermore, these regions are often more difficult to access than lowland sites.

Locally distributed species are expected to be more vulnerable than those which are widespread across the continent. The proportion of widespread species, as judged by their type locality, lies between 5% (2,677 m) and 20% (1,040 m). Type specimen were collected in countries such as Brazil, Panama and Costa Rica. These are minimum numbers because species which were documented in Ecuador and other Andean countries could of course be more widespread. However, the numbers give a good indication of how the degree of endemism rises with altitude. Similar tendencies were found in the much better known flora of Ecuador (Balslev 1988). The latter described the lowland flora as rich in widespread species, whereas mid-elevations housed about half of the species of the country. Prendergast et al. (1993) pointed out that regions with high numbers of species are not necessarily identical to those with a high degree of endemism. The patterns found in the present study support this view since the species richness is very high throughout the gradient (Chapter 5), whereas the ratio of endemism significantly changes. Montane cloud forests are among the world’s most threatened ecosystems, and rates of loss by deforestation exceed those of lowland tropical rainforests (Hamilton et al. 1995). This study therefore confirms the urgent need to conserve Andean montane rainforests with their unique biodiversity, in particular those at higher elevations. Though detailed inventories of insect faunas in the Andean region could reveal clearer patterns of local endemism, no further delay can be brooked in terms of action against further destruction of montane forest habitats.

ARE TAXON RATIOS USEFUL FOR DIVERSITY ESTIMATIONS?

Assuming constant ratios, it might be sufficient to restrict sampling to certain “indicator” taxa. Chapter 5 discusses in more detail the problems associated with such indicators. Some authors have suggested that the diversity of groups can be estimated from that of indicators or “focal taxa” (Colwell & Coddington 1994, Longino 1994, Beccaloni & Gaston 1995). The approximate constancy of such ratios is often not based on empirical evidence (Gaston 1992, Prendergast et al. 1993). This study shows that the ratios of taxa can change rapidly along environmental gradients. Hence, before ratios can be utilised as a basis for extrapolation, it is essential to assess at the outset the influence of environmental gradients in an area. Once a reliable pattern has been identified, the study of indicator taxa might indeed be sufficient for certain purposes. If, for example, the subfamily Larentiinae could have been sampled at a certain altitude in the study area in Ecuador, the diversity of Ennominae could be predicted quite accurately. However, if local changes in species composition are not taken into consideration, results can be highly misleading. In a hypothetical new study at another Andean locality, a new calibration of ratios would be required because altitudinal shifts in composition might vary geographically. Such variations between small and large mountains may result from the Massenerhebungseffekt (Tanner 1977, Holloway 1984, Flenley 1995). As a consequence, extrapolation by the use of ratios has to meet strict requirements before it can be applied. A network of reference sites around the world as suggested by Gaston (1992) would have to be very dense to be reliable, in particular in mountainous areas. There is probably no alternative to a better understanding of global biodiversity than carefully designed and co-ordinated studies at a regional level (Colwell & Coddington 1994).

DOMINANCE STRUCTURE

The overall dominance of a single species is very low in Geometridae and only changes in Ennominae at levels of high significance, but not in the expected direction. The lower structural and floristical diversity of the high-altitude habitats obviously does not support higher dominance of the commonest species, but actually the contrary in ennomines. The underlying mechanism for this phenomenon remains to be resolved. Moreover, nothing is known about competition between herbivorous insects in montane forests that might result in the dominance of one or a few species. However, Jermy (1985) showed that there is little evidence for significant interspecific competition between phytophagous insects.

The Berger-Parker index is unreliable in smaller taxonomic units such as Geometrinae and Sterrhinae. In these cases the index is vulnerable to the effects of erratically changing numbers of the most common species. On the contrary, samples comprising many species are not much affected by such changes because there are a number of relatively abundant species. Furthermore, the data set shows that the absolute level of dominance is dependent on the regarded taxonomic level. The most abundant species in the whole data set (*Psaliodes cedaza*, 382 specimens) is simultaneously the most abundant species in the genus, in the subfamily (Larentiinae) and in the family. This example shows the potential pitfalls of comparing absolute dominance values between different taxa. When, for example, dominance structures are compared between geometrid moths and pyralid moths, it must be considered that geometrid moths are a considerably larger taxon in the study area. According to Süßenbach (2001), the average value of the Berger-Parker dominance index of pyralid moths is distinctly higher than that of geometrid moths (0.19 ± 0.08 compared with 0.08 ± 0.04). At the same time, the total number of species sampled is significantly lower in Pyralidae than in Geometridae (748 compared to 1,010). Hence, at least a part of the difference between the values of both families is explained by different absolute numbers of species involved.

CONCLUSIONS

Although the alpha-diversity of geometrid moths remains at a consistently high level throughout the investigated gradient (Chapter 5), the faunal composition changes significantly at all taxonomic levels regarded. The patterns are remarkably clear and are very similar to those found at latitudinal gradients. Only the subfamily Larentiinae shows a significant increase in its proportion as altitude and latitude rise. Larentiine moths are obviously better adapted to climates that are characterised by low temperatures and high precipitation than all other groups of Geometridae. An advantage of such habitats could be a relatively low predation, e.g. by ants, bats and birds (see also Chapters 5 and 7). Montane cloud forests do not only hold a very high diversity of geometrid moths, but also a significantly higher proportion of locally restricted species than adjacent habitats at lower altitudes. Furthermore, the results clearly indicate the potential pitfalls of diversity estimations which rely on constant ratios between taxa, because such ratios might change rapidly and profoundly along environmental gradients.

5 Andean montane rainforests are a diversity hotspot for geometrid moths

INTRODUCTION

Tropical rainforests cover only 7% of the Earth's surface, but it is estimated that they harbour more than 50% of all existing species on the planet (Myers 1992). The exact number of species is still unknown, and the latest estimates of the number of arthropods range between five to ten million species (Ødegaard 2000). Herbivorous insects probably account for a major fraction of diversity (Erwin 1982, Ødegaard 2000). So far, montane forests were largely neglected with regard to studies on tropical arthropods. For example, although Basset (2001) reviewed 89 studies on canopy arthropods, none of them was conducted in a tropical montane habitat. The northern Andes have recently been recognised as a "hyper hotspot" on Earth for vascular plants and vertebrates (Henderson et al. 1991, Myers et al. 2000). However, apart from a few exceptions (Janzen et al. 1976, Olson 1994, Kling 2000, Ferrer-Paris 2001, Braun 2002), little is known about patterns of insect diversity in Andean montane forest habitats.

This dissertation is part of a broad interdisciplinary project investigating the functioning of a montane rainforest ecosystem in Ecuador (Beck & Müller-Hohenstein 2001, Fiedler 2001). The aim of my study was to evaluate the diversity of a major group of herbivorous insects in such a system. Folivorous insects have been recognised as the most important consumers in tropical forests (Coley & Barone 1996). Their functional role as regulators of primary production and nutrient cycling in temperate forest ecosystems is well documented (Mattson & Addy 1975, Swank et al. 1981, Lovett & Ruesink 1995). The ecology of Lepidoptera is better known than most other major group of insect herbivores are; yet this insect order comprises high species numbers (Solis & Pogue 1999). The moth family Geometridae is one of the three largest clades of Lepidoptera and currently includes more than 21,000 valid described species (Scoble 1999), with some 6,450 (30%) occurring in the Neotropical region. Their taxonomy is relatively advanced because a modern catalogue of all names (Scoble 1999) as well as generic revisions of Neotropical Geometrinae and Ennominae (Pitkin 1996, Pitkin 2002) are available. Studies of geometrids as a target group in tropical rainforests have been carried out e.g. in South East Asia (Holloway 1987, Intachat et al. 1997, Beck et al. 2002). Intachat & Woiwod (1999) described them as a suitable and practical group for detailed studies of biodiversity in tropical forests. Previously to the present study, no detailed ecological studies of geometrids in the Neotropical region have ever been conducted.

The dominant environmental gradient in mountainous habitats is altitude, which is directly related to decreasing temperature and increasing precipitation. Significant changes in the vegetation along altitudinal gradients in the Andes were first documented as early as by Alexander von Humboldt (von Humboldt & Bonpland 1807), and refined later (e.g. Grubb et al. 1963, Gentry 1988). Elevational changes in diversity have also been documented for a variety of animals in the Neotropical region, e.g. birds (Terborgh 1977, Rahbeck 1997), rodents (Sánchez-Cordero 2001) and bats (Matt 2001), but rarely for insects (Janzen et al. 1976, Olson 1994, Braun 2002).

Rahbeck (1995) found that approximately half of the reviewed studies showed a continuous decline in species richness with increasing altitude, whereas the other half detected a peak at medium elevations. In insect groups such as ants, a continuous loss of diversity has been detected (Brühl et al. 1999). Wolda (1987) also found decreasing species numbers of several insect groups such as homopterans and scarabaeid beetles as altitude increased. Although some authors suggested that the occurrence of mid-elevational peaks might be a sampling artefact (e.g. Wolda 1987), there is substantial evidence for the existence of such peaks in a broad range of organisms (McCoy (1990) and Grytnes & Vetaas (2002) with references therein). Among insects, several families of Lepidoptera in South East Asia have been reported to exhibit their largest diversity at medium elevations, between 600 m and 1,000 m above sea level (Holloway 1987, Holloway et al. 1990). However, only a few exceptions to an overall declining diversity at altitudes higher than 1,000 m have been documented for arthropods. Examples include larentiine moths (a subfamily of Geometridae), which are most species rich at high altitudes, and also show an increase with latitude in temperate regions (Chapter 4, Holloway 1987). Schulze (2000) reported that diversity of the families Geometridae and Arctiidae in Borneo reached maxima at altitudes between 1,200 m and 2,000 m. Above this altitude, only declining diversity has been recorded so far. This suggests that environmental conditions at high altitudes in tropical mountains become so harsh that a decreasing number of ectothermic insect species is able to cope with such circumstances.

In this first study of its kind in the Neotropical region, I aimed to investigate the diversity of a “mega-diverse” group of herbivorous insects in a montane Andean rainforest. This chapter focuses on patterns of intra-habitat diversity (alpha-diversity) along an altitudinal gradient covering a range of about 1,700 m, and ecosystem diversity (gamma-diversity, Whittaker (1972)). Analyses were carried out at the level of the family Geometridae, as well as of the level of the two largest subfamilies, Ennominae and Larentiinae. I expected a decline of diversity along the elevational gradient or diversity peaks at medium elevations for all taxonomic levels regarded.

Samples taken from tropical arthropod communities are a methodological challenge for diversity measures. They are almost always incomplete and the numbers of specimens available for analyses often diverge considerably between sites (e.g. Schulze & Fiedler 2002). Moreover, tropical arthropod communities are characterised by a high proportion of rare species that cannot be excluded as artefact or a group of marginal importance (Price et al. 1995, Novotný & Basset 2000). From the plethora of available measures of alpha-diversity (e.g. Hayek & Buzas 1997, Southwood & Henderson 2000), four were selected, their sample size dependence was tested and they were then applied. Suitable diversity measures should be able to discriminate between samples of different diversity *and* be independent of sample size in order to avoid misleading bias in the results.

METHODS

SAMPLING, STUDY AREA, ENVIRONMENTAL FACTORS

The light-trapping and processing methods applied are presented and discussed in Chapter 3, and the study area is described in detail in Chapter 4. Specimens were sorted to the level of morphospecies and subsequently assigned in museums to the level of species (52%), genus (46%) and subfamily (2%) (Chapter 3). Data was entered into a relational database, and the resulting species-site matrix (Appendix 2) was analysed. Subsequently, diversity scores were plotted against altitude. A list of available environmental factors in the study area is provided in Chapter 7. The potential influence of climate, vegetation structure, tree species diversity and other factors on the alpha-diversity of geometrid moths will be discussed (references in the Discussion).

ALPHA-DIVERSITY MEASURES

The analysis was restricted to four selected measures (see below). All measures were first tested for their sample-size dependence. Two commonly used measures were not taken into consideration here because they did not seem to be suitable for the purpose of this study: The Shannon-Wiener index is known to be sample size dependent. Moreover, both the Shannon-Wiener and the Simpson index emphasise the most common species. They tend to ignore rare species, the occurrence of which is rather typical in tropical arthropod samples (Lande 1996, Novotný & Basset 2000). Furthermore, there is no variance estimate available for Simpson's index (Lande 1996).

All analyses were performed separately for Geometridae and the two largest subfamilies Ennominae and Larentiinae. The remaining subfamilies (Geometrinae, Sterrhinae, Oenochrominae, and Desmobathrinae) were not analysed because of their insufficient numbers in the samples. All standard statistical analyses were performed using the software package Statistica 5.5 (StatSoft 1999). Since relationships between data in this study are non-linear, the Spearman rank correlation coefficient was used (Fowler et al. 1998), and multiple tests of significance were Bonferroni-corrected according to Hochberg (1988).

Species number Measurement of species richness by complete census is only feasible for a few organisms. For most organisms, measurement means sampling (Colwell & Coddington 1994). However, species numbers are still used widely as a measure of diversity. Misleading results and biases must be expected in incomplete samples that differ in size.

Alpha of the log-series (Fisher et al. 1943, hereafter: Fisher's alpha, also known as William's alpha) has been used in many studies of temperate and tropical arthropod assemblages (Wolda 1983, Thomas & Thomas 1994, Robinson et al. 1995). Although the underlying mechanisms responsible for the log-series distributions are not yet fully understood (Pachepsky et al. 2001), its mathematical simplicity and almost universal appearance in nature are appealing (Kempton & Taylor 1974, Robinson 1998). In contrast to other diversity indices, Fisher's alpha has been shown to be efficient at discrimination between sites, and is influenced mainly by the frequencies of species of medium abundance (Kempton & Taylor 1974). Samples from disturbed habitats tend to diverge from the log-series (Pachepsky et al. 2001, Beck et al. 2002), but Wolda (1983) showed that Fisher's alpha yields a robust measure even if the distribution of relative abundance significantly differs from a log-series. Several studies showed that Fisher's alpha tends to increase in tropical fauna even after long periods of sampling (Wolda 1987, Intachat & Holloway 2000, Holloway et al. 2001, Schulze & Fiedler 2002), and that consequently, it is not always independent of sample size. The fit of the log-series distribution was tested using a program developed by Henderson & Seaby (1998). It compares expected with observed numbers of species in abundance classes (octaves) using χ^2 test statistics. Fisher's alpha and standard deviations (according to Fisher's original formula, R. Colwell pers. comm.) were calculated with the program EstimateS 6.0 (Colwell 2000).

A minimum number of at least 100 specimens is usually recommended for calculating Fisher's alpha (Hayek & Buzas 1997). This number was not reached in only one sample of the subfamily Larentiinae (site 1a: 65 specimens).

Rarefaction methods offer a suitable alternative and are particularly useful if assemblages are sampled with different intensity or success (Hurlbert 1971). Rarefaction methods were reviewed by Achtziger et al. (1992) and most frequently applied in recent times, e.g. by DeVries et al. (1997), Willott (1999), Lewis (2001), and Schulze & Fiedler (2002). The geometrid samples were rarefied to a shared number of specimens using a program developed by Kenney & Krebs (2000). The program also provided standard deviations. Rarefied expected species numbers were calculated at the levels of 50, 100, 150, etc. specimens. This measure is expected to be independent of sample size since samples are standardised to an equal level.

Extrapolation Even in long-term studies and with effective sampling methods, tropical arthropod assemblages are difficult to assess fully because of their extreme species-richness (e.g. Lande 1996). By using extrapolation methods, the "true" number can be estimated if certain assumptions are not violated (Colwell & Coddington 1994). A number of estimators were tested empirically by Soberón & Llorente (1993), Beck (1998), and Süßenbach & Fiedler (1999). Colwell & Coddington (1994) recommended the use of non-parametric estimators as promising quantitative techniques. The estimator "Chao 1" is one of these estimators and has been used in several studies on moths (Thomas 1996, Schulze 2000, Beck et al. 2002). Analyses were performed using the computer program EstimateS 6.0 (Colwell 2000), and the bias-corrected formula of Chao 1 was used. Non-parametric estimators must underestimate the true richness if the sample is too sparse (Colwell & Coddington 1994). Since all samples contained at least 380 specimens, the use of "Chao 1" appeared to be justified. However, a certain dependence on sample size was expected, because the recorded number of species is an integral part of the formula of the estimator (Colwell & Coddington 1994).

RESULTS

TOTAL NUMBERS OF SPECIES AND SPECIMENS

A total of 13,938 specimens were collected from 22 sites, these included a proportion of 12.6% females (Chapter 3). Four hundred and ten specimens (2.9% of the total catch) could not be reliably sorted and had to be discarded. Figure 1 A shows the fluctuating number of specimens per season and site. Numbers cannot be directly compared because of the differing number of nightly catches analysed. The minimum and maximum number of specimens per site are 384 and 1,200, respectively. Figure 1 B shows the total number of species per site, partitioned into the subfamilies. The total number of observed species and morphospecies is 1,010. No previous study has ever counted anywhere near as many of geometrids in a single study area. The most species-rich subfamily is Ennominae (500 species), followed by Larentiinae (391), Sterrhinae (58), Geometrinae (57), Oenochrominae (3), and Desmobathrinae (1). The number of observed species per site ranges from 134 (site 1a) to 292 (site 7a), but actual numbers are expected to be higher (see below).

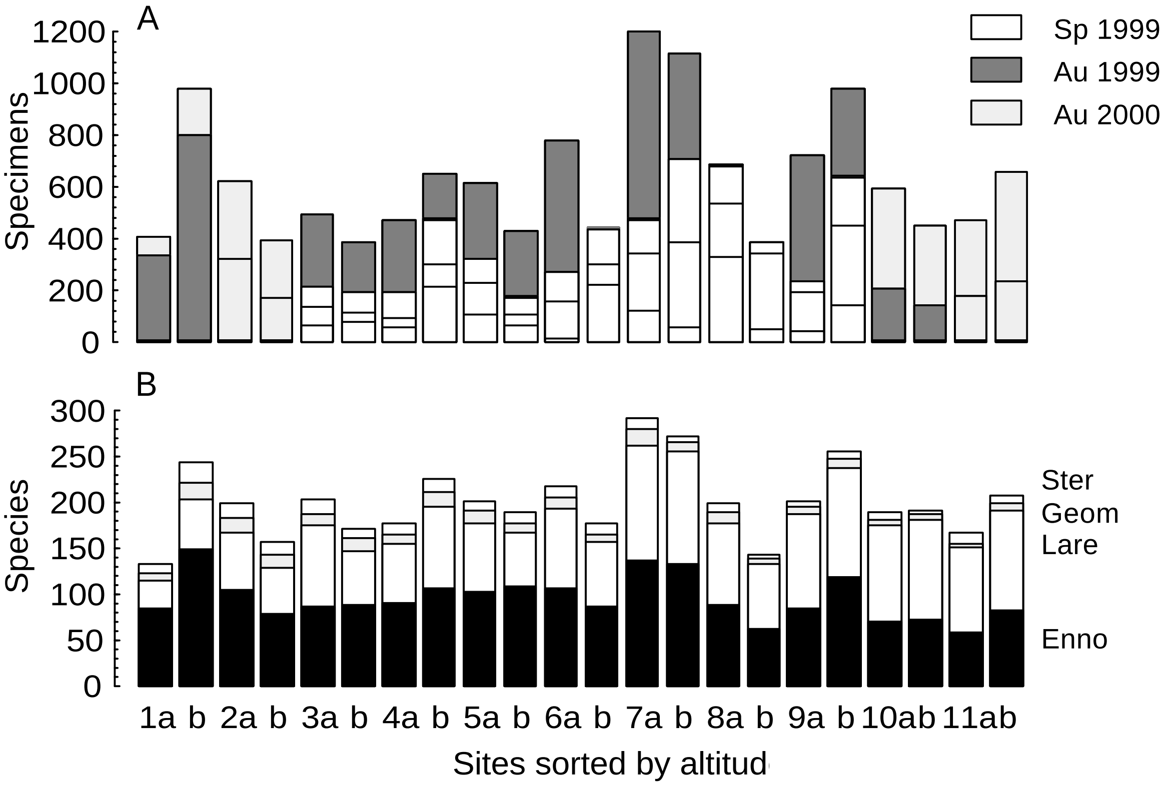


Figure 1 A Number of specimens collected at 22 sites. The sites are sorted by altitude and are partitioned according to the nightly catch and the sampling period. **Sp**ring **1999** (April-May), **Au**tumn 1999 (October 1999-January 2000), **Au**tumn **2000** (October-November 2000). **B** Number of species at 22 sites (sorted by altitude and partitioned across subfamilies). **Ster**rhinae, **Geom**etrinae, **Lare**ntiinae, **Enno**minae. Due to the chosen scale, Desmobathrinae and Oenochrominae are not visible. Desmobathrinae: One species at sites 1a and 1b. Oenochrominae: Two species at sites 1b and 7b, one species at sites 1a, 2a, 5a, 7a, 7b, 8a, 10a, and 11b.

DIVERSITY OF GEOMETRID MOTHS

Fisher's alpha of the log-series A significant deviation from the log-series occurs in ten out of 66 ensembles (Table 1). However, after performing the sequential Bonferroni procedure suggested by Hochberg (1988), the log-series distribution is rejected only in Geometridae and Ennominae at one site (number 1b, Table 2). The observed number of species in the first abundance class is larger than expected, i.e. there are "too many" rare species in the samples. Thus, calculation of Fisher's alpha seems to be appropriate in nearly all samples; the deviations that do occur are often slight, and will not substantially affect the results (see Methods). The pooled value of Fisher's alpha for all samples is 250.1 ± 4.2. Since an environmental (altitudinal) gradient and thus beta-diversity is incorporated in this figure, it can be regarded as an estimate of gamma-diversity for montane rainforests located within the altitudinal range of this study. Figure 2 A shows values for Geometridae at all 22 sites. They range from 69.3 ± 5.4 to 130.6 ± 10.4 and are among the highest values ever measured for local geometrid ensembles. There is no significant consistent change in Fisher's alpha along the altitudinal gradient (Table 2). The values for Ennominae range from 38.2 ± 3.4 to 66.7 ± 6.5, and for Larentiinae from 20.1 ± 4.1 to 64.2 ± 6.2 (Figure 2 A). In both subfamilies, there is no overall significant change in Fisher's alpha along the altitudinal gradient (Table 2). However, in Larentiinae, significant differences occur between the lowest and medium sites.

Table 1 Nominally significant deviations of samples from the log-series distribution. Provided are p-values from χ^2 tests after arranging species-abundances in octaves (between 3 and 4 degrees of freedom) (Henderson & Seaby 1998). Printed in **bold**: significant after sequential Bonferroni correction (Hochberg 1988). Samples from all other sites (levels 2, and 5-11) and all Larentiinae samples do not deviate from the log-series. A complete list of sites and coordinates is provided in Chapter 4.

Site number	Altitude (m)	Geometridae	Ennominae
1a	1,040	0.038	-
1b	1,040	**<0.001**	**0.003**
3a	1,800	0.027	0.048
3b	1,800	0.015	-
4a	1,850	0.010	0.006
4b	1,875	0.015	0.035

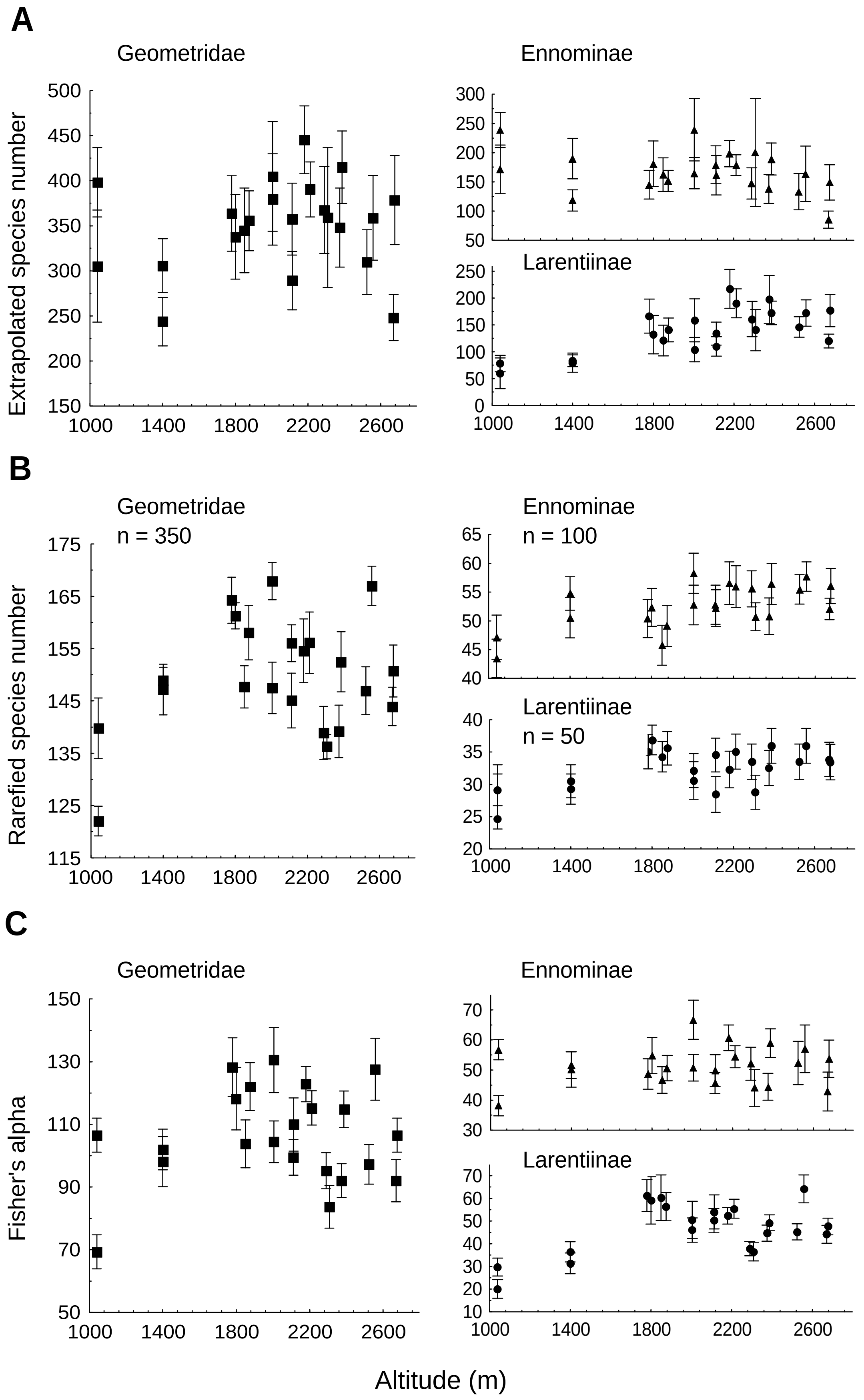


Figure 2 Diversity of Geometridae (left), and Ennominae and Larentiinae (right) along an altitudinal gradient ranging from 1,040 to 2,677 m in a montane rainforest in South Ecuador. Diversity measured **A** by extrapolation with the estimator Chao 1 **B** by rarefaction (the level of specimens to which samples have been rarefied is indicated), and **C** with Fisher's alpha. Only the extrapolated species numbers of Larentiinae are significantly correlated with altitude (Table 2).

Table 2 Spearman rank correlations between four measures of alpha-diversity (species number, Fisher's alpha, rarefied species number, and extrapolated species number (Chao 1)) and (1) specimen number, and (2) altitude. Bottom: ratios of observed species numbers and extrapolated species numbers. Species numbers and extrapolated species numbers are significantly correlated with specimen numbers and are thus unreliable measures of diversity. Only two (unreliable) measures in the subfamily Larentiinae are significantly correlated with altitude. [1]Expected species numbers at the rarefied sample size. **ns** not significant, ** p<0.01, *** p<0.005, **** p<0.001. Printed in **bold** are results that remain significant after sequential Bonferroni correction.

	Geometridae	Ennominae	Larentiinae
Correlations between **specimen number** and			
species number	**0.91 ******	**0.93 ******	**0.94 ******
Fisher's alpha	0.15 ns	0.29 ns	0.11 ns
rarefied species number	-0.07 ns	-0.09 ns	0.32 ns
level [1]	350	100	50
extrapolated species number (Chao 1)	**0.58 *****	**0.54 ****	**0.83 ******
Correlations between **altitude** and			
species number	0.13 ns	-0.39 ns	**0.78 ******
Fisher's alpha	0.08 ns	0.11 ns	0.16 ns
rarefied species number	0.01 ns	0.57 **	0.31 ns
extrapolated species number (Chao 1)	0.18 ns	-0.30 ns	**0.65 *****
Average ratio of extrapolated and observed species number	1.77 ± 0.27	1.80 ± 0.38	1.70 ± 0.26
Minimum and maximum ratio (sites)	1.43 (7b), 2.49 (8b)	1.34 (7b), 3.18 (8b)	1.29 (11a), 2.20 (3b)

Rarefaction Figure 3 shows rarefaction curves of Geometridae at all 22 sites. All curves lie within a relatively narrow band and no clear altitudinal pattern is visible. Figure 2 B shows the expected species numbers for samples rarefied to a standard size of 350 specimens plotted against altitude. While one site (1a at 1,040 m) has a significantly lower rarefied species number (122) than all other sites, the other sites again range in a continuous band between 135 and 168 expected species and show no tendency along the altitudinal gradient (Table 2). Spearman rank correlation coefficients of expected species numbers versus altitude at various other standardised sample sizes are presented in Table 3. There is no significant correlation between all tested rarefied species numbers of Geometridae and altitude.

While rarefaction analyses suggest that there is no significant change in expected species numbers with altitude in Geometridae as a whole, such changes occur at the subfamily level. Figure 2 B shows the rarefied species numbers for the subfamilies Ennominae and Larentiinae at rarefied sample sizes of 100 and 50 specimens, respectively. The patterns resemble each other. Surprisingly, there is a significant increase in species numbers in Ennominae. A conspicuous difference between both subfamilies is visible in plots 3a, 3b, 4a, and 4b (at 1,800-1,875 m). While rarefied species numbers in Ennominae tend to be lower than in the neighbouring sites, those of Larentiinae tend to be higher.

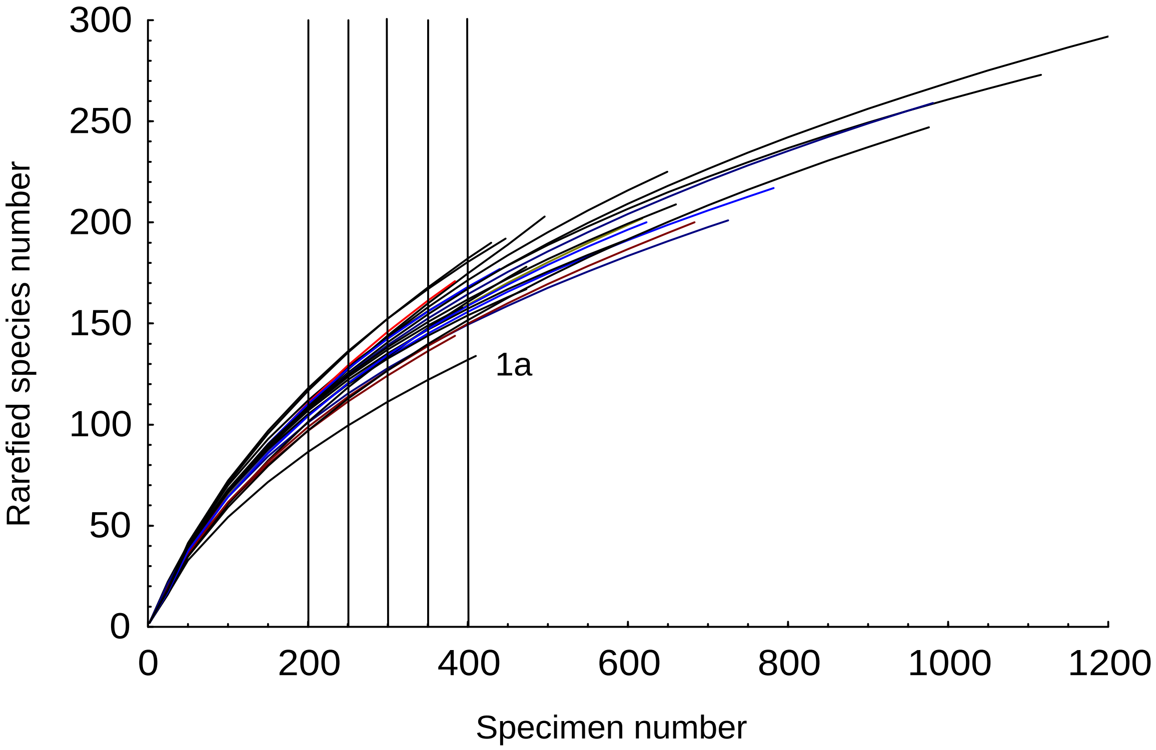


Figure 3 Rarefaction curves for Geometridae at all 22 sites. For clarity, standard deviation curves are omitted. The vertical lines indicate standardised sample sizes for separate analyses, see Table 3. The lowest rarefied species number was calculated for site 1a (1,040 m).

Table 3 Spearman rank correlations between rarefied species numbers and altitude. Correlation coefficients in *italics* indicate that not all sites are included because the number of specimens from at least one site was too low. **ns** not significant, * p<0.05, ** p<0.01, **** p<0.001. All results remain significant after sequential Bonferroni correction.

	400	350	300	250	200	150	100	50
Geometridae	*0.06* ns	-0.01 ns	0.14 ns	0.11 ns	0.07 ns			
Ennominae						*0.56* *	0.57 **	0.67 ****
Larentiinae							*0.04* ns	0.31 ns

Extrapolation The estimated total species number is 1,173 (± 30) and thus only 16% greater than the actual number counted, which was 1,010. In contrast, extrapolated species numbers at the individual sites are on average 70% to 80% larger than the observed numbers in all three taxa (quotients in Table 2). Minimally the estimate is 29% larger than the recorded species number (Larentiinae, site 11a), but the highest divergence is 218% (Ennominae, site 8b). Figure 2 C shows extrapolation results for Geometridae, Ennominae and Larentiinae for all 22 sites. For the Geometridae as a whole, estimates range between 244 (site 2b) and 445 (site 7a) expected species per site. For geometrids as a whole and Ennominae there does not seem to be a relationship between altitude and the extrapolated number of species, while an increase in species numbers for Larentiinae with altitude is notable (Table 2). However, estimates for single sites have to be regarded with caution since extrapolation is not a fully reliable measure of diversity in this particular data set.

SAMPLE SIZE DEPENDENCE OF DIVERSITY MEASURES

Table 2 shows correlations across the 22 study sites of specimen numbers with different measures of alpha-diversity for Geometridae, Ennominae, and Larentiinae. The recorded species number is strongly correlated with the number of specimens collected in all three taxa and must therefore be rejected as a measure of diversity. Extrapolated species numbers also show significant correlations in all taxa, although the relationship is less pronounced than with recorded specimen numbers. The Chao 1 estimator obviously depends too much on recorded species numbers for a reliable discrimination of sites. In contrast, values of Fisher's alpha and rarefied species numbers are independent of sample size.

DISCUSSION

DIVERSITY WITHIN A WORLD CONTEXT

The number of geometrid species and morphospecies collected in this study (1,010) is by all standards the highest ever counted in a single study on such a small spatial scale. The true species richness is even larger because the ensembles are not completely sampled and the extrapolated number is 16% higher. Only a small proportion of species are expected not to be attracted to light, among them diurnal species. Appendix 4 lists 25 such species (24 of them have been recorded exclusively at day), which were thus far collected in the study area. The high rate of singletons (48%), i.e. species with only one specimen recorded, among the diurnal species actually points to a larger number of species that are active during daytime (Chao 1 estimator 32 ± 6 species). Sampling with light generally attracts high proportions of geometrids. For example, Skou (1986) showed that 87% of Northern European geometrid species could be attracted in that way. Some species may be active exclusively late at night, but their proportion e.g. in the Palaearctic region is very low (R. Trusch, pers. comm.). Hence, the true number of geometrid species in the whole study area might be close to 1,300, which would be equivalent to more than 6% of the known fauna of the world. This is more than can possibly be reached in any other region of the world. For example, the total number of Geometridae in Borneo is estimated to be ca. 1,000 species (Holloway 1997) and in Europe ca. 920 species (Hausmann 2001). The 500 species of ennomine moths recorded in the study area in Ecuador surpass the known species total of that subfamily in Borneo (429 species, Holloway 1993), and reach the magnitude of the countrywide inventory of Costa Rica (597 species, Pitkin et al. 1996). These results clearly show that Andean rainforests are the world’s most prominent hotspot for Geometridae, in particular for the subfamilies Ennominae and Larentiinae. If the altitudinal gradient had included the Amazonian foothill region as well as higher altitudes, the number of observed species would have increased further; maybe one would then have found up to ten percent of the world’s fauna in a single altitudinal transect. This would even exceed the percentage of the world’s vascular plants and vertebrates found in the North Andean region. These groups reach 6.7% and 5.7% of the global total in this region, respectively (Myers et al. 2000). Values of Fisher’s alpha up to 131 per site are also among the highest ever measured in the world, and the order of magnitude of gamma-diversity of 250 (Fisher’s alpha) has never been documented before. While geometrid ensembles in temperate regions only reach values between 10 and 20 (Barlow & Woiwod 1989, Thomas & Thomas 1994), the highest values to date have been found in Peninsular Malaysia and Borneo, with alpha scores of 127 and 128, respectively (Barlow & Woiwod 1989, Beck et al. 2002). Since the sites in Ecuador were sampled only between two and four times, a year-round sampling would probably lead to even higher values of Fisher’s alpha. Since a considerable number of species are endemic to the region, an efficient conservation of these threatened habitats is urgently required to sustain this tremendous biodiversity (Myers et al. 2000, Chapter 4).

ALTITUDINAL PATTERNS OF DIFFERENT GEOMETRID TAXA

All diversity measures reveal overall similar results along the altitudinal gradient for Larentiinae, whereas the patterns in Ennominae and Geometridae differ slightly depending on the selected measures. All observed patterns are remarkable since a decline of insect diversity towards higher altitudes was expected as shown in many other studies (Wolda 1987, Hanski & Niemelä 1990, McCoy 1990 with a review, Brühl et al. 1999). However, there is growing evidence that diversity often does not decrease linearly along elevational gradients, but peaks at medium elevations (Janzen et al. 1976, Holloway 1987, Olson 1994, Chey 2000). Grytnes & Vetaas (2002) showed a broad medium-elevation hump of plant diversity in the Himalayas. According to Holloway (1987) and Schulze (2000), such peaks often occur at ca. 1,000 m. Above 2,000 m, only declining arthropod diversity has been detected so far. In this study, I found no decline of diversity above 1,000 m, but recorded a high and partly increasing diversity up to nearly 2,700 m, depending on the focal group. No study has ever shown a maximum diversity of a species-rich insect group occurring at such high elevations.

The diversity of the family Geometridae remains high along the whole gradient, but in particular one of the lowest sites (site 1a) tends to be lower in diversity than all other sites. This is probably due to the low diversity of Larentiine moths (see below). Subfamilies like Geometrinae and Sterrhinae tend to be more diverse and increase in their proportion towards lower altitudes (Chapter 4). Further investigations at lowland sites (<1,000 m) are necessary to reveal the overall altitudinal diversity pattern of Geometridae. I do not expect geometrids in Amazonian lowlands to be generally more diverse than at medium to high elevations because members of the large subfamily Larentiinae are mainly distributed at higher elevations.

Ennominae show a uniformly high level of diversity measured by Fisher’s alpha and extrapolated species numbers across all sites, whereas a more asymptotic pattern like in Larentiinae is indicated by rarefied species numbers. Diversity patterns still need to be investigated at lower altitudes than in this study. It remains to be seen whether diversity of Ennominae would really be constant along an extended altitudinal gradient or whether there is an increase in diversity towards medium elevations. Irrespective of these uncertainties as to Ennominae diversity at lower altitudes, the results clearly show that the diversity of this subfamily remains stable and exceptionally high over an altitudinal range of over 800 m at very high elevations. Such a pattern has never been documented before. The diversity of the group in South East Asia has been shown to be greatest in the lower montane zone (Holloway et al. 1990). Ennomines mostly feed on trees and shrubs, and their host-plant specialisation ranges from extreme polyphagy (which is widespread) to restriction to a particular plant family (Holloway 1993, Chapter 2). Although the diversity of trees declines as altitude increases in the study area (see next section), ennomines remain abundant. An explanation could be offered by an increasing ratio of unspecific species that do not depend on a narrow range of hosts. A number of species might also switch from trees to feed on the shrub-like vegetation that becomes more dominant at higher altitudes (see next section). It is not known whether patterns of chemical defence in plants change along the altitudinal gradient and whether this might have an impact on the diversity of herbivores. “Poisonous” plant families such as Solanaceae might be replaced by plants that are protected by more “quantitative” defence mechanisms (Waterman & McKey 1989).

Larentiine moths definitely increase from low diversity at the lowest sites (1,040 m) and reach an approximately constant level of diversity from 1,800 m onwards. A low level of diversity of larentiine moths in lowlands has also been found in several studies in other regions, such as South East Asia (Holloway 1987, Schulze 2000). In the Neotropical region, Herbulot (2001) found only very few species of the large genus *Eupithecia* at elevations below 1,000 m. Bornean Larentiinae are most diverse at altitudes between 1,000 and 2,000 m, but decrease above that level (Holloway et al. 1990, Schulze 2000). In contrast, the diversity of this group is expected to decline in the Ecuadorian Andes only at much higher altitudes, which were not covered in this study. The diversity pattern of Larentiinae in the study area can best be described as a very broad medium to high elevation hump. The underlying mechanisms for this most exceptional distribution of Larentiinae are uncertain. One reason could be the better availability of specific host-plants that are more diverse at high altitudes. For example, larvae of several species of the genus *Eupithecia* were found in the study area feeding on flowers of the family Asteraceae (Chapter 2). This family, which contains many species of shrubs, reaches its highest diversity in Ecuador at altitudes higher than 2,000 m (Jørgensen & León-Yanez 1999). The clear increase of *Eupithecia* towards higher altitudes might indicate greater resource availability. Herbaceous rather than woody plants might thus also play an important role for Larentiinae moths, as they do in temperate regions (e.g. Ebert 2001). A substantial number of species of herbaceous plants occur in the open structures of upper montane forests in the study area (R. Bussmann, pers. comm.). However, this interpretation remains largely speculative as long as the knowledge of the natural histories of Neotropical larentiine species remains scarce.

DIVERSITY PATTERNS AND ENVIRONMENTAL FACTORS

Lawton et al. (1987) listed four possible explanations for declining diversity of herbivorous insects towards higher altitude: (1) reduction of habitat area, (2) reduction of resource diversity, (3) reduction of primary productivity, (4) increasingly unfavourable environments. Despite these constraints, diversity of geometrids and subfamilies remains constant or is even lower at low altitudes. How can this be explained? The points listed by Lawton et al. seem either not applicable in the study area (1 and 2), or are compensated for by other factors (3 and 4).

Habitat area is not expected to be a limiting factor in this study, because the highest site is situated ca. 500 m below the mountain summit. However, a limitation of area might also come into play at higher altitudes in the Andes. Rahbeck (1997) and Körner (2000) emphasised the importance of decreasing area at high altitudes, and Holloway (1987) discussed a higher diversity of moths in montane Papua New Guinea compared to Borneo, as a consequence of greater land area situated above 2,000 m. The Andes are folded mountains with a habitat area at high altitudes that is by far larger than in relatively isolated mountains such as Mount Kinabalu in Borneo or Mount Kilimanjaro in East Africa. Furthermore, the biogeographical conditions in the Andes support the isolation of local populations (e.g. during glacial periods), subsequent speciation events, and a later co-existence of species. These features might explain a considerable part of the exceptional diversity of geometrid moths in Ecuador.

The possible reduction of resource diversity (including spatial niches) is difficult to assess because of widely lacking information describing which resources are actually used by Neotropical geometrid moths. However, some conclusions can be drawn from the available information on host-plant use (Chapter 2), and from vegetation data covering the study area.

The structural complexity of the forests clearly declines along the altitudinal gradient (Paulsch 2002). Upper montane forests in the study area provide a far poorer offer of structural niches, e.g. because of the lower height and the absence of lianas. As a consequence, structural niches do not seem to be a limiting factor in the diversity of geometrids. On the other hand, a declining offer of structural niches might be compensated for by a declining species number of (potentially competing) other groups of herbivores. Such a decline has been shown in the study area for bushcrickets and pyralid moths (Braun 2002, Süßenbach in prep., respectively)

The level of floristic diversity is more difficult to interpret, but there is evidence that the diversity of potential host-plants of geometrid moths generally decreases along Andean altitudinal gradients (e.g. Gentry 1988). In a few cases there are indications of specialism towards certain host plant groups that decline towards high altitudes (Chapters 2 and 4). For example, the ennomine tribes Cassymini and Macariini are expected to be specialised towards the plant family Fabaceae and are not present at the highest sites of the study area. Only a very few members of this plant group have been found in the study area (Homeier in prep.). Another example of declining plant diversity is provided by the woody vines (lianas), which show a decrease of diversity along the altitudinal gradient in the study area whereas in herbaceous vines this trend is less pronounced (Matezki in prep.). According to Homeier (in prep.) the number of trees (>5 cm diameter at breast height, 400 m^2 plots) of ridge forest in the area decreases from ca. 30 species at 1,850 m to ca. 20 species at 2,450 m. In contrast, the diversity of shrubs might be constant or even increasing. This probably also applies for the diversity of epiphytic plants, which is generally known to be very high in Neotropical montane forests (Gentry & Dodson 1987, Nieder et al. 2001). However, epiphytic plants are hardly exploited by geometrids, since most such species in these habitats are monocotyledons and ferns (Rauer & Rudolph 2001, Werner 2002). These plant groups are most probably not used as larval host plants (Chapter 2, see also Benzing 1990, Stuntz 2001). Overall, the total diversity of hosts that are actually exploited can be expected to decrease with altitude. However, the extent of this decrease remains unknown and might be rather small. This could offer an explanation as to how the exceptionally high diversity of geometrids can be supported by the ecosystem even at high altitudes.

This study shows that many species of the family are able to resist the unfavourable cold and humid weather conditions at high altitudes. The monthly average temperature decreases linearly by approximately 10 K throughout the gradient, and the precipitation more than doubles from ca. 2,000 mm to more than 5,500 mm per annum (P. Emck in prep., Chapter 7). While alpha-diversity is virtually independent of this great change in abiotic conditions, beta-diversity (species turnover) is strongly associated with ambient temperature (Chapter 7). Other factors such as primary productivity are also known to decrease along altitudinal gradients (Bruijnzeel & Veneklaas 1998, Waide et al. 1998, but see Singh et al. 1994). According to Tanner et al. (1998), nutrient limitation is widespread in montane soils and foliar nitrogen decreases with increasing altitude. Significant changes in soil properties have also been documented along the elevational gradient in the study area by Schrumpf et al. (2001). They reported e.g. decreasing pH values and decreasing nitrogen availability with rising altitude. Thus, one would expect also from a nutrient-balance perspective that habitats within tropical montane forests become ever more unfavourable for herbivores with rising altitude.

From the viewpoint of a herbivorous insect, high-altitude habitats offer very few advantages. One such advantage could be that these habitats are characterised by a low predation pressure (enemy-free space) with regard to both vertebrate and invertebrate predators. However, evidence is required to support this hypothesis, since there is a scarcity of studies that have investigated the role of antagonists on very species-rich arthropod groups in tropical regions (but see Novotný et al. 1999). Williams et al. (2001) pointed out that resources may often be less important than natural enemies in determining herbivore distributions. The diversity of insectivorous species of birds and bats in the Andes rapidly decreases with altitude (Terborgh 1977, Rahbeck 1997, and Matt 2001, respectively). Up to 38 species of insectivorous species occur in lowland rainforests in Panama (Kalko 1997), while only very few occur above 2,000 m in Ecuador (Matt 2001). Mixed species flocks of birds that forage in rainforests are expected to have a large impact on leaf-chewing insects (Braun 2002) and occur more prominently in lowland rainforests than montane forests (Thiollay 1999). A lower predation pressure could also be assumed for bats, although geometrid moths are adapted to co-exist with these predators. Like most other nocturnal Lepidoptera, geometrids are able to hear echolocational sounds (Rydell 1995).

Ants are the most prevalent invertebrate predators in many tropical forests (Wilson 1987, Hölldobler & Wilson 1990). However, they strongly decrease in diversity as altitude increases (Stork & Brendell 1990, Brühl et al. 1999). At higher altitudes in the Ecuadorian study area (above ca. 2,000 m), only very few ant species occur (own observation). Therefore, habitats are indeed an enemy-free space with regard to this otherwise very important group of potential predators (Novotný et al. 1999). Whether they are possibly replaced in their functional role by spiders or carabid beetles, as suggested for Sulawesi by Stork & Brendell (1990), still needs to be investigated in Neotropical montane rainforests.

ARE THE RESULTS REPRESENTATIVE OF OTHER GROUPS?

This study has shown exceptional altitudinal patterns and overall very high diversity of one major group of herbivorous insects. However, sampling would be required to confirm whether the results of this study are also applicable for other taxa. Holloway

(1987) showed that geometrid moths grow in their relative importance along altitudinal gradients, mainly due to the increasing number of Larentiinae moths. Similar patterns were reported by Hausmann (2001) from samples collected in Europe. Other moth groups in the Ecuadorian study area, such as Pyralidae and Arctiidae, exhibit completely different altitudinal diversity patterns (Süßenbach in prep.). Beccaloni & Gaston (1995) found a relatively constant ratio of species of the subfamily Ithomiinae among all butterflies, and Longino (1994) reported a number of tropical invertebrate “focal taxa” that might represent suitable “survey taxa” (see also Chapter 4). The transfer of results from one group to others is part of the controversial debate about the usefulness of biodiversity indicators. Although several studies have established parallels between the diversity patterns of different groups of organisms (Wolda 1996, Kerr et al. 2000), others found that there were none (Lawton et al. 1998, Ricketts et al. 2002). Simberloff (1998) criticised the concept of biodiversity indicators because of lacking consensus as to what indicators should indicate at all and which organisms are the best groups. If various taxa exhibit fundamentally different diversity patterns even among the herbivorous Lepidoptera, there is no reason to assume that patterns of, for example, detrivorous or predatory insects are better reflected.

CHOICE OF MEASUREMENT AND SAMPLE SIZE DEPENDENCE

The results confirm that unless complete inventories are possible to achieve, the recorded species number is an unreliable measure of diversity because of its extreme dependence on the number of specimens collected (correlation coefficients all >0.9, $p<0.001$). As expected, it has to be rejected as a meaningful measure of diversity for the purpose of discriminating between sites. However, the total number from all sites pooled (1,010) gives a good idea about the order of magnitude of species numbers in the entire study area. A regional pool of around 1,100 to 1,300 species is supported by extrapolation, which is quite close to the number observed.

The estimator Chao 1 has also been shown to be significantly sample size dependent, though not to the same extent as species number. It is very probable that the true local richness is still substantially underestimated at most sites. This is illustrated by the very high ratios of singletons at single sites, i.e. species that were collected only once. Ratios range between 0.41 and 0.60. A very high ratio of rare species is typical for samples of tropical arthropods. For example, Novotný & Basset (2000) found very similar singleton rates of 0.45 in samples of herbivorous insects in New Guinea. Underestimation occurs if samples are too sparse (Colwell &

Coddington 1994). This study shows that even samples of at least 134 species and 384 individuals can be “too sparse” for extrapolation in extremely rich moth ensembles. According to Colwell & Coddington (1994), estimators correlate with sample size until about half the total fauna is observed and thereafter become gradually independent of sample size. Obviously, this level has not been reached at many sites because they could not be sampled more than two to four times. In a study of geometrid moths in Borneo, Beck et al. (2002) collected samples containing much fewer species (62 to 192) and specimens (118 to 619) per site. However, extrapolated species numbers (Chao 1) did not significantly correlate with specimen numbers in their study ($r = 0.36$, $p = 0.19$). The reason for this discrepancy could be the more homogenous set of data from Ecuador compared to the Bornean data set, and the consequently better fit of Chao 1 with the observed species number. The ratio of extrapolated species number and observed species number for Ecuador is 1.76 ± 0.26, and for Borneo it is 2.05 ± 0.70, i.e. there is a much higher variability in the Bornean data. This example shows that extrapolation might be a relatively unreliable measure even if it is not strongly correlated with the species number. In conclusion, in the “mega-diverse” fauna of Andean montane rainforests a reliable species number can be extrapolated only on a regional scale, but on a local scale, even large samples might be insufficient for reliable estimation.

Fisher’s alpha values do not correlate with specimen numbers. The measure is thus superior over the former diversity measures with regard to sample size dependence. In addition, results can easily be compared with those from other places in the world, such as South East Asia. Nevertheless, this result does not rule out the possibility of increasing values of Fisher’s alpha with an increasing number of samples as described e.g. by Wolda (1987) and Intachat & Holloway (2000). Schulze & Fiedler (2002) showed that Fisher’s alpha of pyralid moths samples still tended to increase even after 13 nightly catches and with over 2,000 moths recorded per site. This could also be the case if the sites in Ecuador were to be sampled more often. Moreover, goodness-of-fit of the log-series model was not always satisfactory. Thus, it does not seem to be appropriate to rely solely on this measure.

Rarefied species numbers have also been shown to be independent of sample size. The measure can overestimate diversity if species have clumped distributions (Achtziger et al. 1992). However, this is of relatively little importance in large samples and will not affect the results presented in this study.

In conclusion, the use of several different measures can be recommended since they complement each other in different aspects of diversity as well as in the mathematical assumptions underlying their usage. Furthermore, the risk of possible misinterpretations can be minimised to an even greater extent if all these measures yield concordant results.

POTENTIAL METHODOLOGICAL PROBLEMS

Methodological problems such as sampling with light and possible effects of seasonality are discussed more in-depth in Chapter 3 and are only briefly treated here. Sampling with light is undoubtedly the most effective method for collecting moths in a quantitative manner. Like with virtually any other comparable method, activities rather than true abundances are measured, but this does not seem to have any serious implications for this study. At all sites, light-traps were operated at the ground. It could be argued that the fauna of the canopies might be underrepresented, in particular at the lowest sites where trees are considerably larger than at higher elevations (Paulsch 2002). However, in high-grown hill forests of Borneo, Beck et al. (2002) found that combined canopy and understorey geometrid samples never significantly exceeded the diversity scores for understorey ensembles alone. Moreover, by applying the same sampling and analytical methods in a parallel study on pyralid and arctiid moths, Süßenbach (in prep.) found the highest diversity at the lowest sites in the study area. Hence, the described patterns are expected to be reliable.

Insect communities in tropical regions frequently show temporal variation in numbers of species and specimens. In particular, numbers diverge in regions with marked seasonal changes between wet and dry periods (e.g. Wolda 1978b, Novotný & Basset 1998, Wagner 2001). In contrast, Lepidoptera ensembles were apparently not seasonal in climates with constant rainfalls (Hebert 1980). The study area in Ecuador receives substantial rainfall throughout the year, with a short drier period during November (P. Emck in prep.). Some species indeed showed differences in abundance in different seasons, and more specimens were caught in the drier time of the year (Figure 1). This might correspond to a higher availability of young leaves, which can be observed in many tree species in September and October (Homeier, in prep.). Basset (2001) emphasised the high importance of young foliage for leaf-chewers. Year-round sampling, combined with monitoring the phenology of potential hosts could substantiate these observations. The overall influence of temporal changes of moth ensembles on measures of alpha-diversity in this study is expected to be rather low.

Some sites at lower altitudes are affected by anthropogenic disturbance such as selective logging, mostly at level 2 (1,400 m), but also sites at the levels 1, 3 and 4 (1,040 to 1,960 m). This might have an unknown impact on certain specialised species. Beck et al. (2002) showed that disturbed old-grown forests in Borneo have a diversity of geometrid moths similar to primary forests. Moderate disturbances might even have a positive, scale-dependent impact on Lepidoptera diversity (Hamer & Hill 2000). The higher diversity of Larentiinae at levels 3 and 4 could be interpreted as a consequence of higher availability of herbaceous plants due to the moderate disturbance at these sites. Herbs are expected to be important for Larentiinae (see above and Chapter 2). The impact of habitat disturbance on moth ensembles in the study area needs to be investigated in the future.

CONCLUSIONS

This chapter provided evidence that Andean montane rainforests are the “hottest hotspot” on Earth with regard to one large taxon of herbivorous insects. Despite the enormous diversity of geometrid moths, analyses were manageable at a high taxonomic resolution and allowed ecological interpretations at a relatively fine scale (Chapter 4). Geometrids are predestined to serve as study organisms for further ecological studies in the Neotropical region. The diversity patterns that emerged in this study are unique and raise a number of questions, e.g. how the extremely high diversity can be achieved despite increasingly unfavourable climatic conditions. Investigations along comparable altitudinal gradients in the Andes offer an excellent opportunity to learn more about the generality of the patterns uncovered here and the mechanisms that are responsible for the diversity of herbivorous insects. Such investigations could also reveal patterns of large-scale beta-diversity of a species-rich arthropod group (Chapter 7) and the association between altitudinal and latitudinal gradients. A better understanding of the natural histories of Neotropical geometrids is urgently required in order to shed more light on the functional role played by herbivorous insects in tropical ecosystems. The results provided in this chapter also emphasise the enormous importance of montane rainforests in conservation issues (Chapter 4).

6 Appropriate ordination methods and similarity indices for species-rich arthropod communities

INTRODUCTION

Changes in communities of animals or plants along habitat gradients have attracted attention since Alexander von Humboldt's investigations of altitudinal changes in phytodiversity in the Andes (von Humboldt & Bonpland 1807). Natural habitat gradients offer experimental systems "designed" by nature in which complex entities such as species-rich communities can be studied (Körner 2000).

A large number of statistical methods have been developed in order to describe, visualise and interpret such changes. Some were adopted by ecology from other disciplines such as psychometry (e.g. non-metric multidimensional scaling, Kruskal 1964), while many others were specifically developed for use in biological disciplines (e.g. the NESS-index of similarity, Grassle & Smith 1976). It is often very difficult to choose the most appropriate method from the great number of available multivariate techniques and similarity indices because no definitive guideline exists. For example, Kenkel & Orlóci (1986) concluded that none of the currently available ordination strategies could be regarded as being appropriate under all circumstances.

This chapter focuses on methodological aspects of the assessment of beta-diversity of extremely diverse tropical arthropod samples. These provide a particular methodological challenge because the investigated ensembles (Fauth et al. 1996) of geometrid moths are characterised by a very high diversity as well as by the occurrence of many rare species (Novotný & Basset 2000). The diversity of the investigated ensembles of geometrid moths reaches values of Fisher's alpha between 69-131 with estimated species numbers up to 400 and more per site (Chapter 5). Furthermore, samples from such very species-rich ensembles are usually incomplete unless thousands of specimens are caught over long time periods (Chapter 5).

In the first part of this chapter, the choice of ordination methods and similarity indices from those that are potentially appropriate is explained. In the second part, I compare the performance of ordination methods and similarity indices against my empirical data. Classification is briefly discussed as a potential alternative to ordination. While this chapter focuses on methodological aspects involved in interpreting the data, their ecological significance is profoundly analysed in Chapter 7. Figure 1 gives an overview of the methods that were employed and tested.

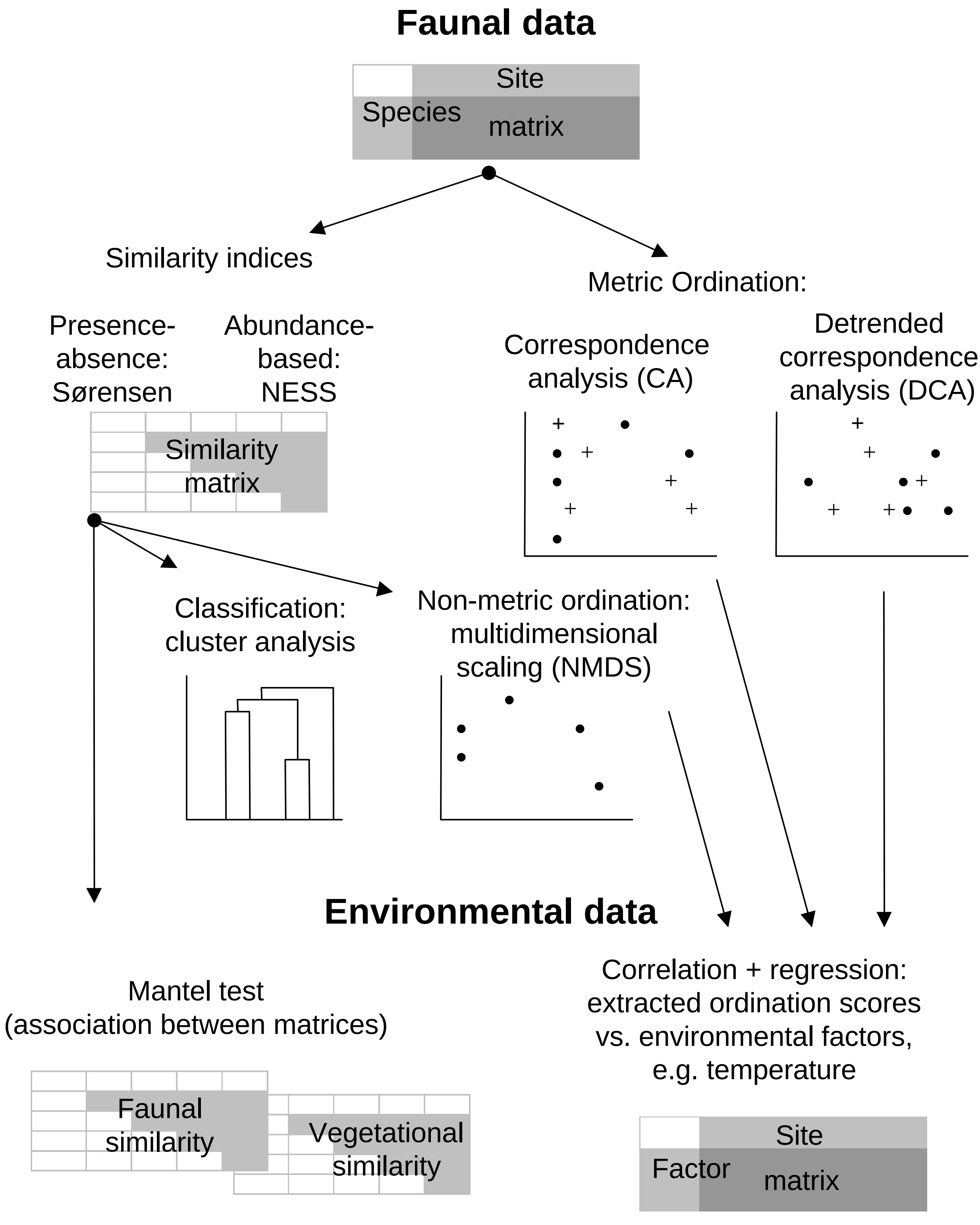


Figure 1 Diagram of methods applied to analyse beta-diversity of geometrid moths sampled at 22 sites in South Ecuadorian montane rainforests. Data are fictitious. Field data of moth ensembles can be directly ordinated by metric ordination techniques such as correspondence analysis (CA) and detrended correspondence analysis (DCA). Classification by cluster analysis as well as ordination by non-metric mulitdimensional scaling (NMDS) requires an intermediate step: Similarity has to be calculated using an index (e.g. the Sørensen or Normalised Expected Species Shared (NESS) index). Associations between similarity matrices and matrices derived from environmental data can be evaluated with Mantel tests. In addition, extracted data derived from ordination techniques can be subjected to statistical tests (e.g. correlations with environmental parameters).

METHODS

APPLIED STATISTICS PROGRAMS

All standard statistical methods were performed using the software package Statistica 5.5 (StatSoft 1999). The Sørensen and NESS indices were calculated with a program provided by S. Meßner (1996). A modified version of the program DECORANA in the software PC-Ord (26 segments) was used to perform detrended correspondence analysis. Mantel tests (1000 permutations) were also performed with PC-Ord (McCune & Mefford 1999).

RESULTS AND DISCUSSION

CHOICE OF ORDINATION TECHNIQUES

The objective of ordination techniques is to find a parsimonious representation of individuals in a space of low dimensionality (Kenkel & Orlóci (1986) offer a comprehensive overview). In the context of this chapter, “individuals” means either sites or species. These are often so numerous as to render simple bivariate analyses unrealistic (Jackson & Somers 1991). Ordination should be interpretable in terms of underlying environmental gradients. If only one gradient is responsible for changes in community structure, the term “coenocline” has been coined for simulated data structures (Hill & Gauch 1980). Two or more gradients form a “coenoplane” (Kenkel & Orlóci 1986). Data are ordinated in a multidimensional space, but the first axis usually explains most of the variability of the data. Two-dimensional representations are interpretable and most readily compared visually (Shepard 1974, Jackson & Somers 1991).

Unfortunately, no objective method exists that enables the assessment of the efficiency of ordination methods (Kenkel & Orlóci 1986). However, there are only relatively few techniques that are commonly employed. Three of them were applied here: The metric techniques correspondence analysis (CA) and detrended correspondence analysis (DCA), and non-metric multidimensional scaling (NMDS). The parallel application of several methods is probably the best way to ensure that the patterns found are stable (e.g. Kenkel & Orlóci 1986).

Linear models underlay all metric ordination techniques. Principal component analysis (PCA) and correspondence analysis (CA) are mathematically related. CA has been shown to have some advantages over PCA in summarising non-linear trends and to be efficient when dealing with highly heterogeneous non-linear data

(Gauch et al. 1977, Kenkel & Orlóci 1986). CA directly analyses data matrices and results in a multidimensional plot. One advantage of CA and DCA is that both species and sample ordinations are produced simultaneously. Using simulated data, Faith et al. (1987) found the use of chi-square distances in CA is often inappropriate. Legendre & Legendre (1998) stated that rare species are relatively over-emphasised in CA, and Legendre & Gallagher (2001) suggested a transformation of data before the application of CA and other ordination methods. However, the emphasis of rare species could turn out as an advantage in the analysis of tropical communities that are characterised by the occurrence of a great number of rare species.

Hill & Gauch (1980) criticised CA because it often shows an “arch”-like form in the first two dimensions if a coenocline is investigated. In addition, distances at the lower and upper end of the parameter space covered by the samples to be ordinated are compressed relative to the middle. The nature of this “arch” is a controversial issue and it has been interpreted as an artefact (Hill & Gauch 1980). In strong contrast, it was also described as an important and inherent property of successive replacement data (Wartenberg et al. 1987). Arch-like structures appear prominently in ordinations of the present empirical data set and are discussed below and more profoundly in Chapter 7. Hill & Gauch (1980) developed a technique to eliminate the arch and to rescale the axes in order to minimise the problems they recognised in CA. They termed their method detrended correspondence analysis (DCA). DCA became very popular in the following years, but some severe problems soon became apparent. Kenkel & Orlóci (1986) emphasised that detrending can distort underlying data structure. Wartenberg et al. (1987) fundamentally criticised the concept as having no empirical or theoretical justification. Peet et al. (1988) defended detrending and rescaling as necessary steps in order to make higher dimensions interpretable. However, Jackson & Somers (1991) showed that the choice of axis segmentation in DCA could substantially affect the interpretation of the results. The selection of the number of segments is arbitrary, since no guidelines exist for different numbers of samples. Jackson & Somers concluded that multidimensional configurations obtained by using DCA might be unstable and potentially misleading.

Another variant of CA is canonical correspondence analysis (CCA) (Palmer 1993, ter Braak 1995). CCA is a constrained form of ordination that involves multiple regression of environmental data. Økland (1996) pointed out the conceptual differences between ordination and constrained ordination. While, for example, a CCA requires a complete set of environmental variables and then allows a-priori hypotheses to be tested (ter Braak 1995), unconstrained ordination is superior in generating new hypotheses. For the purpose of the present study, the latter approach was deemed more appropriate, because at the onset of the project neither the moth fauna nor its potential determinants were known.

Non-metric methods circumvent the linearity assumption inherently underlying all metric ordination methods. Since ecological data sets often do not conform to such assumptions, using methods such as non-metric multidimensional scaling (NMDS) is frequently more statistically appropriate than using metric techniques. NMDS is probably the most often used non-metric ordination method and has been recommended as robust and unlikely to mislead (Kenkel & Orlóci 1986, Minchin 1987, Clarke 1993). Unlike in metric ordinations, the total number of dimensions can a priori be fixed to a low number (e.g. two or three dimensions). The underlying rank statistic minimises the influence of outliers on the results. A disadvantage of NMDS is that no biplots can be drawn as in metric techniques such as CA and PCA. In contrast to these methods, NMDS can easily cope with data that involve even many null abundances. Moreover, transformation of data as suggested by Legendre & Gallagher (2001) for metric techniques is not required.

Until the 1980s, NMDS was criticised as being computationally more demanding than CA (Gauch & Hill 1980, Kenkel & Orlóci 1986), but this problem has vanished following progress in computer technology. This historical background might be one of the reasons why NMDS is still less commonly used than CA, despite its statistical advantages.

CHOICE OF SIMILARITY INDICES

While correspondence analysis can be calculated directly from the original species-site matrices, NMDS requires an intermediate step (Figure 1). A resemblance matrix (similarity or distance) must be calculated from the original matrix. Conceptually, any measure of pairwise resemblance between objects can be used with NMDS, including correlation coefficients, Euclidean distances or one of the many available indices of faunal similarities (Kruskal 1971).

The choice of the “correct” index is an important step, since different indices might lead to completely different results. From the vast number of available algorithms (more than 60 according to Lamont & Grant (1979), see also Legendre & Legendre (1998)), 22 were performance tested by Wolda (1981). He used model data and concluded that only the Morisita index is independent of sample size and species diversity of the sample, whereas all other indices failed to be independent to a varying extent. However, he recognised that Morisita’s index is sensitive to changes in abundance of the more common species. At this time, Wolda did not seem to be aware of the existence of the NESS index derived by Grassle & Smith (1976), because two years later he described this latter index as far superior over any other (Wolda 1983). The NESS index (Normalised Expected Species Shared) is a generalisation of the Morisita index (Grassle & Smith 1976). In contrast to other indices, it considers that two random samples drawn from the same community are usually not identical but differ due to stochastic effects. In species-rich communities that are incompletely sampled, similarity will be seriously underestimated by all other indices. This phenomenon will be illustrated by empirical data later in this chapter. The NESS index is sensitive to the less common species that account for a major fraction of the data, in particular in tropical communities. Moreover, it is not dependent on fluctuations in a few abundant species that occur in temperate as well as in tropical insect communities (Wolda 1978a, Novotný & Basset 1998). The NESS index is still rarely used, but has become more widely applied in the past ten years, e.g. by Wolda (1992, 1996), Willott (1999), Beck et al. (2002), and Schulze & Fiedler (2002). It is computationally more demanding than other indices, but by no means problematic any longer. Similarly to NMDS, this may be one "historical" reason why the concept of NESS has remained widely unaccepted.

NESS can be adjusted by choice of the sample size index, m (Grassle & Smith 1976). Therefore, NESS is not just one similarity index, but rather a "family" of indices. For example, in the empirical data of all geometrid moths, 193 indices are available (from $m = 1$ to $m_{\max} = 193$, see Table 1, p. 106). At its minimum of $m = 1$ NESS is identical to the Morisita index (Morisita 1959) and emphasises the dominant species. At the other extreme, maximum m values correspond to a strong emphasis on less abundant species. The number of m values that are available increases with sample sizes (notice the much lower $m_{\max}$ in smaller taxa in Table 1). Grassle & Smith (1976) recommended studying the role of dominant and rare species by varying m, but there is no guideline which m is most appropriate to apply. Hence, NESS demands a decision regarding which m to use. Some authors have set m to 20 without explaining their choice (e.g. Wolda 1983, Willott 1999), while others have alternatively presented $m = 1$ and $m_{\max}$ (Schulze & Fiedler 2002). The performance of NESS with different values of m was investigated on the Ecuadorian geometrid data set. Maximum values of m were found to perform best (see below and Figure 2 A, B and C, p. 105).

A popular and widely used index of similarity is the Sørensen index (Sørensen 1948). It is identical to the Czekanowski index (Czekanowski 1913) and closely related to the Bray-Curtis- and Jaccard indices, as well as to several other indices. In contrast to the NESS / Morisita index, it is not based on species abundances, but on presence-absence data. Wolda (1981) showed that the Sørensen index has the best mathematical properties of the binary measures tested in that paper. The Sørensen index was compared with the performance of the NESS index (see Figure 2).

POST-HOC TESTING OF ENVIRONMENTAL FACTORS

Two methods were chosen to “blend” geometrid moth data with environmental factors (Figure 1, lower part). Ordination scores were extracted and correlated with environmental factors. This method is restricted to studying the effect of “one-dimensional” data like ambient temperature or altitude and does not allow searching for correlations with structurally more complex data, e.g. matrices derived from vegetation structure. This problem can be solved by using Mantel tests for associations between distance matrices (Mantel 1967). For example, dissimilarity matrices of geometrid moth ensembles can be directly compared with matrices of geographical (Euclidean) distances or any other similarity matrices derived e.g. from vegetation data.

EMPIRICAL DATA: WHICH ORDINATION METHOD IS APPROPRIATE?

Figure 2 in **Chapter 7** (pp. 118-119) shows two-dimensional ordinations of NMDS (Sørensen-index), CA and DCA of all geometrid moths and separately of the subfamilies Ennominae and Larentiinae. Figure 1 in **Chapter 7** (p. 117) shows further NMDS ordinations based on two NESS indices (m = 1 and $m_{\max}$). All results are readily interpretable since a gradual structure from site levels 1 to 11 (i.e. revealing the altitudinal sequence) is clearly depicted. Hence, it can be expected that scores from the first dimension are strongly correlated with environmental parameters such as altitude or temperature (Chapter 7). In contrast, the interpretation of the second axis or even higher (CA- and DCA-) axes is difficult. CA shows the clearest picture, whereas NMDS and DCA plots appear more scattered. NMDS and CA both show a clear arch-like structure, which has been interpreted alternatively as artefact, or as an inherent property of successive replacement data (see above and Chapter 7). The arches intelligibly indicate one dominant gradient, i. e. a coenocline situation. In the second axis, sites from the extremes of the gradient have similar values despite their very low similarity (Sørensen values between 0.05 and 0.11, NESS ($m_{\max}$) values between 0.06 and 0.10). This phenomenon can be interpreted as involution, i.e. the closeness of dissimilar extremes of an environmental gradient (Wartenberg et al.

1987). Hence, a meaningful analysis of the second dimension by correlation of environmental parameters is not possible. An in-depth discussion of the ecological meaning of the data follows in Chapter 7, where additional model data are analysed. In DCA, the arch is eliminated by the detrending algorithm. Whether the resulting structure in the second dimension can be interpreted better than in the other ordination techniques is questionable.

In conclusion, all chosen ordination techniques performed well in the empirical data set. NMDS might be preferred because its statistical assumptions are minimal and the data can be ordinated in a fixed number of dimensions. Both metric methods have a number of further axes (not shown) that explain a decreasing proportion of the variability of the data. CA performed surprisingly well despite its linearity assumptions and produced the most “proper” ordinations, whereas DCA ordinations are not “better” and sites appear more scattered in the two-dimensional space.

EMPIRICAL DATA: WHICH SIMILARITY INDEX PERFORMS BEST?

Figure 1 in **Chapter 7** (p. 117) shows NMDS ordinations of Geometridae, Ennominae and Larentiinae, each based on the two NESS indices m = 1 and $m_{\max}$. Figure 2 in **Chapter 7** (pp. 118-119) shows further NMDS ordinations, based on the Sørensen index of similarity. The clearest ordinations are revealed by NESS $m_{\max}$, followed by the Sørensen index and NESS m = 1. However, the overall differences are slight. In order to assess this qualitative observation by an objective measure, I investigated the behaviour of “stress” in NMDS and compared its values in different taxa and with the three different similarity measures. Stress is a measure that reflects the degree of deviation of NMDS distances from true matrix distances. These distances can be plotted against each other in a “Shepard diagram”. A line denotes the best-fit monotonic (increasing) regression while the scatter about this line is defined as stress (Clarke 1993). Figure 2 (A and B) shows two such Shepard diagrams for Geometridae (m = 1 and $m_{\max}$ = 193) after two-dimensional scaling. Both results are readily interpretable, but ordination using $m_{\max}$ is even more convincing than with m = 1 because the value of stress with $m_{\max}$ is only half of that with m = 1. In addition, the Shepard plot of the $m_{\max}$ ordination almost shows a linear relationship. According to Clarke (1993), stress values below 0.2 still produce a usable picture, values below 0.1 correspond to a good ordination with no real risk of drawing false conclusions, and values below 0.05 give an excellent representation with no prospect of misinterpretation.

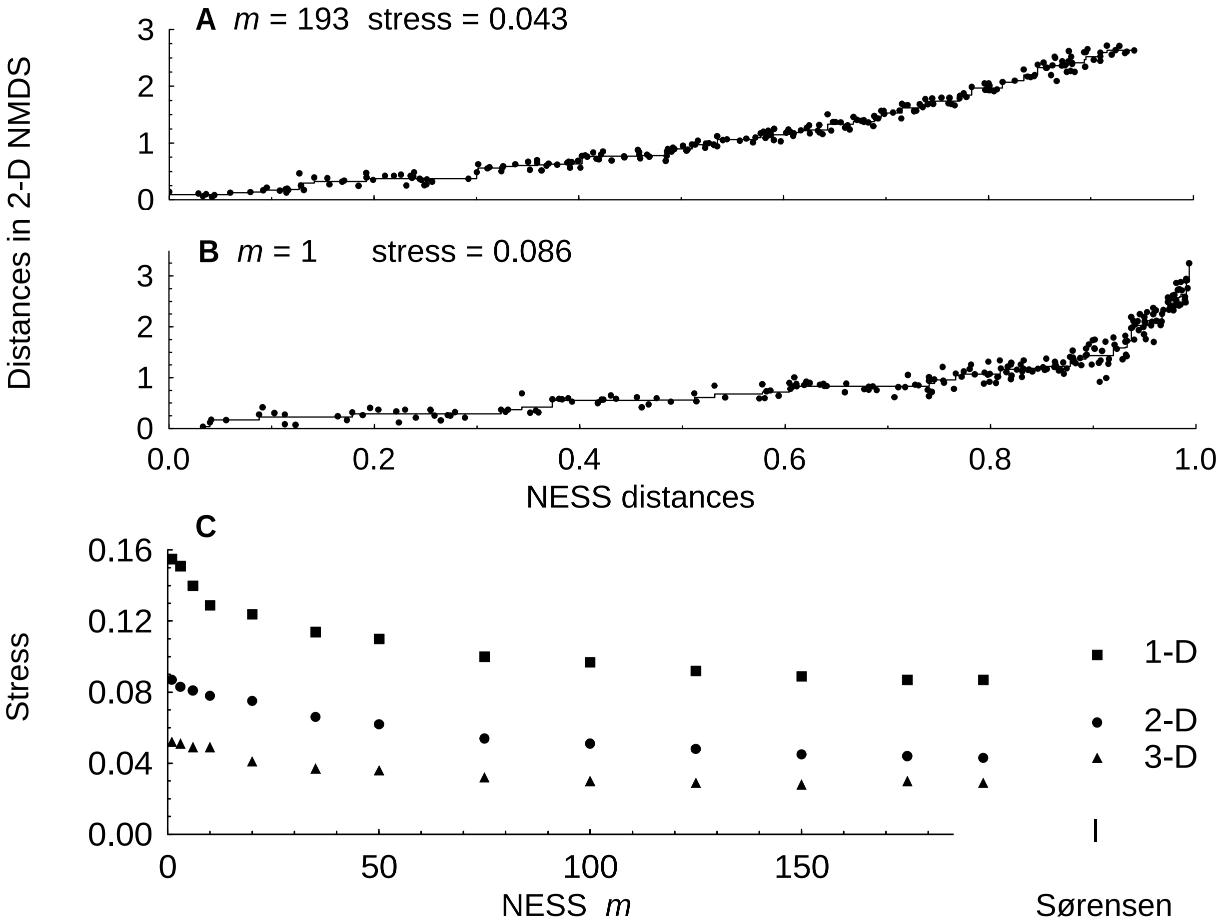


Figure 2 **A** and **B** Shepard diagrams of NMDS ordinations of two different NESS indices of Geometridae (*m* = 1 and m_{max} = 193 respectively). The diagrams correspond to the ordinations A and D shown in Figure 1 in Chapter 7 (p. 117). Multidimensional scaling was performed with two dimensions. Stress is defined as scatter around the best-fit monotonic regression line. **C** NMDS stress as a function of the size of the parameter *m* of the NESS index and of the Sørensen index. Data are from 13,938 specimens of 1,010 species of geometrid moths from 22 sampling sites in South Ecuador (see Chapter 7). As expected, the stress is systematically higher in one-dimensional ordinations (**1-D**) than in two-dimensional (**2-D**) and three-dimensional (**3-D**) ordinations. Stress decreases monotonically in all cases with increasing *m*, except in three-dimensional ordinations where *m*>150. Stress in the ordination based on Sørensen's index has intermediate values.

In a next step, I compared stress values at a range of intermediate *m* values, and for the Sørensen index for one-, two- and three-dimensional scaling (Figure 2 C). The results show two major tendencies: Firstly, stress decreases monotonically with increasing *m* in asymptotic curves. Major changes occur in the range from *m* = 1 to *m* = 20, whereas the changes at higher levels of *m* are less pronounced. Stress in the ordinations using the Sørensen index has intermediate values. Secondly, as theoretically expected, stress is lower in three dimensions than in two dimensions or one dimension. However, the difference between one and two dimensions is about twice as large compared to that from two to three dimensions. Since relatively little would be gained from using a three-dimensional ordination, the visually more comprehensible two-dimensional plots are preferred in this study.

The results show that for ordination purposes a maximum *m* performs much better than a low *m*, and that intermediate *m* values do not differ strongly in their performance from very high *m*. Therefore, in comparable studies, m_{max} should be preferred over an arbitrarily chosen intermediate *m*, since the results are the easiest to interpret. These findings are supported when larger subgroups of Geometridae are considered. Table 1 gives an overview of stress values in two-dimensional scaling for eight taxa. Only in the three largest groups, high m_{max} values (>30) are available. In these cases, m_{max} clearly performs better than $m = 1$ and the Sørensen index. In the remaining smaller taxa, m_{max} reaches only values between 3 and 10, and no consistent stress pattern can be seen within the similarity measures.

Table 1 Stress values of two-dimensional NMDS of eight taxa of geometrid moths: Sørensen index, NESS $m = 1$, NESS m_{max}. Additionally, information is provided for species and specimen numbers as well as average and minimum specimen number per site. Printed in **bold** is the lowest stress value for each taxon. Taxa are arranged according to the number of specimens found. Ennominae and Larentiinae are subfamilies of Geometridae; *Eupithecia*, *Eois* and *Psaliodes* are genera within Larentiinae, and Boarmiini and Ourapterygini are tribes within Ennominae.

	Sørensen index	NESS index			Species	Specimens	Average number	Minimum number
		$m = 1$	m_{max}	m_{max}				
	NMDS Stress							
Geometridae	0.063	0.086	**0.043**	193	1,010	13,938	634	384
Ennominae	0.077	0.112	**0.068**	62	498	6,646	302	140
Larentiinae	0.084	0.103	**0.065**	32	390	5,714	259	65
Eupithecia	**0.113**	0.137	0.125	7	139	2,139	97	17
Eois	0.143	**0.101**	0.104	10	85	1,582	72	20
Boarmiini	0.148	0.118	**0.117**	3	68	1,371	62	6
Psaliodes	**0.136**	0.184	-	-	69	1,167	53	3
Ourapterygini	0.171	0.138	**0.132**	5	82	1,023	44	8

The absolute values for stress decrease with a growing number of species and specimens. For the smaller taxa, values are below 0.2, whereas in the three largest taxa, values are below 0.11. The smallest stress value is achieved for the total geometrid sample with 0.04 for m_{max} (Figure 2 A). Hence, if the performance of similarity indices is tested using NMDS stress, they can be arranged in the order NESS m_{max} > Sørensen > NESS $m = 1$ (identical to Morisita's index), provided that a large m_{max} can be obtained.

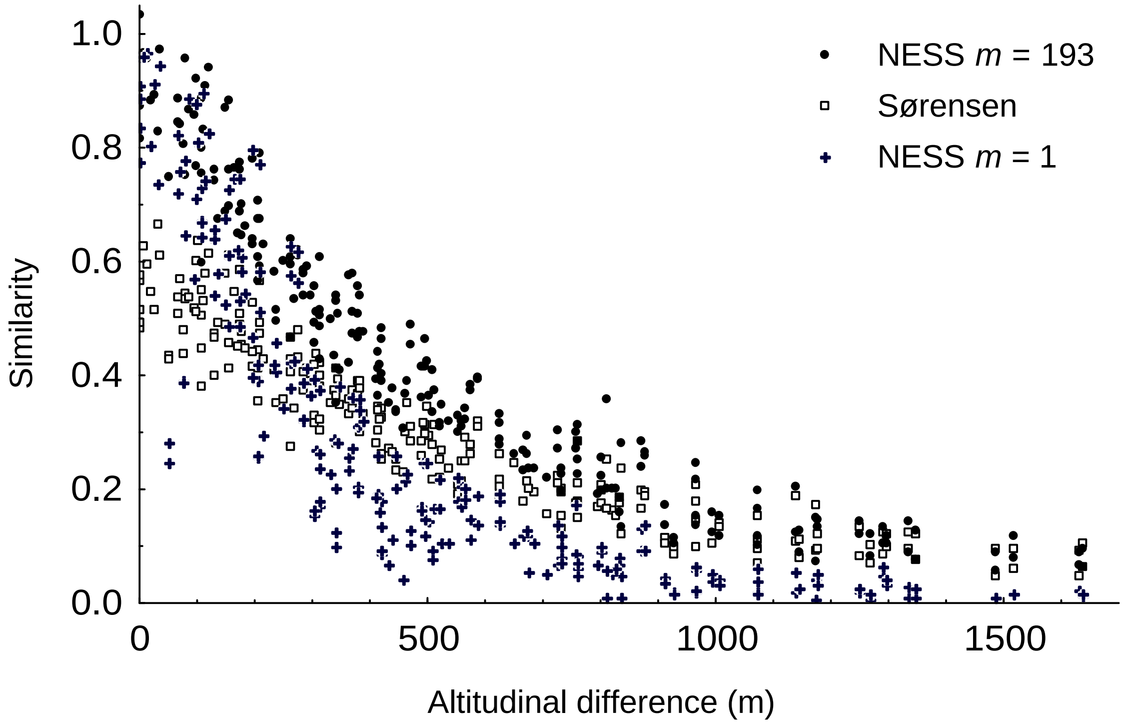


Figure 3 Values of three similarity indices (Sørensen index, NESS $m = 1$, NESS m_{max}) of the whole geometrid data set plotted against the pairwise altitudinal differences between all sites (n = 231). NESS $m = 193$ values are by far the highest, whereas NESS m=1 reaches high values only in sites in close proximity. Sørensen values are generally lower than NESS $m = 193$ (see Table 2).

Table 2 Average values of the Sørensen index, and two NESS indices ($m = 1$ and m_{max}) for all pairs of 231 sites, and for 11 pairs of sites situated at the same altitudinal level. Printed in **bold** are indices with the highest values.

	All 231 pairs ± SD		11 pairs ± SD	
NESS $m = 193$	**0.44**	0.25	**0.92**	0.07
NESS $m = 1$	0.28	0.27	0.88	0.08
Sørensen	0.31	0.15	0.56	0.06

While relative values of all similarity indices can readily be interpreted and ordinations reveal similar results, absolute values differ greatly. Figure 3 shows similarity values of the three indices used plotted against the altitudinal differences between all sites (n = 231 pairs). The average values of the whole data are presented in Table 2, together with average values of eleven site-pairs that are situated at the same level of altitude (<35 m of altitudinal difference).

NESS $m_{\max}$ yields the highest similarity values, whereas values of NESS $m = 1$ and Sørensen are much smaller. Very similar results very obtained by Süßenbach et al. (2001) for pyralid moths. Both NESS indices show high similarities at sites that are situated at the same altitudinal level (average values ca. 0.9), i.e. they indicate that the ensembles from which the samples had been drawn are essentially identical. In contrast, Sørensen values are noticeably lower (0.56). There is a lot of evidence that the Sørensen index dramatically underestimates similarity (see also Wolda 1981). The investigated samples are incomplete and species occur by chance in only one or a few samples. The proportion of “singletons”, i.e. species that were collected only once, ranges between 0.41 and 0.60 at single sites (but accounts for only 20% when all samples are pooled, see Chapter 5). The NESS index accounts for the effect that samples usually differ by chance alone to some extent by involving probability calculus in its formula (see Grassle & Smith 1976). Simple presence-absence indices like the Sørensen index do not account for such probability effects. Hence, in terms of the interpretation of absolute values, both NESS indices appear to reflect the “true” situation better than presence-absence indices.

Many studies that are based on presence-absence data draw the conclusion that they found a high beta-diversity. The findings presented here suggest that beta-diversity might often have been overestimated. For example, Gentry (1988) reported a very small overlap of tree species in lowland rain forests at Tambopata, Peru. Only 3-24 species out of ca. 200 species sampled for any habitat were shared with an adjacent habitat. He interpreted this as an example of an extremely high beta-diversity due to a high diversity of different habitats. However, Gentry had noticed that some of the lack of overlap could be due to inadequacy of the sampling technique. Species-area curves of plant samples did not reach an asymptote, i.e. the samples represented very incomplete subsets of the communities. Gentry would probably have found a considerably higher similarity between his samples if he had used the NESS index instead of presence-absence data of species.

Gentry (1986) found that many of the Amazonian forests were clearly richer in tree species than equivalent Central American forests. However, his conclusion that the very rich Amazonian forests also have a much higher beta-diversity than other forests due to greater habitat differentiation raises some doubts. The high beta-diversity might partly have resulted as a methodological artefact from the very high alpha-diversity of the Amazonian sites.

IS CLASSIFICATION A USEFUL ALTERNATIVE TO ORDINATION?

An alternative approach to ordination is classification of dissimilarity data by clustering (see Figure 1). Cluster algorithms might help to find outliers and to split data into discrete categories. Among a variety of cluster algorithms, agglomerate single-linkage cluster analysis is probably the most widely used in biogeography and evolutionary biology. Figure 4 shows a comparison between a cluster analysis and an NMDS ordination of geometrid moths (NESS $m_{\max} = 193$). Other cluster algorithms such as the Ward method reveal overall similar patterns (not shown).

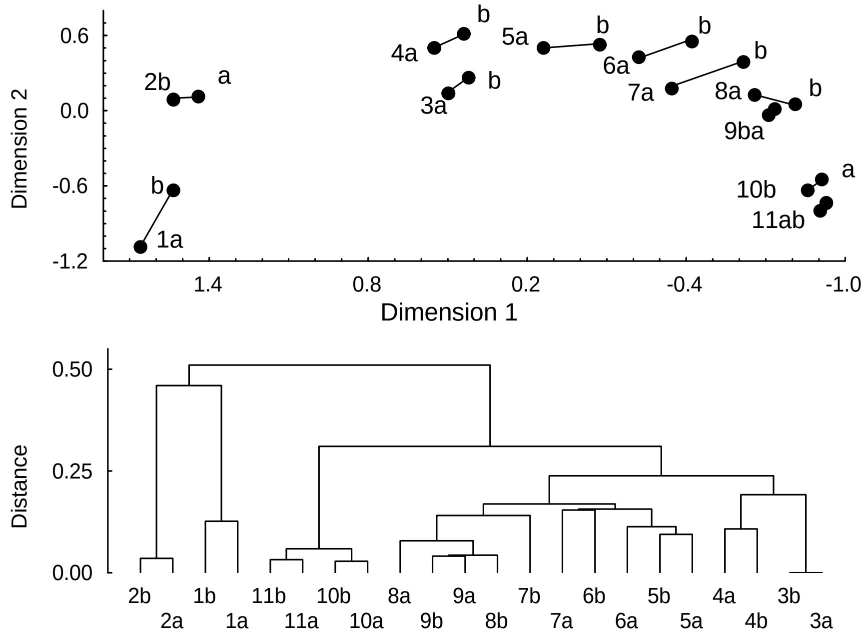


Figure 4 NMDS ordination (NESS $m_{\max} = 193$) and a dendrogram derived by agglomerate single-linkage cluster analysis of geometrid moths collected from 22 sites in a montane rain forest in South Ecuador. Numbers indicate altitudinal levels (1 low, 1,040 m, 11 high, 2,670 m; a and b replicates at each level, see Chapter 4). While NMDS arranges the samples according to their altitudinal order, cluster analysis fails to reflect the altitudinal gradient with equal precision.

The resulting dendrogram depicts a clear, interpretable pattern and reflects e.g. the outstanding nature of the samples from the levels 1 and 2. However, the method cannot reflect a smooth transition between samples as is suggested by all ordination methods (see above). Clarke (1993) criticised cluster analysis because “it is something of a hair-line decision as to how groups combine. This is precisely the reason why the continuum of an NMDS ordination is preferred to the discreteness of a cluster analysis.” I agree with Clarke that ordination methods are more powerful tools in the analysis of gradual changes, as is the case in the empirical data set of geometrid moths. Furthermore, the choice of the cluster algorithm is somewhat arbitrary and might lead to varying results. In contrast to NMDS or metric methods, cluster analysis does not allow further exploration via correlation (Figure 1) or statistical testing. I conclude that ordination has all the advantages of cluster analysis in depicting interpretable patterns, but none of its potential disadvantages.

CONCLUSIONS

Selected unconstrained ordination techniques and similarity indices were compared with respect to their behaviour with a very large empirical set of data from moths in tropical montane rainforests. Among the ordination methods, non-metric multidimensional scaling is advantageous because of its minimal statistical assumptions. However, both tested metric methods, correspondence analysis and detrended correspondence analysis, like NMDS, provide readily interpretable results. While CA shows the clearest ordinations, DCA does not have any advantages over the other methods. This is emphasised in Chapter 7 where DCA fails to reflect patterns of simulated model data. Furthermore, cluster analysis did not reveal any structure in the data set which would not be accessible through ordination.

The NESS index has fundamentally important advantages over other similarity indices, in particular its ability to cope with incomplete samples and many rare species. Since these are typical properties of tropical arthropod samples (Novotný & Basset 2000), the index deserves to attract much wider usage than it currently has. If a large parameter *m* can be achieved (in large data sets), there is evidence that the maximum *m* yields the clearest results, whereas a NESS index with a minimum *m* (= Morisita index) is vulnerable to fluctuations in the dominant species (Wolda 1981). The Sørensen index has also been shown to be a suitable measure of similarity on this particular data set because sample sizes and coverage of actual species numbers differ only moderately (see Chapter 5). In data sets that are more heterogeneous, Sørensen's index will be less appropriate, as shown e.g. for data of pyralid moths in the same study area (Süßenbach in prep.). Moreover, absolute similarities are systematically underestimated since presence-absence based indices do not account for stochastic effects in samples, which are especially problematic with very species-rich communities.

A combination of NMDS ordination and the NESS index seems to be the most appropriate solution for the analysis of incompletely sampled and species-rich communities. So far, only very few studies have applied this combination (Schulze & Fiedler 2002, Beck et al. 2002). In addition, alternative techniques should always be explored in order to check the robustness of resulting patterns since no single method will perform perfectly under any given set of circumstances.

7 Beta-diversity of geometrid moths in an Andean montane rainforest

INTRODUCTION

Communities of organisms change along environmental gradients such as from dry to moist, cold to warm, and nutrient-poor to nutrient-rich. Whittaker (1972) named this phenomenon ‘beta-diversity’ and defined it as the “extent of differentiation of communities along habitat gradients”. One of the central aims of community ecology is to discover the mechanisms responsible for such changes in community structure and diversity. Tropical communities are the most diverse but probably also among the least understood on Earth. For example, Gentry (1988) described patterns of diversity in plant communities and floristic composition along environmental and geographical gradients and concluded that plant diversity in the Neotropics correlates strongly with annual precipitation. However, the role of soil nutrients remains a more controversial issue (Sollins 1998). Scale is an important issue in the analysis of diversity (Lawton 1999). Large-scale patterns have been successfully analysed for a range of organisms in macroecology, a relatively new discipline of ecology (Lawton 1999, Gaston 2000). While there is an increasing understanding of the mechanisms responsible for tropical phytodiversity at smaller scales, this cannot be said to be true for the majority of animal groups, including herbivorous insects. So far, relatively few studies have analysed beta-diversity and the possible underlying mechanisms responsible for changes in diversity in this guild across small spatial scales in tropical ecosystems (e.g. Schulze 2000, Basset 2001, Hill et al. 2001).

In this chapter, I attempt to identify determinants for the beta-diversity (i.e. the change in species composition) of a very species-rich group of tropical herbivorous insects. Investigations were carried out into the diversity of geometrid moths (Lepidoptera) in a montane rainforest in South Ecuador, along an gradient ranging in altitude from 1,040 m to 2,677 m above sea level. The structure and alpha-diversity of the species ensembles (terminology according to Fauth et al. 1996) are discussed in Chapters 4 and 5, while methodological techniques of measuring beta-diversity are considered in Chapter 6. The study area is described in Chapter 4.

This chapter has the following aims:

- Description and interpretation of beta-diversity of geometrid moths and two major subfamilies (Ennominae and Larentiinae) along an altitudinal gradient

- Establishing correlations between faunal data and biotic and abiotic environmental factors
- Development of simulation models which reflect empirical patterns of geometrid beta-diversity and assist in the interpretation of ordinations

METHODS

ORDINATION AND SIMILARITY INDICES

Data was ordinated by three different methods: Non-metric Multidimensional Scaling (NMDS), correspondence analysis (CA) and detrended correspondence analysis (DCA). The Sørensen index and the NESS index were selected as similarity measures. Theoretical justification and performance of different ordination methods and similarity indices are discussed in-depth in Chapter 6. NMDS and the NESS index were recognised as being the most appropriate for species-rich and incompletely sampled ensembles. The similarity indices were calculated with a program provided by S. Meßner (Meßner 1996). The DECORANA program (26 segments) in PC-Ord (McCune & Mefford 1999) was used to perform DCA. Mantel tests (1000 permutations) were also carried out with the program PC-Ord. All other statistical methods were carried out using the Statistica 5.5 software package (StatSoft 1999).

AVAILABLE ENVIRONMENTAL DATA

An interdisciplinary group has been investigating the upper part of the study area (i.e. a range from 1,800 m upwards) since 1997 (Beck & Müller-Hohenstein 2001). Some environmental data is already available in the literature, and various colleagues kindly provided as yet unpublished results (see Table 1). Some additional measures were carried out in order to obtain a more complete data set (Table 1). At all 22 sites in the study area, altitudinal and geographical coordinates were measured with a Garmin GPS III (geographical positions are provided in Chapter 4). Data was available from three weather stations, situated at 980 m (Zamora), 1,870 m and 2,677 m (area of the Estación Científica San Francisco, P. Emck (in prep.)). Since these climate data points were too few for correlation with faunal data, temperature was also measured during the catches (three to eleven nights, every 30 minutes during 6.30 and 9.30 p.m. local time) with a Casio alti-thermo twin sensor. Although the type and quantity of these measurements did not fit regular meteorological standards, they were sufficient for the purpose of this study, and matched well with data from climate stations in the study area. Temperature measured at all seven times per night linearly monotonically decreased with altitude. Braun (2002) provided very similar data on temperature changes along the altitudinal gradient from the study area. During the three-hour moth catching period the temperature declined at an average of 1.26 K (± 0.36) (Chapter 3). Average temperatures of measures taken at 8 p.m. were subsequently used as standard.

Table 1 Available data sources of abiotic and biotic environmental factors which are discussed in the text. Correlations (**C**) were performed with suitable data sets.

Factor	Source	Correlation
Soil	Schrumpf et al. (2001)	
Climate	Emck (in prep.)	
Vegetation structure	Paulsch (2002)	x
Floristic composition	Bussmann (2001)	
Diversity of trees	Homeier (in prep.)	x
Diversity of lianas	Matezki (in prep.)	
Diversity of epiphytic plants	Werner (2002)	
Diversity of pyralid and arctiid moths	Süßenbach (in prep.)	x
Diversity of bushcrickets	Braun (2002)	
Diversity of bats	Matt (2002)	
Temperature during the catches	own data	x
Visible sky (canopy closure)	own data	x
Geographical distances	own data	x

In order to find an objective measure of canopy closure, hemispherical photographs were taken with a Nikon SLR 8 mm lens and a Nikon camera. From these, the “visible sky” value was calculated with the HemiView program (Delta-T Devices 1999). Five photographs were taken at each site: one in central position (i.e. exactly at the light trap’s position) and four at a distance of each 15 m from the central point to the four points of the compass. Values of visible sky and their average for each site were calculated, and the latter used for further analysis (values are provided in Appendix 5). Due to technical problems, data is available for only 19 of the 22 sites (missing at sites 10a, 10b, 11b, see Chapter 4).

Available data on vegetation structure as well as on tree diversity is restricted to the upper part of the study area, i.e. covering the range between 1,800 and 2,677 m.

For each of the 16 sites where moths were sampled, I chose sites where vegetation structure had been documented in close proximity (Paulsch (2002), see Appendix 5). A perfect match between the sites could not always be achieved because light-trapping sites require some few square metres of fairly even ground and open vegetation. The mean altitudinal distance between sites was 30 ± 29 m. However, forest structure was in all cases apparently very similar between light-trapping sites and the plots where vegetation structure was studied. Paulsch (2002) originally recorded a total of 146 structural parameters from a low and a high forest stratum (his strata 1 and 3) in plots of 400 m^2 size. An intermediate stratum 2 was available from only a few sites and was consequently discarded from the present analyses. Structural parameters included rank scale data of canopy shape, stem form, branch patterns, leaf size, leaf form, bark, occurrence of mosses, lichens, lianas, palms, bamboo, and ferns, as well as of epiphytic bromeliads and orchids. Variables with zero values at all 16 sites were ignored for subsequent analyses (stratum 1: 119 variables left, stratum 3: 123 variables left). Since an immediate effect on moth ensembles cannot be expected from all aspects of vegetation structure, a subset which included exclusively leaf parameters was selected and analysed separately. A high proportion of geometrid moths is known to be folivorous (see Chapter 2) and a consequent response of the moths to changes of leaf structures was anticipated. Leaf parameters originally comprised 54 variables, of which 41 (stratum 1), and 47 (stratum 3) remained after discarding variables with zero values.

Data on the diversity of trees in the study area was provided by J. Homeier (in prep.). He recorded all tree individuals ≥ 5 cm diameter at breast height (dbh) in plots of 400 m^2 size. A total of seven plots were chosen in close proximity to light trapping sites within an range in elevation of 1,850 to 2,450 m, and with a mean altitudinal distance between vegetation sites and light-trapping sites of 26 ± 26 m.

CORRELATIONS WITH ENVIRONMENTAL DATA

Two principal methods were applied in order to correlate moth faunal data with environmental parameters (see Chapter 6, Figure 1). Dimensional scores of moth samples extracted from different ordinations were directly correlated with altitude, temperature and with the structural vegetation parameter of visible sky. For more complex (i.e. higher dimensional) data sets such as geographical distance, vegetation structure and tree diversity, Mantel tests for associations between matrices were performed with the program PC-Ord (McCune & Mefford 1999). Matrices based on Euclidean distances were derived from data on geographical distance and vegetation structure, whereas a similarity matrix was derived from tree species data, based on the NESS index ($m_{\max} = 19$, see Chapter 6 for further details on this index). These matrices were subsequently tested for their association with faunal similarity matrices. In order to compare the performance of methods on the data sets, such matrices were also derived from (“one-dimensional”) data on altitude and temperature. These procedures were all aimed at identifying those environmental factors which can be used to explain patterns of faunal change.

SIMULATED MODEL DATA

Relatively simple simulation models of species distributions along an elevational gradient were developed (two examples in Figure 4). Models generally contain no “data noise”, as empirical data sets often do, and are intended to simplify complex real patterns. By creating models in this study, I wanted to learn about the essential properties of the empirical data sets with regard to their beta-diversity. The models also provided the possibility of comparing the performances of the applied ordination techniques.

The simulation models are characterised by the following features and assumptions:

(1) They are based on presence-absence information for simplicity.

(2) All species have the same span of altitudinal distribution, and each species occurs continuously within its complete range.

(3) Sites which are situated at the same altitude are more similar to each other than to sites of a different altitude with regard to their species composition. In the models, this is reflected by a turnover of one species from one site to the next at the same level, and a turnover of two species to a site at the next higher (or lower) level.

(4) Altitudinal change is modelled at elevational steps of 100 m. This reflects the empirical data set, where light-trapping sites are roughly spaced at steps of ca. 100 m.

(5) Due to difficulties of access in the lower part of the study area, the altitudinal steps between real sites are much larger than in the upper part. In order to mimic this in the model, a step between the three lowest levels in the model data is reflected in a species turnover which is four times higher than in a “normal” step.

A number of models were eventually developed, in which the (equal) altitudinal range of the species was varied from 300 m to 1,600 m (maximum range of the gradient).

This simultaneously changed the number of species involved in the models. I decided not to further vary the models to include a higher (and more “realistic”) number of species (see Discussion), or to change altitudinal distributions, (1) in order to sustain the most simplistic assumptions, and (2) because the models exhibited an excellent fit with the empirical data set (see below). Figure 4 shows graphically two such models with all species’ altitudinal ranges of 700 m and 900 m, respectively. Models were developed for Geometridae as a whole and the two large subfamilies Ennominae and Larentiinae. From the simulated data sets, matrices of similarity between sites were calculated with the Sørensen index which is the most appropriate for presence-absence data (Wolda 1981). These matrices were subsequently compared with matrices derived from the empirical data set by using Mantel tests (see Chapter 6). The overall best-fitting model (species distributional range: 700 m) was chosen then to perform ordinations. In this way it was possible to compare ordinations derived from simulated data with those derived from empirical data.

RESULTS

ORDINATIONS

Figures 1 and 2 show ordinations performed by NMDS, CA and DCA for Geometridae, the two large subfamilies Ennominae and Larentiinae, and model data. All ordinations very clearly reflect the relative altitudinal positions of sites from level 1 to level 11. In all taxa as well as in model data, NMDS and CA ordinations have a U-shaped arrangement of sites in common. In ecological literature, this form has been described as arch (Wartenberg et al. 1987). The similarity of arrangements across the different methods is striking. Even more surprising is the similarity of model ordinations to those based on empirical data. Results clearly suggest that one dominant gradient is responsible for the arrangements, and arches have to be interpreted as the result of this gradient (see Discussion). As a consequence, meaningful scores can be extracted only from the first dimension in order to perform correlations with environmental factors (see below). As suggested in Chapter 6, comparable extractions cannot be performed with scores from the second or higher dimensions.

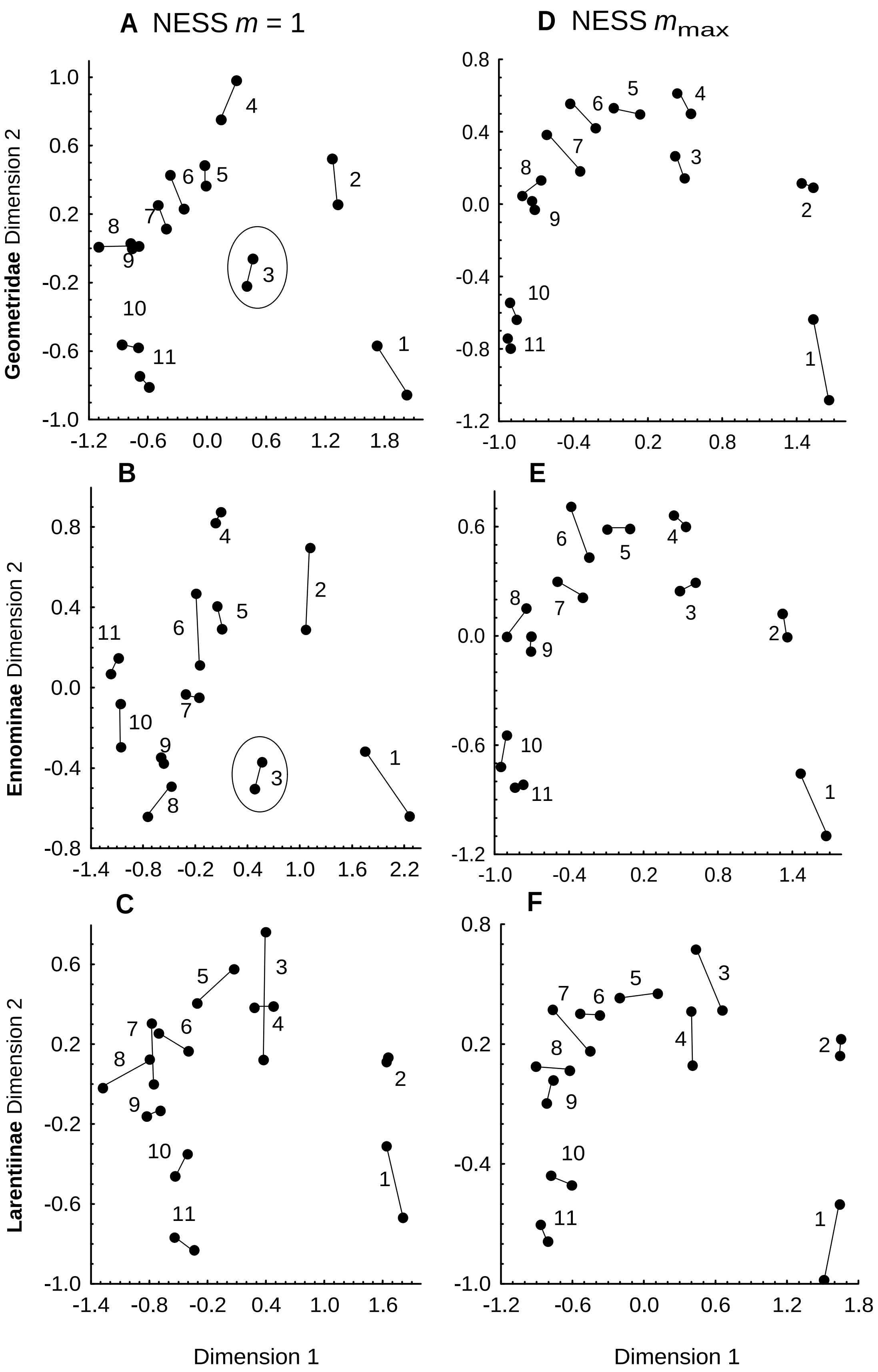


Figure 1 Non-metric multidimensional scaling (two dimensions) of samples of Geometridae (**A, D**), Ennominae (**B, E**) and Larentiinae (**C, F**), based on matrices calculated with NESS similarity indices. **A, B, C** NESS m = 1, **D, E, F** NESS m = 193. Numbers from 1 to 11 correspond to altitudinal levels from low (1,040 m) to high (2,677 m), see Chapter 4. Ellipses indicate deviations from the arch-patterns in Figures A and B at sites adjacent to disturbed areas.

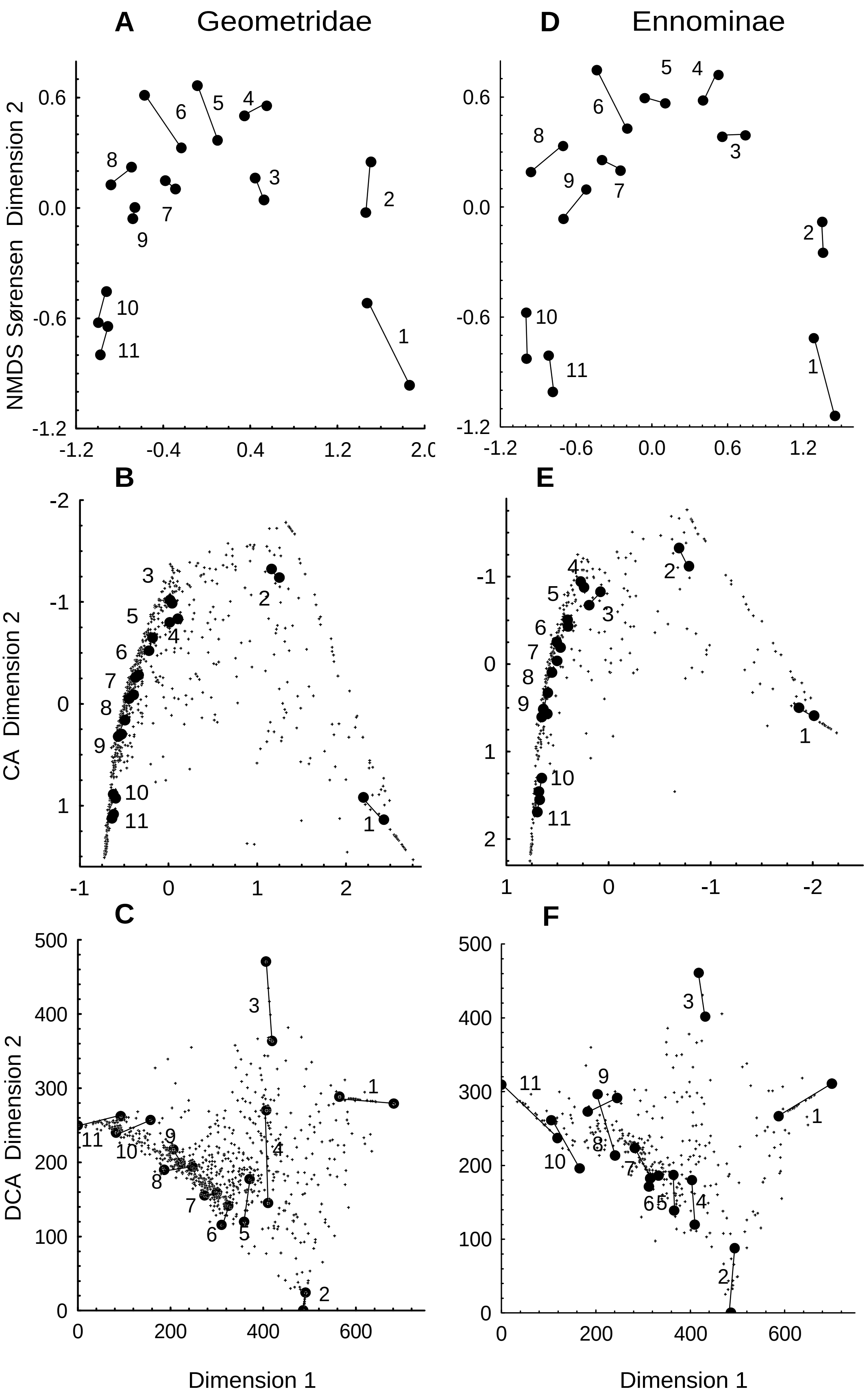
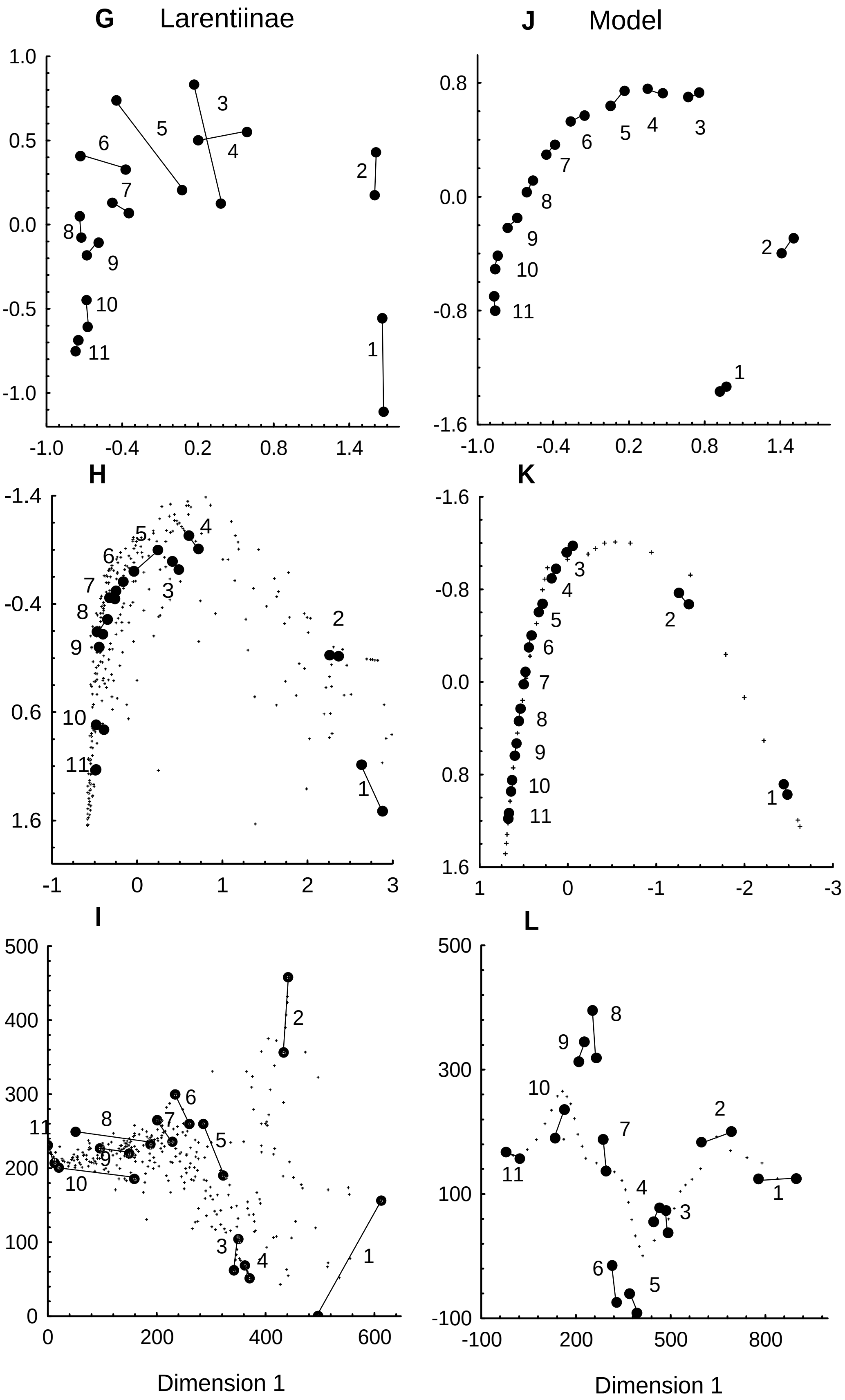


Figure 2 Ordinations of samples of Geometridae (**A, B, C**), Ennominae (**D, E, F**) and Larentiinae (**G, H, I**), and model data (**J, K, L**; underlying model: see Figure 4A). First row: non-metric multidimensional scaling, based on matrices calculated with the Sørensen index, second row: correspondence analysis, third row: detrended correspondence analysis. Further NMDS ordinations



see Figure 1. Numbers from 1 to 11 correspond to altitudinal levels from low (1,040 m) to high elevations (2,677 m), a complete list of altitudes and geographical positions of all sites is provided in Chapter 4. Little dots in CA and DCA represent single species.

There are only minor deviations in CA and NMDS from the commonly found arch, occurring in NMDS ordinations of Geometridae and Ennominae based on the NESS index ($m = 1$, indicated with ellipses in Figure 1 (A and B)). As discussed in Chapter 6, this index (identical to the Morisita index) is sensitive to abundance fluctuations in common species. Subsequent interpretations are not influenced by such deviations since the arrangement along the first dimension is not affected.

As expected, in contrast to NMDS and CA, no arch is visible in DCA. An algorithm in this technique “detrends” the arch form. Model data also suggest that the second dimension cannot be interpreted because sites are arranged arbitrarily along this axis and there is no underlying structure in the model which corresponds to the DCA patterns. After detrending, however, the arrangement of sites along the first axis from low to high elevations remains stable, although it is more scattered than in CA and NMDS.

CORRELATIONS WITH ENVIRONMENTAL DATA

Table 2 shows correlations between environmental data (altitude, temperature and visible sky) and scores extracted from the first dimensions of three ordination techniques. Across all examined taxa there are extremely high correlations between altitude and temperature and the first dimensions of all ordinations ($r = -0.89$ to -0.99 and $r = 0.87$ to 0.98, all $p<0.001$). In contrast, visible sky is not significantly correlated with them ($r = -0.26$ to -0.56, no result significant after sequential Bonferroni procedure). Relatively small differences can be detected between different ordinations. For example, DCA corrrelations are always stronger than CA correlations. Figure 3 shows graphically the correlation of temperature and scores with the first dimension of NMDS of Geometridae.

Table 2 Pearson correlation coefficients between **altitude**, mean temperature during moth sampling at 8 p.m. (**Temp**), the **visible sky** parameter (canopy closure) and the extracted scores of the first dimension of five different ordinations in three taxa (Geometridae, Ennominae and Larentiinae). The first three ordinations in each taxon are non-metric multidimensional scaling ordinations, based on three different similarity indices (Sørensen index and NESS index with $m = 1$ and m_{max}). The other two ordinations are correspondence analysis (CA), and detrended correspondence analysis (DCA). All correlations of scores of the first dimensions of all ordinations with altitude and temperature are highly significant. In contrast, the structural canopy parameter "visible sky" does not correlate significantly with extracted scores from the first dimensions (available due to technical reasons only for 19 of 22 sites). **ns** not significant, (*) not significant after sequential Bonferroni correction. **** p<0.001.

	Altitude		Temp		Visible Sky	
	r	p	r	p	r	p
Geometridae						
Sørensen	-0.97	****	0.96	****	-0.39	ns
NESS $m = 1$	-0.96	****	0.94	****	-0.31	ns
NESS $m_{max} = 193$	-0.97	****	0.96	****	-0.39	ns
CA	-0.94	****	0.91	****	-0.29	ns
DCA	-0.97	****	0.98	****	-0.56	(*)
Ennominae						
Sørensen	-0.96	****	0.95	****	-0.37	ns
NESS $m = 1$	-0.99	****	0.98	****	-0.45	ns
NESS $m_{max} = 62$	-0.97	****	0.96	****	-0.38	ns
CA	-0.92	****	0.89	****	-0.27	ns
DCA	-0.97	****	0.98	****	-0.53	(*)
Larentiinae						
Sørensen	-0.94	****	0.93	****	-0.31	ns
NESS $m = 1$	-0.89	****	0.87	****	-0.20	ns
NESS $m_{max} = 32$	-0.95	****	0.93	****	-0.34	ns
CA	-0.94	****	0.92	****	-0.30	ns
DCA	-0.95	****	0.97	****	-0.56	(*)

Figure 3 Correlation of ambient temperature (measured at 8 p.m.), and scores of light-trapping sites according to the first dimension of non-metric multidimensional scaling (Geometridae, NESS index with $m_{\max}$ = 193). r = 0.96, p<0.001.

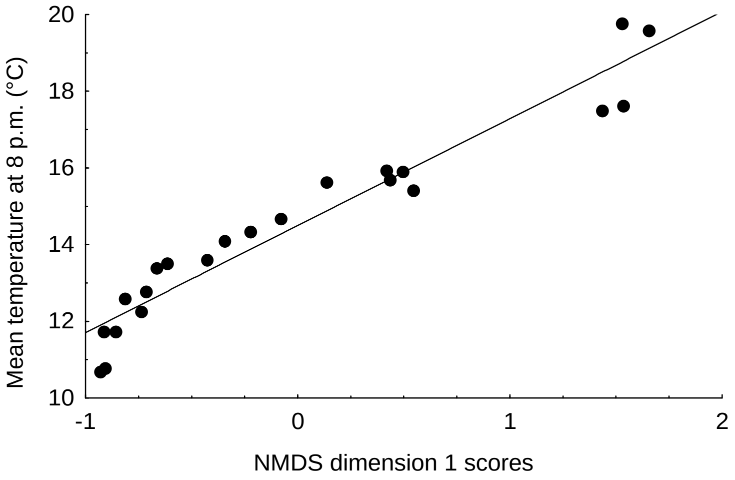


Table 3 Mantel correlations of similarity matrices of three moth taxa (Geometridae, Ennominae and Larentiinae) versus distance matrices of different environmental factors. Faunal similarity matrices are based on data from 22 sites from a montane rainforest in South Ecuador (1,040 – 2,677 m). Matrices were derived from the Sørensen index and with two NESS indices (m = 1 and $m_{\max}$). Not all environmental data sets were available from all the 22 sites where moths were sampled: full sets include altitude, temperature (**Temp**), and geographical distance. Data on vegetation structure were available from 16 plots in the upper part of the study area (1,850 – 2,677 m, Euclidean distance matrices). **Strat**um 1 and 3 (Paulsch 2002). Data on tree diversity (**Tree div**) was available from seven sites within the same range. The tree diversity matrix was derived from the NESS index ($m_{\max}$). * p<0.05, ** p<0.01, *** p<0.005, **** p<0.001, (*) not significant after sequential Bonferroni correction (Hochberg 1988).

	Altitude		Temp		Distance		Vegetation structure								Tree div	
Sites	22		22		22		16								7	
Distances	Euclidean		Euclidean		Euclidean		Euclidean								NESS $m_{\max}$	
							All parameters				Leaf parameters					
							Strat 1		Strat 3		Strat 1		Strat 3			
	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p
Geometridae																
Sørensen	0.90	****	0.88	****	0.66	****	0.27	(*)	0.45	****	0.33	***	0.35	***	0.85	****
NESS m = 1	0.78	****	0.76	****	0.58	****	0.33	**	0.40	****	0.41	****	0.41	****	0.84	****
NESS $m_{\max}$	0.90	****	0.88	****	0.65	****	0.36	**	0.43	****	0.43	****	0.41	****	0.83	****
Ennominae																
Sørensen	0.87	****	0.85	****	0.60	****	0.24	*	0.38	***	0.29	*	0.28	*	0.79	****
NESS m = 1	0.76	****	0.74	****	0.56	****	0.34	***	0.39	****	0.42	****	0.41	***	0.78	****
NESS $m_{\max}$	0.87	****	0.85	****	0.63	****	0.35	***	0.41	****	0.41	****	0.37	***	0.81	****
Larentiinae																
Sørensen	0.88	****	0.84	****	0.71	****	0.29	(*)	0.46	****	0.34	**	0.35	**	0.80	****
NESS m = 1	0.78	****	0.76	****	0.58	****	0.34	**	0.37	***	0.41	****	0.41	****	0.73	****
NESS $m_{\max}$	0.88	****	0.85	****	0.65	****	0.37	**	0.40	****	0.45	****	0.42	****	0.82	****

The significant correlations of altitude and temperature with moth data shown in Table 2 and Figure 3 are confirmed by Mantel tests for associations between entire matrices (Table 3), but are generally less strong. Correlation coefficients range from r = 0.76 to 0.90 for altitude, and from r = 0.74 to 0.88 for temperature (all $p<0.001$). Geographical distance is also correlated with faunal matrices, but to a considerably lesser extent than are altitude and temperature (r = 0.56 to 0.71, $p<0.001$). While correlation coefficients are almost identical between the Sørensen index and the index NESS $m_{\max}$, values of NESS $m = 1$ are consistently lower. The direct comparison of matrices might be regarded as a more sensitive method of detecting associations between data sets than the indirect method of extracting scores from ordinations. Matrices of vegetation structure are also significantly correlated with faunal matrices, but the correlations are substantially weaker (r = 0.24, $p<0.05$, to r = 0.45, $p<0.001$). There are relatively small and inconsistent differences between the forest strata as well as between the full data set and selected leaf-parameters. Correlations tend to be stronger for the full data set in stratum 3 compared with stratum 1; however, for leaf parameters correlations are stronger in stratum 1 compared to stratum 3. Among the various similarity indices used, the strongest correlations are obtained from the NESS index ($m_{\max}> m = 1 >$ Sørensen index). In contrast to matrices derived from vegetation structure, those derived from tree species similarity (NESS $m_{\max}$) are highly significantly correlated with faunal matrices (r = 0.73 to 0.85, $p<0.001$). Hence, the beta-diversity of trees is strongly associated with the beta-diversity of moths.

MODELS

The two models shown in Figure 4 correspond very well with the empirical data set of Geometridae, based on the NESS index of similarity ($m_{\max} = 193$). The correlations between the matrices are very strong (r = 0.95 and r = 0.94 for models A and B, respectively, $p<0.001$). They have the same magnitude as the correlations of faunal data have with temperature and altitude (correlation of ordination scores: r = -0.96 and -0.97 respectively; matrix correlation r = 0.88 and 0.90 respectively, see above).

Other models (not shown graphically) also fit well the with matrices derived from empirical data. Figure 5 shows the matrix correlation coefficients of model data which differ in the (equal) altitudinal distribution of species in a range from 300 m to 1,600 m. In all three taxa considered, the best matches are obtained at elevational ranges of individual species that span between 600 and 800 m. The match rapidly decreases as altitudinal ranges become smaller whereas models with larger ranges still fit empirical data quite well.

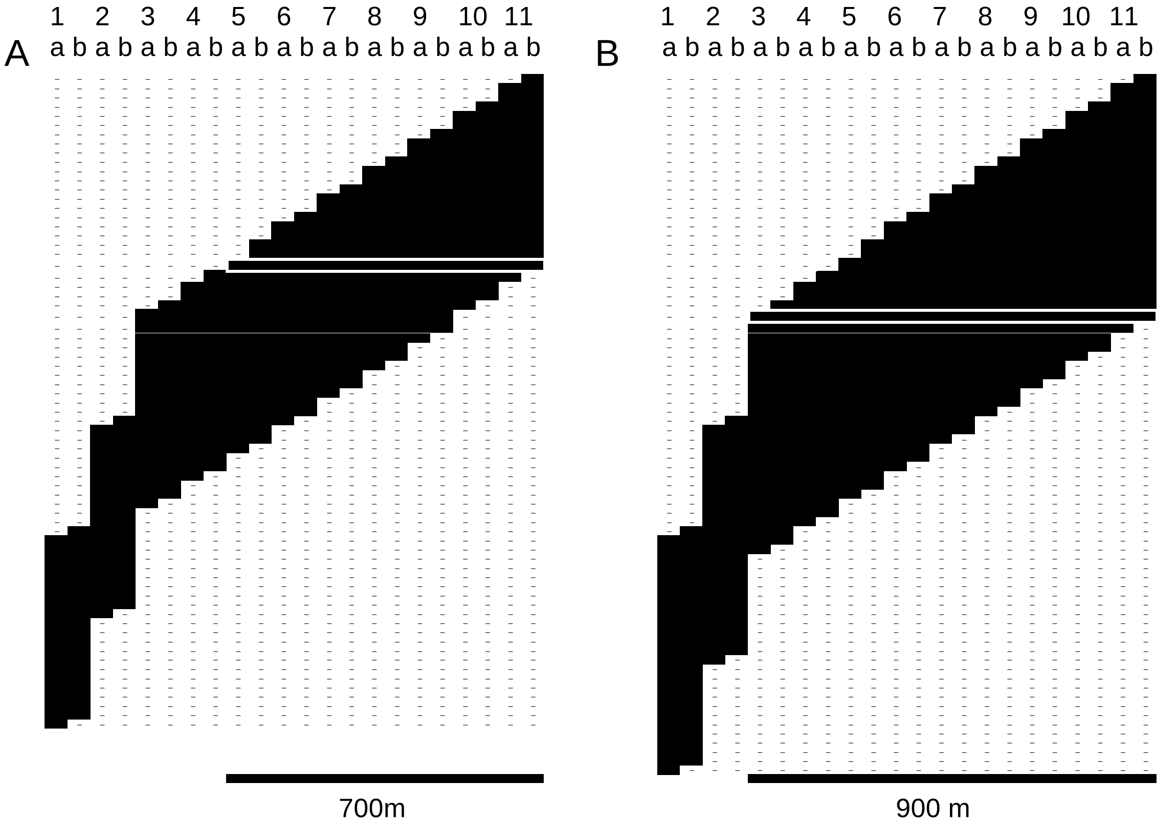
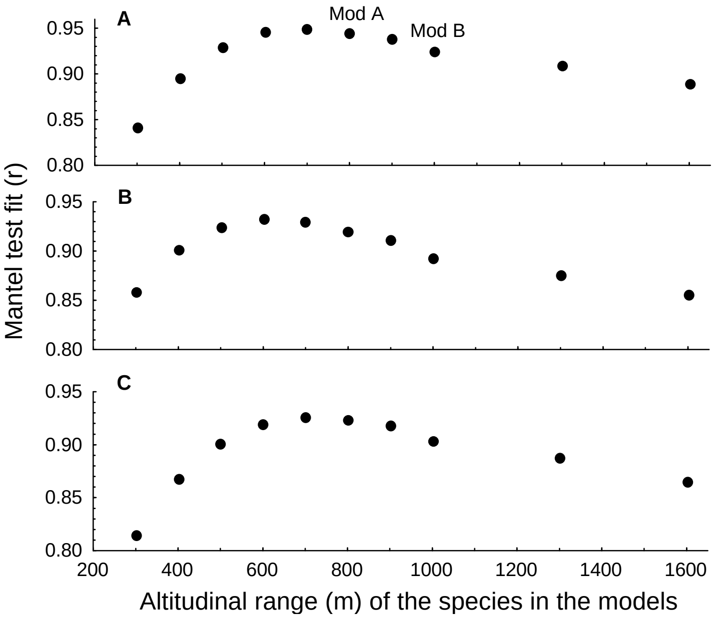


Figure 4 Two models of simulated species distributions along an altitudinal gradient of 1,600 m. Both models fit empirical data very well. **First row** altitudinal levels 1-11, separated by 400 m (1-3), and 100 m (3-11). **Second row (ab)** replicate sites at the same altitudinal level. **Remaining rows** species distributions with species present (black rectangles), and species absent (-). Sørensen similarity matrices were calculated and tested from the models for associations with a matrix derived from empirical data (Geometridae, NESS $m_{\max} = 193$). Model A (70 species, range of all species: 700 m): Mantel r = 0.95, p<0.001. Model B (75 species, range of all species: 900 m): Mantel r = 0.94, p<0.001.

Figure 5 Mantel test associations of model data matrices with empirical data matrices (**A** Geometridae, **B** Ennominae, **C** Larentiinae). **Mod A, Mod B** corresponding to the models presented in Figure 5. The latter matrices are based on the NESS index of similarity ($m_{\max}$: Geometridae: 193, Ennominae: 62, Larentiinae: 32). Model matrices were derived from simulated data of species distributions (see text and Figure 4). Models differ in the altitudinal range of species. Irrespective of the considerable differences in the altitudinal range of species in the models, all model data matrices fit the empirical data well (all r>0.70, all p<0.001).



DISCUSSION

INTERPRETATION OF THE ORDINATIONS

The very similar ordinations achieved by the application of principally different methods (both metric and non-metric) argue for the validity and robustness of the results. NMDS and CA ordinations clearly indicate the dominant altitudinal gradient and reveal arch-like forms in two-dimensional plots. The interpretation of arches is a controversial issue (see also Chapter 6). Hill & Gauch (1980) described arches as mathematical artefacts with no real corresponding structure in the data. Wartenberg et al. (1987) stated that, on the contrary, arches are an accurate representation of the data and the curvature is a result of the partially overlapping distribution of each species along a one-dimensional environmental gradient. In this study, the ordination of simulated data argues in favour of Wartenberg's interpretation. Arches result from changes along one single gradient (coenocline) in the simulated data, both in NMDS and CA. These coenocline patterns are very similar to those obtained from the empirical data. It can therefore be assumed that the empirical data also reflects a coenocline. As described in the results and in Chapter 6, there is evidence that the scores of only the first dimension can be extracted for the purpose of correlation with environmental factors, whereas data from the second dimension cannot be used in a comparable way. Probably a better approach is to interpret occurring arches as an indication for underlying coenocline data, rather than to eradicate them as is carried out in detrended correspondence analysis. DCA removes arches but does not replace them with interpretable patterns. Therefore, I agree with Wartenberg et al. (1987) who stated that DCA is no better and perhaps worse than other ordination methods.

The ordinations clearly show a gradual change of geometrid ensembles along the elevational gradient, and similar patterns appear in the two large subfamilies Ennominae and Larentiinae. Süßenbach (in prep.) found corresponding patterns in the two moth families Pyralidae and Arctiidae. These results give no hint as to the occurrence of distinct categories of communities, such as "lower montane forest geometrid ensembles" or "cloud forest geometrid ensembles". Rather, a smooth transition occurs and species are successively replaced by others. Irrespective of this, ensembles found at different altitudes have "typical" properties, such as a certain composition of taxa. For example, cloud forest is clearly characterised by a high proportion of larentiine moths, whereas ennomine moths dominate in lower montane forests (Chapter 4). However, the ratios of these subfamilies do not alter abruptly within the gradient but change gradually. Homeier (in prep.) also discovered gradual changes in tree diversity in the same study area. In contrast, Paulsch (2002) categorised distinct forest types, based on structural features (see above). Classification algorithms generally aim to find distinct categories to illustrate differences. It appears to be a rather philosophical question as to whether ordination or classification is preferred. Since my results do not indicate any clear distinctness, I prefer to describe and analyse patterns as gradual changes (Chapter 6).

INTERPRETATION OF MODEL DATA AND RAPOPORT EFFECT

The discovery that moth ensembles change gradually rather than abruptly is underpinned by the extremely good fit of simulated data with empirical data. All models assume a monotonic turnover of species rather than distinct communities which partially overlap. Moreover, the altitudinal ranges exhibited by the most abundant species show qualitatively the same patterns. Fifty-three species which comprised at least 50 individuals were tabulated in Appendix 3. As in the models (Figure 4), sharp boundaries occur only at the lower and upper end of the gradient, as well as between the sites which are 400 m apart in elevation. The mean altitudinal range of 51 species which occur at least at two different elevations is 920 ± 418 m. The actual mean range will exceed this value because 34 species are distributed up to the limits of the investigated gradient and can be assumed to be distributed beyond these limits. Hence, the overall best-fitting models assume even a lower altitudinal range (600 to 800 m) than actually displayed by many of the common species (>1,000 m). I assume that the less common species in the empirical data set are responsible for this difference as they will often be more widely distributed than they appear. Furthermore, the high standard deviation derived from the empirical data suggests that the elevational distributions vary between species to a certain extent. However, neither discrepancies affect the basic properties (monotonic replacement of species) of the models. It must also be emphasised that the models are not aimed at reflecting the other properties of the communities, such as alpha diversity. In fact, they are a gross abstraction with regard to the number of species and their abundance. The two illustrated models (Figure 4) comprise only 70 and 75 species respectively, compared with empirical numbers of between 390 and 1,010 species per taxon observed (Chapter 5). In contrast with the uniform occurrence of species in the models, the species sampled in the field differ significantly in abundance (log-series distribution, see Chapter 5). Insect samples from tropical rainforests usually contain high numbers of rare species (Novotný & Basset 2000) which is also the case here.

Available data does not indicate any systematic changes of the species' ranges along the altitudinal gradient as suggested by Stevens (1992) in his extension of Rapoport's latitudinal rule (Rapoport 1980) to altitude. However, such effects cannot be ruled out reliably without expanding the range of this study to lower and higher elevations. General evidence for Rapoport's rule is, at the very least, equivocal (Gaston et al. 1998 with a review).

THE ROLE OF ENVIRONMENTAL FACTORS: METHODOLOGICAL CONSTRAINTS

The search for the mechanisms responsible for diversity and its changes in natural ecosystems is methodologically constrained. Arguments often rely on plausibility rather than on rigorous evidence because of the immense number of variables which are beyond control. There are approaches towards the experimental manipulation of relatively simple ecosystems (e.g. grasslands in Minnesota and Europe (Tilman 1999)), but this is impractical in highly diverse systems such as tropical rainforests (e.g. Moon et al. 1999). Therefore, precise descriptive analysis along existing gradients is probably the only method of obtaining an understanding of diversity patterns in species-rich real ecosystems. I was searching for correlations by using two different approaches. Generally, the fact that variables are correlated does not necessarily mean that one causes the other (e.g. Fowler et al. 1998). However, correlative studies are the appropriate first step in understanding causal relationships and in the building of hypotheses before field experiments can be carried out (e.g. Sollins 1998). The results suggest the clear dominance of an altitudinal gradient which is responsible for the beta-diversity of geometrid moths. Geographical distance correlates far less with faunal matrices than do altitude and temperature. Geographical distance and altitude are autocorrelated ($r = 0.78$, $p<0.001$). This autocorrelation is undesirable, but was unavoidable when the study sites were selected. Geographical distance will play a subordinate role compared with altitude and temperature. This is well illustrated by the high similarity between ensembles which were sampled at the same altitude but at relatively large distances from each other (ca. 1.5 km) (see the map in Chapter 4).

Unfortunately, altitudinal gradients comprise a large number of intercorrelated variables. Abiotic factors change, as do the diversity and functional roles of organisms. For example, as elevation decreases, temperature decreases linearly (see Chapter 3), precipitation increases (Emck in prep.), and nitrogen availability and primary productivity decrease (Waide et al. 1998, Schrumpf et al. 2001). The diversity of many groups of organisms decreases at least from medium altitudes as elevation increases. In the study area (above 1,800 m) this is true for trees >5 cm diameter at chest height (Homeier in prep.), lianas (Matezki in prep.), birds (Rahbeck 1997), bats (Matt 2001), bushcrickets (Braun 2002), and pyralid moths (Süßenbach in prep.) (see Chapter 5). Beta-diversity in all these groups will show a certain degree of similarity in the way that species are replaced by others as elevation rises. Very strong correlations between groups of organisms might indicate a casual relationship, but they might also hint at a common underlying environmental factor. As a consequence, the underlying mechanisms which drive the beta-diversity of a certain group, such as geometrid moths, can never be precisely understood in a complex ecosystem, unless the ecological requirements of all species are exactly known.

INTERPRETATION OF ENVIRONMENTAL FACTORS

Despite the constraints on its interpretation the available data gives some very clear indications about dominant factors. Altitude, ambient temperature and tree diversity match the observed beta-diversity patterns very well. While altitude per se is not meaningful in a biological sense, ambient temperature and tree diversity are. Climatic influences were e.g. detected as the most important factors for population changes in British butterflies (Roy et al. 2001). The excellent fit of temperature argues in favour of different ecophysiological (i.e. thermal) constraints on geometrid species. This hypothesis could be tested with experiments which explore the performance of different species at different temperatures (e.g. in terms of larval growth, survival, pupal weight, flight physiology, e.g. Thompson 1988, Fischer 2000). Such experiments could also reveal whether the ecophysiological range of species (i.e. their fundamental niches) corresponds well to the patterns found in the field (i.e. their actual niches).

According to Gentry (1988), the diversity of plant species generally decreases with rising altitude in the Neotropics. Nevertheless Andean forests are more species-rich at altitudes >3,000 m than are temperate forests. For example, Madsen & Øllgard (1994) found an extraordinarily high tree diversity near the treeline in Podocarpus National Park. A relationship between the beta-diversity of trees and that of geometrid moths appears to be readily interpretable because geometrid moths are dominated by species which are arboreal defoliators (Chapter 2). At much lower elevations in Borneo, understorey vegetation diversity emerged as the single most important predictor of geometrid moth diversity (Beck et al. 2002). A certain proportion of the species in the Ecuadorian study area is known to be adapted to certain resources as is the case for the ennomine tribe Macariini and Fabaceae (Chapters 2, 4 and 5). A turnover in species of the plant group might result in a turnover in moth species. However, the majority of geometrid species is not expected to be specialised but polyphagous. For these species, the turnover in potential host-plant species will not be very important since the moths can easily switch to different hosts. Rather, for most tropical herbivores, food supply is likely to be a function of the availability of young foliage (Basset 1992). Therefore, I assume that a common underlying gradient for both trees and moths (such as ambient temperature) actually plays a greater role than a direct causal relationship. This hypothesis could be tested with future investigations: Paulsch (2002) and Homeier (in prep.) found that forest structure and tree diversity show considerable differences between stands on ridges (where moth sampling was performed) and in ravines. A systematic comparison of sites which are situated at the same altitude but differ with regard to aspect could reveal whether temperature or tree diversity is the more important environmental factor responsible for the beta- (and alpha-) diversity of geometrid moths.

In contrast to temperature and tree diversity, the available data on vegetation structure fits the beta-diversity patterns of geometrid moths much less well. While the beta-diversity of moths and trees changes more or less linearly as elevation increases, vegetation structure as measured by Paulsch (2002) does not. Areas of vegetation structure might be relatively heterogeneous because of landslides which often occur in the study area (Stoyan 2000). Differences in aspect, steepness, nutrient availability and successional age of sites will have a considerable effect on vegetation. On the contrary, many tropical successions may represent a relatively permanent and predictable habitat for insects (Lepš et al. 2001). Furthermore, most insects are mobile, and vegetation mosaics on very small scales will not be reflected by the insect communities present. The relatively weak correlations between vegetation structure and the beta-diversity of geometrid moths indicate that forest structure is not a dominant factor for ectophagous herbivorous insects. However, habitat structures have to fulfil a number of criteria in order to be appropriate to geometrids. These include the provision of a suitable microclimate, as well as host-plants and feeding sources for the adults. Since geometrid moths are known as a group of mainly forest-dwelling insects, they respond sensitively to habitat alterations (e.g. Kitching et al. 2000, Beck et al. 2002).

The suggestion that climatic factors, such as temperature, are the dominant driving force behind species turnover rates, rather than vegetation factors, is further supported by the remarkably high similarity of beta-diversity patterns among different taxa. For example, similarity matrices derived from the two subfamilies Ennominae and Larentiinae correlate with r = 0.95 ($p<0.001$). However, the groups show contrasting patterns of alpha-diversity (Chapter 5), and also differ with regard to host-plant relationships (Chapter 2). Even more astonishing is the similarity of matrices derived from the geometrid data set and a data set of pyralid moths collected in the same study area, despite the profound differences with regard to the ecology of the groups. The Mantel correlation between the similarity matrices of both taxa (NESS index with m_{max}) is r = 0.87 ($p<0.001$) (Süßenbach in prep.). Species' life histories of the families are expected to differ considerably. While geometrid moths are mostly ectophagous herbivores, a major proportion of species of Pyralidae are endophagous. Endophagous insects are generally more specialised than their ectophagous counterparts (Basset 1992, Loder et al. 1998 with references therein), and this is also assumed to be the case with Neotropical pyralid moths (Süßenbach in prep.) The groups also differ fundamentally with regard to their patterns of alpha-diversity (Chapter 5, Süßenbach in prep.).

CONCLUSIONS

Temperature is likely to have the greatest influence on the beta-diversity of the large herbivorous group Geometridae and is also expected to be a significant factor on a range of other organisms along the investigated altitudinal gradient. In contrast to commonly employed classificational approaches in botany (e.g. Sierra 1999, Bussmann 2001, Paulsch 2002), there are no hints from ordinations and raw data that ensembles of geometrid moths can be categorised into distinct classes. Simulated data sets confirm this view and underpin the continuous coenocline structure of the faunal samples. Furthermore, available data does not indicate systematic changes of the range of elevational distributions (Rapoport's rule). In order to solve this latter question, the investigation of even larger elevational gradients at a fine spatial resolution would be required. As suggested in Chapter 5, further studies of geometrid moths as a suitable and manageable "mega-diverse" group can shed light upon large-scale patterns of beta-diversity and confirm the conclusions drawn in this chapter.

8 Bergmann's rule does not apply to tropical Andean geometrid moths

INTRODUCTION

Changes in body sizes of animals along environmental gradients have attracted the attention of ecologists since Bergmann's famous publication in 1847. He found that endothermic vertebrate species tend to be smaller in warmer climates and larger under cooler conditions. According to his hypothesis, animals with larger body masses suffer smaller losses of energy due to their more favourable relation between volume and surface. Since then, several re-definitions of his rule have been formulated. For example, Rensch (1938) restricted the rule to intraspecific body size variations of endothermic animals, while Blackburn et al. (1999) redefined it as "the tendency for a positive association between the body mass of species in a monophyletic higher taxon and the latitude inhabited by those species". Hence, the latter concept explicitly included ectothermic animals, considered phylogenetical relationships, and excluded all gradients other than latitudinal gradients. Some of the alterations to Bergmann's rule appear to be arbitrary, such as the restriction to latitudinal gradients as suggested by Blackburn and co-workers. Climatic changes, as mentioned by Bergmann, occur not only along these gradients, but also very prominently along elevational gradients (Körner 2000). As a consequence, the definition of Bergmann's rule remains a controversial issue. Furthermore, the underlying mechanisms for the rule are not understood, and there are serious doubts as to whether a consistent phenomenon of changing body sizes along environmental gradients exists at all (Blackburn et al. 1999).

For ectothermic organisms such as insects, no convincing general hypothesis that would explain body size patterns along climatic gradients is currently available. However, experimental approaches have revealed that ectothermic insects often respond with larger body sizes in low temperature environments. For example, Fischer & Fiedler (2002) showed that univoltine and multivoltine populations of the butterfly *Lycaena hippothoe* responded differently with regard to their body size to increasing temperatures. Experiments on *Drosophila melanogaster* showed that body size can be influenced by the manipulation of ambient temperature (larger males at lower temperatures) (e.g. Reeve et al. 2000).

A number of studies have analysed body sizes along environmental gradients. Loder et al. (1998) stated that Bergmann's rule most likely does not apply to insects in general, and Blackburn et al. (1999) concluded that there is probably more than one single mechanism responsible for observed body size changes. In fact, from the divergent results of previous studies no consistent overall tendency can be detected. Body size patterns were often analysed in only one or a few species. For example, Hepburn et al. (2001) investigated one bee species which increases in body size with increasing altitude. On the contrary, Sota (1996) showed a decline of body size with increasing altitude in several species of carabid beetles. Krasnov et al. (1996) recovered a heterogeneous pattern in seven species of tenebrionid beetles along an elevational gradient. Other studies included much larger numbers of species. Body size of ant species in Europe has been shown to increase with increasing latitude (Cushman et al. 1993). Hawkins & Lawton (1995) analysed butterfly body sizes along latitudinal gradients in several regions and found no consistent patterns. Existing changes were explained by historical patterns of speciation. Hawkins & DeVries (1996) concluded that there were no general trends in butterfly body sizes across environmental gradients in Costa Rica, although different families exhibited varying patterns.

In the first study of its kind in the Neotropical region, I investigated the diversity of geometrid moths along an altitudinal gradient in a montane rainforest in South Ecuador (see previous chapters). In contrast to many previous studies on tropical arthropods, analyses were carried out on a very fine taxonomical scale (Chapter 3). With a total of 1,010 species, the very large data set offered the unique chance to analyse body size patterns of a monophyletic group of herbivorous insects along an elevational gradient in their natural habitat. I investigated wingspan patterns along the elevational gradient as well as the variability of the data, measured as relative coefficient of the variation of wingspan. It was expected that high-altitude environments constrain the body sizes of moths towards a certain optimum and that the variability in body size is lower in these habitats compared to lower elevations.

Analyses were carried out at the level of Geometridae and the seven largest subordinated taxa (>60 species in the study area: Ennominae with the tribes Boarmiini and Ourapterygini, and Larentiinae with the genera *Eupithecia*, *Eois* and *Psaliodes*). Sampling methods are discussed in Chapter 3, the study area is described in Chapter 4, alpha-diversity patterns are analysed in Chapter 5, and numbers of species and specimens of all analysed taxa are provided in Chapter 6 (Table 1).

METHODS

There are various ways to quantify body size in arthropods. Morphometric measures have frequently been used, e.g. the body length (Cushman et al. 1993, Sota 1996, Krüger & McGavin 2000, Smith et al. 2000) or the elytra length in beetles (Krasnov et al. 1996). Studies on single species evaluated up to even 55 quantitative morphological characters (Hepburn et al. 2001). In Lepidoptera, at least three measures have frequently been taken into consideration: body length (Wasserman & Mitter 1978), forewing length (Hawkins & DeVries 1996), and wingspan (Lindström et al. 1994, Loder et al. 1998). All these variables are strongly positively intercorrelated (Loder et al. 1998). Since all specimens available in the present study were spread in a standardised way (Chapter 3), I chose to measure the wingspan of the moths. This measure appeared to be a reliable and rapid method, in particular for the smaller moths (wingspan <20 mm). Measures were performed with a calliper rule (Mitutoyo model no. CD-15CP absolute digimatic) at a degree of accuracy of 1 mm.

Table 1 Numbers of species sampled, and numbers of species in which males were available for analysis of the three largest taxa analysed (Geometridae, and the two large subfamilies Ennominae and Larentiinae). Provided are total numbers and proportions in brackets. ^{1}Proportions refer to the species numbers in which males were available for analysis. Not shown: numbers for the subordinated taxa Boarmiini and Ourapterygini (Ennominae), and *Eupithecia*, *Eois* and *Psaliodes* (Larentiinae).

	Geometridae	Ennominae	Larentiinae
Total number of species	1,010	500	391
At least one male present	953 (0.94)	468 (0.94)	372 (0.95)
Two males present^1	739 (0.78)	363 (0.77)	298 (0.80)
Three males present^1	590 (0.58)	304 (0.65)	231 (0.62)

Analysis was restricted to males because sexes are often dimorphic in body size (Hawkins & Lawton 1995), and males were much more abundant in the samples than females were (Chapter 3). In 94% of all geometrid species sampled, males were available for analysis (Table 1). However, the data set contains many rare species (Chapter 5). Since this is a typical feature of tropical arthropod samples and rare species should not be excluded from community studies (Novotný & Basset 2000), I decided to include these species in the analysis. As a consequence, wingspan data is based on a variable number of specimens (one to three). Measures based on single specimens were accepted because (1) variability of wingspan of other species appeared to be modest, and (2) the overall effect on the results was expected to be very low because of the high species numbers analysed per site. If two or three specimens were available, the arithmetic mean was calculated and used for subsequent analyses. In 58% of the geometrid species in which males were present, three male specimens were available for measurement. In a further 20%, two males could be measured, while in 22% of the species only one male could be analysed. Table 1 provides species numbers of Geometridae and the two large subfamilies Ennominae and Larentiinae. A total of 2,282 specimens were measured. Standard statistical analyses were performed using the software package Statistica (StatSoft 1999).

RESULTS

Figure 1 shows histograms of wingspan sizes of Geometridae, Ennominae and Larentiinae. The pattern in Geometridae is left-skewed which is probably due to the occurrence of the many small larentiine species (values for skew and kurtosis are provided in the legend of Figure 1). Within this subfamily, small species of the category between 15 and 20 mm of wingspan dominate. The effect is mainly caused by the three most species-rich genera *Eupithecia*, *Eois* and *Psaliodes.* These genera account for more than 70% of all species in the subfamily Larentiinae (Chapter 4), and comprise predominantly small species. On the contrary, wingspan sizes in Ennominae appear to be normally distributed. Ennomine species are significantly larger than larentiine species (Kolmogorov-Smirnov test: wingspan Ennominae 34.4 ± 9.7 mm, Larentiinae 21.2 ± 6.9 mm, Geometridae 28.1 ± 10.6 mm, see also Figure 1).

All correlations between altitude and wingspan sizes are weak ($-0.17 \leq r \leq 0.18$, Table 2) and reveal no consistent pattern. However, the correlation is highly significant in Geometridae and Ourapterygini, where a decreasing wingspan with increasing altitude is revealed (Figure 2). On the contrary, wingspan is significantly increasing in the genus *Eupithecia*. The decrease of body size in the whole family is most probably caused by a shift in the structural composition of the family along the elevational gradient. While the larger-bodied ennomines dominate at low altitudes, the proportion of the smaller-sized larentiine species continuously increases as altitude increases (Chapter 4). This is also illustrated in Figure 3. In contrast to geometrids as a whole, no significant relationships can be found within each of the two large subfamilies, if analysed separately.

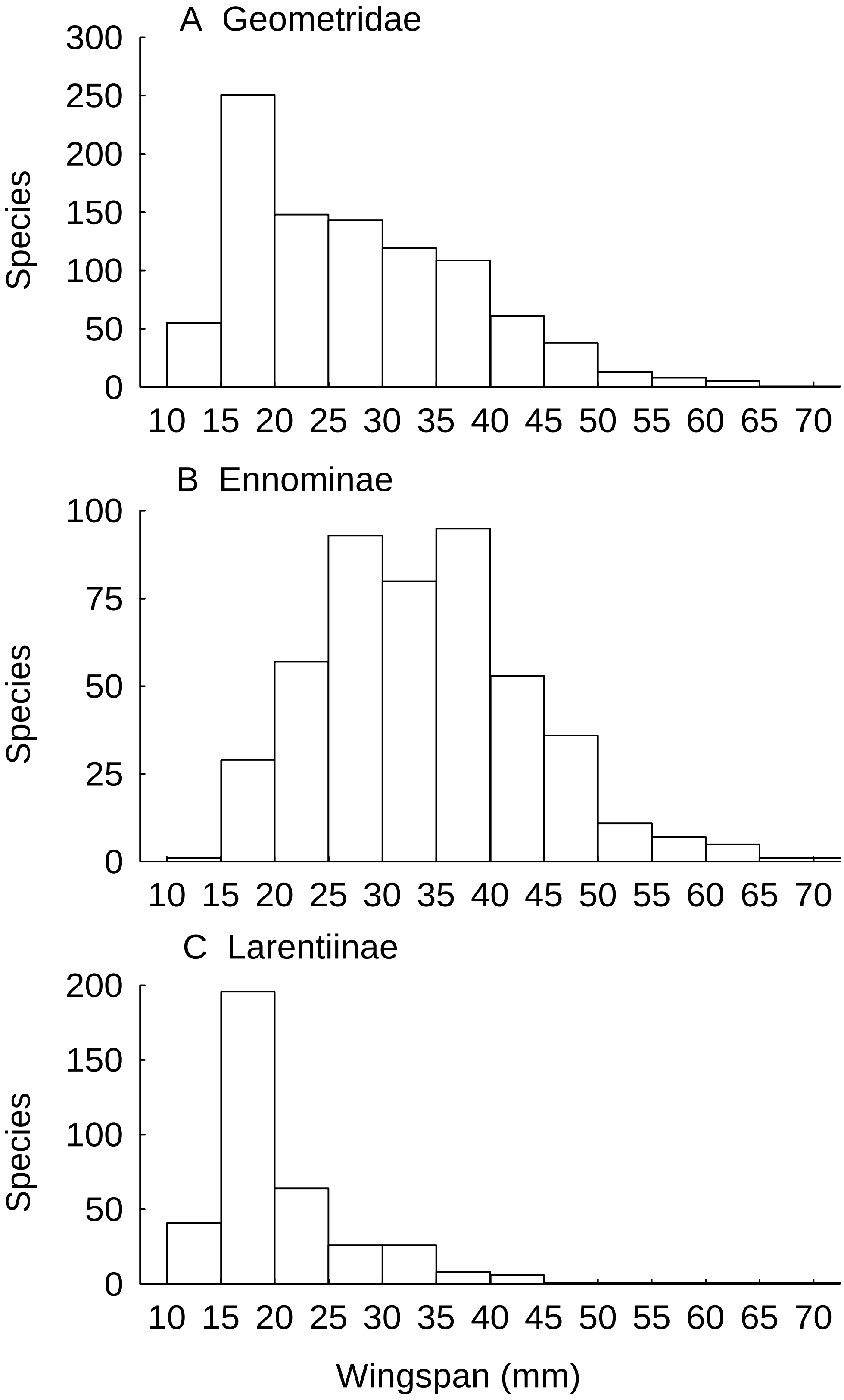


Figure 1 Frequency distributions of wingspan sizes of the three largest taxa analysed **A** Geometridae (skew: 0.81 ± 0.08, kurtosis: 0.25 ± 0.16), **B** Ennominae (skew: 0.57 ± 0.11, kurtosis: 0.37 ± 0.23), and **C** Larentiinae (skew 1.92 ± 0.13, kurtosis: 4.44 ± 0.25) in class intervals of 5 mm. Kolmogorov-Smirnov test for normal distribution: Geometridae d = 0.10, $p<0.01$, Ennominae d = 0.06, no significant deviation from normal distribution, Larentiinae d = 0.22, $p<0.01$.

Table 2 Pearson correlation coefficients between wingspan and altitude, as well as between the coefficient of variation of wingspan and altitude. **ns** not significant, * p<0.05, ** p<0.01, **** p<0.001. Results in brackets: not significant after sequential Bonferroni correction (Hochberg 1988).

	Wingspan vs. altitude r, p		Coefficient of variation vs. altitude r, p	
Geometridae	-0.06	****	0.38	ns
Ennominae	0.04	ns	0.56	**
Boarmiini	-0.02	ns	-0.37	ns
Ourapterygini	-0.17	****	0.27	ns
Larentiinae	-0.03	ns	0.70	****
Eupithecia	0.18	****	0.83	****
Eois	0.01	ns	0.27	ns
Psaliodes	0.11	(*)	0.45	(*)

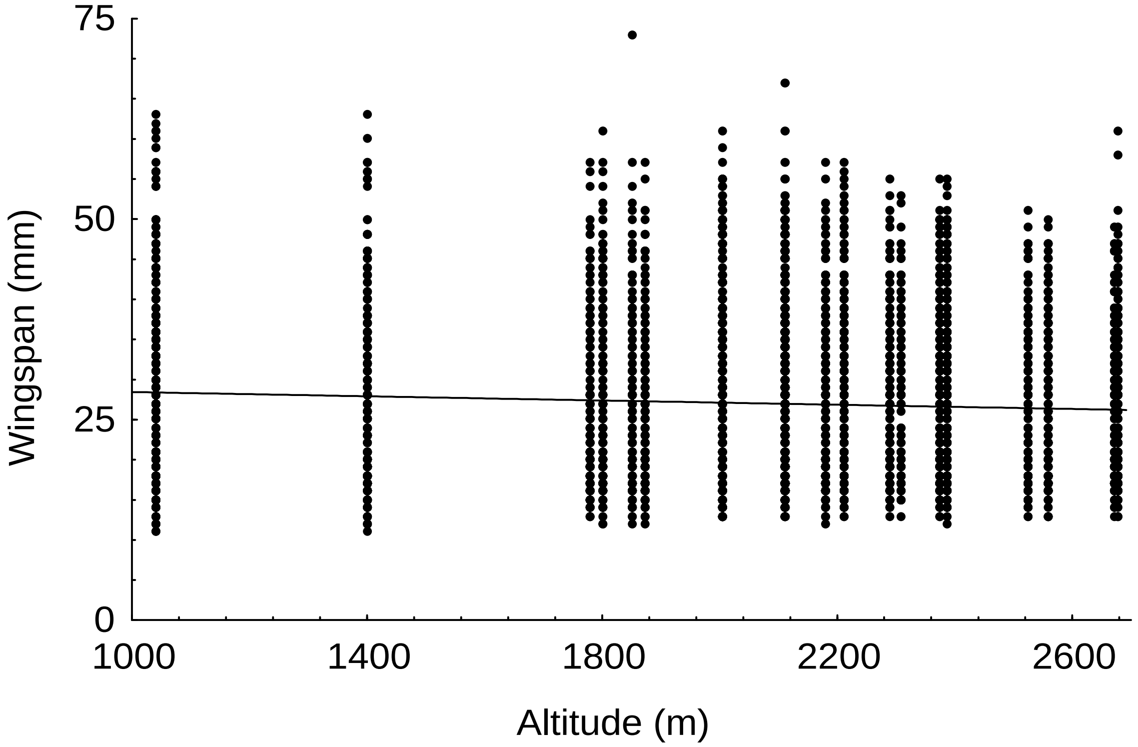


Figure 2 Wingspan size of all geometrid moths is weakly negatively correlated with elevation (r = -0.06, p<0.001). Each dot represents one species (measurements only taken for males). No significant relationship has been found in the two large subfamilies Ennominae and Larentiinae, respectively (see Table 2).

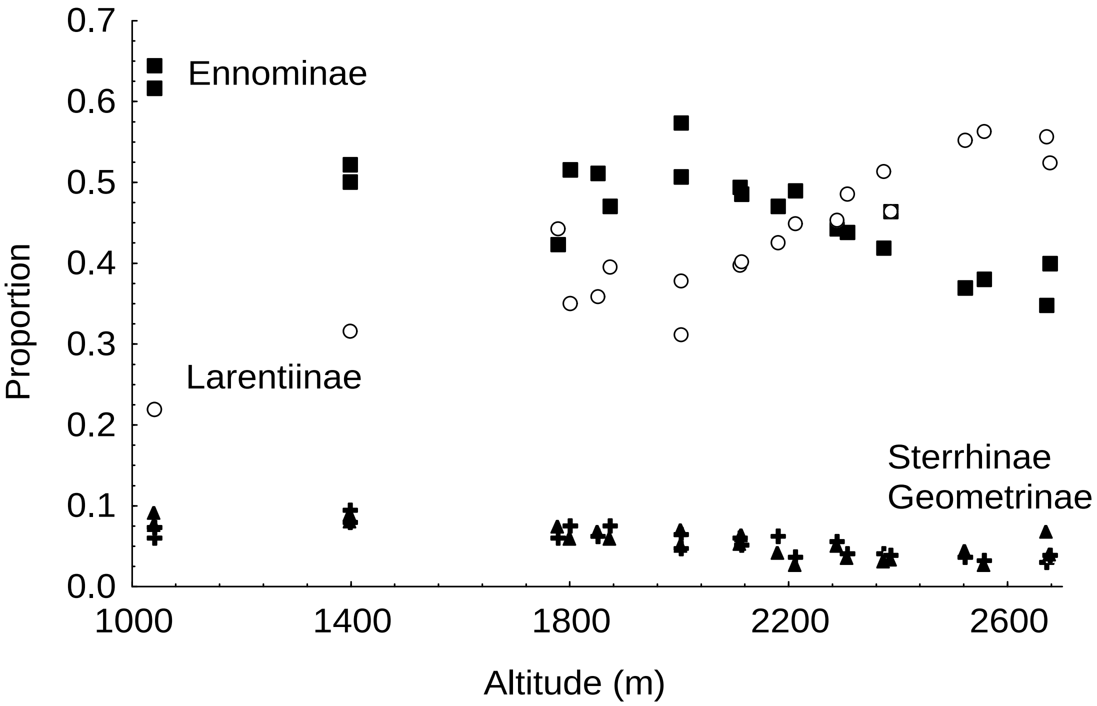


Figure 3 Structural changes in the faunal composition of geometrid moths along the elevational gradient. While the subfamilies Ennominae (squares), Sterrhinae (triangles) and Geometrinae (crosses) decrease in the proportion of species numbers, the subfamily Larentiinae (circles) increases with increasing altitude. Proportional changes in all four subfamilies are highly significant (values of r and p are provided in Chapter 4, Table 2).

Against the expectations, the variability of the data showed no decrease, but tended to increase in all taxa regarded except for the ennomine tribe Boarmiini. The results are significant in the subfamilies Ennominae, Larentiinae and the genus *Eupithecia* (Table 2). Hence, while only weak patterns of wingspan size can be found across the elevational gradient, there is a higher variability of wingspan at higher elevations compared to lower altitudes.

DISCUSSION

A very weak overall decrease in body size with increasing altitude was found in Geometridae. This decline is clearly caused by changes in the structural composition of the family with smaller-sized Larentiinae replacing larger Ennominae at higher altitudes. No significant changes occur in the two large subfamilies analysed. These results suggest that the decrease in body size in geometrid moths is not a “true” pattern, but only a side effect of structural shifts in faunal composition. Phylogenetic relatedness could potentially generate a spurious relationship between body size and altitude (see Harvey & Pagel 1991), and is most probably the dominant factor in this study. Possible reasons why larentiine moths are so species-rich and increase in their proportion at high altitudes in the study area have already been discussed in Chapter 4. Larentiines are generally adapted to unfavourable weather conditions and might particularly benefit from low predation pressures at high altitudes as they are relatively weak flyers. However, there is no evidence that larentiines are successful at high elevations because of their small body sizes. This is (1) because there is no overall significant change in body sizes within the subfamily along the gradient, and (2) genera within the subfamily show no tendency towards smaller body sizes with rising altitude. On the contrary, species of the genus *Eupithecia* tend to be even larger at high elevations compared with lower altitudes. It is surprising that three of the taxa analysed show an increase in the variability of their body size. Obviously, harsher environmental conditions do not restrict the body sizes to a certain optimum range. At the same time, it is probable that some of the biotic constraints such as predation pressure become smaller with increasing altitude (see Chapters 4, 5 and 7). Such constraints might have a canalising effect with regard e.g. to the manoeuvrability of the moth species, including features of the body architecture. Species at high altitudes might be released to a certain extent from these biotic constraints and subsequently exhibit a broader range of body sizes.

The results also show that the separate analysis of body sizes of subordinate taxa can be very important for the interpretation of the pattern of the focal group. If the analysis had been restricted to geometrid moths as a whole, the significant decrease would have been regarded in another light than with additional information on body sizes of subfamilies, tribes and genera as well as on their proportional changes. The example *Eupithecia* clearly shows that results might change fundamentally when different taxonomical levels are regarded. While the genus itself shows a significant increase in wingspan, no tendency can be detected in the corresponding subfamily, even an opposite trend in the family becomes apparent. Hence, if phylogenetical effects are not considered, results are likely to be misinterpreted.

For example, in a study on Finnish geometrid species, Lindström et al. (1994) concluded that hostplant specialists were smaller than oligophagous or polyphagous species, and that small species were more frequently focused on herbs. However, their result is very probably severely biased because they did not consider phylogenetical relatedness of the taxa involved. Larentiines are not only smaller than ennomine species, but they are also often more narrowly specialised – many of them on herbaceous plants (see e.g. Skou 1986, Chapter 2). This is particularly true for the genera that comprise many of the smallest and simultaneously most specialised species, i.e. *Eupithecia* and *Perizoma*. Thus, unless similar body-size patterns could be unravelled within genera such as those mentioned, gross patterns as established by Lindström et al. are suspect of suffering from phylogenetic bias.

Among the Andean geometrid taxa analysed here, weak support for Bergmann's rule was only sporadically found. e.g. in *Eupithecia* or *Psaliodes*. Even in these genera effect size was small, explaining but 1.2 – 3.2% of the intraspecific variation. Moreover, a significant opposite trend on the same magnitude occurred in Ourapterygini, and on higher taxonomic levels (subfamilies, family) patterns vanished almost altogether. This is in line with earlier observations (Hawkins & DeVries 1996) on Neotropical butterflies that body size relationships are characterised by taxonomic idiosyncrasies, and are much less shaped by ecological and physiological constraints as one would expect under the concept of Bergmann's rule. The general suggestion that large-bodied insects might be buffered against environmentally-induced physiological stress (Wasserman & Mitter 1978) cannot be confirmed in the present study because Andean geometrid species show striking inconsistent patterns. My results clearly agree with those found in previous analyses of body-sizes in diurnal Lepidoptera, and confirm that there are probably no general trends of body sizes of insects across environmental gradients (Hawkins & Lawton 1995, Hawkins & DeVries 1996). In conclusion, more meaningful comparative analyses require to include phylogenetic relationships in an adequate manner (Harvey & Pagel 1991). As shown here, the analysis of data of smaller (and monophyletic) units is a first suitable step towards this goal.

9 Synopsis and perspective

This study is an important step towards a better understanding of tropical montane rainforest ecosystems, although many more topics need to be investigated. For the first time ever, the diversity of a very species-rich group of herbivorous insects has been inventoried in such an ecosystem in the Andes. The detailed quantitative analysis of the existing diversity and structure of assemblages of herbivorous insects lays the groundwork for more experimental approaches and detailed investigations on their functional role in the future.

The study has revealed a number of unexpected and surprising results. Probably the most striking finding is that the diversity of geometrid moths remains exceptionally high throughout the complete elevational range investigated. This is in contrast to any previous study on insect diversity along elevational gradients. Whether a low predation pressure, the availability of large habitat areas even at high altitudes, or historical factors are responsible for the patterns revealed remains to be investigated more thoroughly. In particular, Larentiinae species are exceptionally distributed – a pattern shared with other high altitude areas (e.g. Holloway 1997). A total of 1,010 nocturnal and 24 exclusively diurnal species of geometrid moths was collected – a number that has never been sampled before in a comparably small geographical area. Hence, my study parallels earlier "records of diversity", for example those of Gentry & Smith (1988) who found the world's highest diversity of tree species in a lowland rainforest in Peru. Other examples were provided by Wilson (1987) and Robbins et al. (1996), who found in Peruvian lowland rainforests the world's highest numbers of arboreal ant species and butterfly species, respectively. This points out two phenomena: Firstly, for many organisms the Neotropics are the most diverse region in the world, and the rainforests of the Andes and Western Amazonia appear to be prominent hotspots within the large region. Secondly, it is alarming how little we still know about such fundamental issues as how many species of organisms there are on the Earth, and where the hotspots of diversity really are. In this respect, tropical montane rainforests are even less well known than lowland rainforests, although evidence is accumulating (including the data presented in this study) that diversity and endemism might be as high or even higher in the mountainous ranges. For most groups of organisms, in particular arthropods, such data are not yet available. While little is known about the raw species numbers, even less is known about the habitat requirements of the vast majority of species. The data that is available on geometrid moths suggests that species are polyphagous more often than previously thought, and that diversity extrapolations that were based on a high proportion of specialised species have probably overestimated species numbers. However, much needs to be done to improve the available database (see below). The hypothesis that many geometrid species are polyphagous is further supported by the fact that their beta-diversity is less associated with vegetational factors rather than with ambient temperature. It was shown that even within the large family Geometridae, patterns varied substantially across subordinated taxa such as subfamilies, tribes, and genera. It is more than questionable that other large taxa of herbivorous arthropods, will turn out to behave in exactly the same manner as Geometridae do. Hence, simple generalisations cannot be made concerning tropical montane insect diversity.

Natural habitats vanish worldwide at an alarming rate. Most Andean rainforests have already been destroyed and many of the remnant habitat islands are threatened by fire, agriculture and timber-logging. This study has not only shown that the diversity of geometrid moths is tremendous, but also that habitats at higher altitudes are richer in locally restricted species than habitats at lower elevations. It has often been stated that an understanding of ecosystems is essential for their preservation. In my opinion, this is not necessarily the case, because the political will to protect areas is usually much more important for conservation issues than the scientific analysis of the ecosystem. However, scientists can provide facts and arguments which can be used to decide upon the most effective conservation efforts. A network of protected areas in the whole region that represents habitats of all types is definitely desirable, but the land use in non-protected areas is also an important issue (Kessler 2001). For example, secondary forest may harbour a considerable proportion of insect diversity (for moths: Schulze 2000, Beck et al. 2002). However, nothing is so far known with regard to moth diversity in secondary habitats that formerly were covered by primary rainforests in the Andean region. It must be acknowledged that Ecuador has already put a considerable proportion of its territory under legal protection (18% National Parks and similar reserves (EcoCiencia 2000), much more than e.g. Germany has). Conservation efforts in countries such as Ecuador need to be further supported by industrialised countries. Otherwise, much of the unique biodiversity will probably disappear within in the next few decades (Laurance 1998, Chapin III et al. 2000, Terborgh 2000, Peres 2001).

Geometrid moths have already proven to be a suitable model group of herbivorous insects elsewhere in the world. This study has shown that this is also the case in the Neotropial region. A specific feature of the family is that they are a “mega-diverse” group of tropical herbivores which can easily be sampled, while analyses can be performed at species level. This contrasts with many previous studies in the tropics, where analyses were performed at a low taxonomical resolution (e.g. specimens sorted by orders, or tentatively assigned to feeding guilds) with subsequent relatively coarse results (e.g. Watt et al. 1997, Stuntz 2001). Moreover, a high degree of identified species enhances the comprehensibility of studies and the later re-analysis of the data. By collecting larvae, the current knowledge of the early stages, habitat requirements and host-specificity can be further improved with relative ease. The sampling of geometrids using light-traps is not free of problems, but overall provides a reliable, effective, rapid and well-established method. Analytical tools for the investigation of alpha- and beta-diversity of incomplete assemblages that consist of many rare species are available. Some methods such as non-metric multidimensional scaling or the NESS index of similarity still need to be established more widely as appropriate analytical instruments. These methods help to reliably identify and analyse patterns in species-rich ensembles without the necessity of data transformations or the questionable discarding of rare species.

There are various directions in which further studies of geometrid moths as a model group of tropical herbivorous insects could lead. Since this study was the first of its kind in the Neotropical region, the question is raised as to how unique the recovered patterns are. Therefore, a similar gradient should be investigated in a region nearby. Furthermore, the gradient needs to be extended in both directions: despite its wide span, lowland rainforests were not included in the study area, and the natural forest limit could not be reached. A continent-wide investigation of similar gradients, e.g. in Bolivia or Costa Rica, could reveal large-scale latitudinal patterns, and establish the degree of continent-wide beta-diversity. At the moment it is uncertain how similar or dissimilar the geometrid faunas on other even nearby mountains are. Furthermore, the reaction of geometrid ensembles upon natural and anthropogenic disturbances should be investigated. One such approach has recently been started in the Ecuadorian study area. Climate and morphology in the Andes also allow the investigation of the diversity and structure of geometrids along wet-dry gradients. Finally, much more needs to be done in order to learn more about the species' habitat requirements and host-plant relationships across the entire family. Systematic feeding trials could reveal the degree of host-specificity of many more species. So far, very little is also known about effects of predation by insectivorous bats and birds as well as the role of parasitoids of tropical montane herbivorous insects. Hence, after these first promising steps, much still needs to be done.

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Appendix 1 Neotropical Geometridae and their host-plants. **NA** Species that also occur in North America, from where further host-plant records are often available. **N** number of observations (if available), **S** sources: **A** Aiello (pers. comm.), **D** d'Araujo e Silva et al. (1968), **I** INBio (1999), **J** Janzen & Hallwachs (2001), **R** Robinson et al. (2001), **C** Country: **Ar** Argentina, **Br**azil, **Ch**ile, **Co**lombia, **CR** Costa Rica, **Cu**ba, **Ec**uador, **Me**xico, **Pe**ru, **PR** Puerto Rico, **TT** Trinidad & Tobago, *****not specified. Some different undetermined species might belong to the same taxon. This is the case e.g. in *Semiothisa* species in the database of Janzen & Hallwachs (2001); many *Semiothisa* are possibly actually *Macaria* (see Scoble & Krüger 2002). Not all records are listed for the very polyphagous species *Iridopsis herse*, see Janzen & Hallwachs (2001) for further records. Fabaceae are divided into three subgroups: Mimosoideae (m), Caesalpinioideae (c) and Papilionoideae (p).

Subfamily, tribe, species, plant family	**Plant species**	**NA**	**N**	**S**	**C**
Ennominae (169 species)					
Azelini					
Pero sp.					
Fabaceae (m)	*Senna pallida*		1	J	CR
Pero sp.					
Bignoniaceae	*Arrabidaea chica*		1	J	CR
Bignoniaceae	*Cydista diversifolia*		1	J	CR
Bignoniaceae	*Pithecoctinium crucigerum*		1	J	CR
Bignoniaceae	*Xylophragma seemannianum*		1	J	CR
Convolvulaceae	*Ipomoea trifida*		1	J	CR
Rubiaceae	*Alibertia edulis*		1	J	CR
Rubiaceae	*Calycophyllum candidissimum*		1	J	CR
Pero sp.					
Solanaceae	*Cestrum* sp.			I	CR
Pero? sp.					
Fabaceae (m)	*Inga vera*		1	J	CR
Boarmiini					
Anavitrinella pampinaria Guenée, [1858]		NA			
Asteraceae	*Parthenium hysterophorus*			R	Me
Bryoptera sp.					
Solanaceae	*Witheringia solanacea*			I	CR
Epimecis conjugaria Guenée, [1858]					
Annonaceae	*Annona purpurea*		29	J	CR
Annonaceae	*Desmopsis bibracteata*		13	J	CR
Lauraceae	*Ocotea veraguensis*		89	J	CR
Lauraceae	*Persea americana*		8	J	CR
Piperaceae	*Piper amalago*		1	J	CR
Epimecis sp.					
Lauraceae	*Ocotea* sp. (data base #13537)		1	J	CR
Epimecis sp.					
Piperaceae	unknown			A	Pa
Epimecis sp.					
Annonaceae	*Guatteria verrucosa*			I	CR
"Eutomopepla" artena Druce, 1891					
Flacourtiaceae	*Hasseltia floribunda*		11	J	CR
Glena bipennaria Guenée, [1858]					
Myrtaceae	*Eucalyptus grandis*			R	Br
Glena bisulca Rindge, 1967					
Pinaceae	unknown			R	Ec
Pinaceae	*Pinus patula*			R	Ec
Cupressaceae	*Cupressus* sp.			R	Ec
"polyphagous"	-			R	Ec

Glena demissaria Walker, 1860

Clusiaceae	*Kielmeyera coriacea*		R	Br

Glena sp.

Clethraceae	*Clethra* sp. (data base #13653)	1	J	CR
Fabaceae (m)	*Inga punctata*	2	J	CR
Juglandaceae	*Alfaroa guanacastensis*	1	J	CR

Glena sp.

Annonaceae	*Annona purpurea*	2	J	CR
Cochlospermaceae	*Cochlospermum vitifolium*	2	J	CR
Rubiaceae	*Calycophyllum candidissimum*	4	J	CR
Sapindaceae	*Thouinidium decandrum*	1	J	CR

Glena sp.

Cochlospermaceae	unknown		A	Pa

Glena sp.

Flacourtiaceae	*Casearia sylvestris*	1	J	CR

Glena sp.

Myrtaceae	*Callistemon lanceolatus*		I	CR

Glena unipennaria Guenée, [1857]

Myrtaceae	*Eucalyptus grandis*		R	Br

Hymenomima extersaria Warren, 1897

Rubiaceae	*Coffea* sp.		R	Br

Hymenomima memor Warren, 1906

Euphorbiaceae	*Acalypha diversifolia*		I	CR

Hymenomima sp.

Myrtaceae	*Eucalyptus* sp.		R	Br

Hymenomima umbelularia Hübner, [1825]

Euphorbiaceae	*Phyllanthus mocinianus*		I	CR

Iridopsis fragilaria (?) Grossbeck, 1909

NA

Asteraceae	*Parthenium hysterophorus*		R	Me
(many further records from US)				

Iridopsis herse Schaus, 1912

Anacardiaceae	*Spondias mombin*	5	J	CR
Araliaceae	*Sciadodendron excelsum*	1	J	CR
Bignoniaceae	*Arrabidaea patellifera*	1	J	CR
Cochlospermaceae	*Cochlospermum vitifolium*	5	J	CR
Combretaceae	*Combretum farinosum*	2	J	CR
Erythroxylaceae	*Erythroxylon havanense*	1	J	CR
Fabaceae (m)	*Albizia adinocephala*	2	J	CR
Fabaceae (c)	*Caesalpinia exostemma*	1	J	CR
Fabaceae (m)	*Calliandra tergermina*	2	J	CR
Fabaceae (c)	*Cassia emarginata*	1	J	CR
Fabaceae (p)	*Diphysa americana*	3	J	CR
Fabaceae (p)	*Gliricidia sepium*	2	J	CR
Fabaceae (c)	*Hymenaea courbaril*	2	J	CR
Fabaceae (p)	*Indigofera costaricensis*	1	J	CR
Fabaceae (m)	*Inga vera*	2	J	CR
Fabaceae (p)	*Lonchocarpus acuminatus*	5	J	CR
Fabaceae (p)	*Lonchocarpus minimiflorus*	1	J	CR
Fabaceae (m)	*Lysiloma auritum*	2	J	CR
Fabaceae (m)	*Mimosa pigra*	2	J	CR
Fabaceae (m)	*Pithecellobium oblongum*	1	J	CR
Fabaceae (c)	*Senna hayesiana*	1	J	CR
Fabaceae (c)	*Senna pallida*	2	J	CR
Fabaceae (c)	*Tamarindus indicus*	1	J	CR
Fagaceae	*Quercus oleoides*	7	J	CR
Flacourtiaceae	*Casearia corymbosa*	5	J	CR
Hippocrateaceae	*Semialarium mexicanum*	1	J	CR
Loranthaceae	*Phoradendron quadrangulare*	3	J	CR
Malpighiaceae	*Byrsonima crassifolia*	1	J	CR
Myrtaceae	*Psidium guajava* (introduced)	1	J	CR
Opiliaceae	*Agonandra macrocarpa*	1	J	CR
Polygonaceae	*Triplaris melaenodendron*	1	J	CR
Rubiaceae	*Calycophyllum candidissimum*	2	J	CR
Rubiaceae	*Genipa americana*	2	J	CR
Rubiaceae	*Randia monantha*	5	J	CR
Rutaceae	*Essenbeckia berlandieri*	1	J	CR

Sapindaceae	*Dilodendron costaricensis*		2	J	CR
Sapindaceae	*Thouinidium decandrum*		8	J	CR
Sterculiaceae	*Guazuma ulmifolia*		2	J	CR
Iridopsis herse (?) Schaus, 1912					
Asteraceae	*Parthenium hysterophorus*		2	R	Me
Meliaceae	*Swietenia mahagoni*			R	Cu
Iridopsis rufisparsa Warren, 1906					
Fabaceae (m)	*Pithecellobium dulce*			R	Cu
Iridopsis perfectaria McDunnough, 1940		NA			
Asteraceae	*Parthenium hysterophorus*			R	Me
Euphorbiaceae	*Maprounea guianensis*			R	Br
Iridopsis sp.					
Fabaceae (c)	*Senna papillosa*			I	CR
Iridopsis sp.					
Malpighiaceae	*Byrsonima coccolobifolia*			R	Br
Iridopsis syrniaria Guenée, [1858]					
Fabaceae (p)	*Glycine max*			R	Br
“Iridopsis” validaria Guenée, [1858]					
Lauraceae	*Ocotea* sp. (data base #14016)		1	J	CR
Melanochroia aterea Stoll, 1781					
Rubiaceae	*Cephalanthus sarandi*			D	Br
Melanochroia chephise Stoll, 1782		NA			
Euphorbiaceae	*Phyllanthus acidus*			R	Cu
Euphorbiaceae	*Phyllanthus acidus*			R	PR
Euphorbiaceae	*Phyllanthus* sp.			D	Br
Melanochroia geometroides Walker, 1854		NA			
Euphorbiaceae	*Phyllanthus acidus*			R	Cu
Euphorbiaceae	*Phyllanthus acuminatus*			R	Cu
Melanochroia regnatrix Grote & Robinson, 1867					
Euphorbiaceae	*Phyllanthus acuminatus*			R	Cu
Melanolophia commotaria Maassen, 1890					
Myrtaceae	*Eucalyptus* sp.			R	Co
Pinaceae	Pinus patula			R	Co
Melanolophia sp.					
Fabaceae (m)	*Inga longispica*		1	J	CR
Sapindaceae	*Cupania glabra*		1	J	CR
Melanolophia sp.					
Verbenaceae	*Lippia alba*			I	CR
Perigramma immaculata Dognin, 1902					
Proteaceae	*Grevillea robusta*			D	Br

Caberini + Baptini

Cyclomia disparilis Schaus, 1911					
Rhamnaceae	*Colubrina spinosa*			I	CR
Cyclomia mopsaria Guenée, [1858]					
Erythroxylaceae	*Erythroxylum havanense*			R	Cu
Erythroxylaceae	*Erythroxylum tortuosum*			R	Br
Cyclomia sp.					
Rhamnaceae	*Colubrina spinosa*			I	CR
Cyclomia sp.					
Erythroxylaceae	*Erythroxylum havanense*			R	Cu
Erastria decrepitaria Hübner, 1823					
Rhamnaceae	*Gouania polygama*		2	J	CR
Lomographa sp.					
Rosaceae	*Prunus annularis*		1	J	CR

Microgonia rhodaria Herrich-Schäffer, [1855]					
Asteraceae	*Vernonia* sp.			I	CR
Numia terebintharia Guenée, [1858]					
Rhamnaceae	*Zizyphus guatemalensis*		105	J	CR
Paragonia cruraria Herrich-Schäffer, [1854]					
Euphorbiaceae	*Acalypha leptospachya*			I	CR
Paragonia tasima Cramer, [1779]					
Myrtaceae	*Eugenia salamensis*		1	J	CR
Paragonia sp.					
Convolvulaceae	unknown			A	Pa
Paragonia sp.					
Hypericaceae	unknown			A	Pa
Paragonia sp.					
Meliaceae	*Guarea* sp.			I	CR
Paragonia sp.					
Sterculiaceae	*Theobroma cacao*			R	TT
Sphacelodes vulneraria Hübner, 1823		NA			
Rhamnaceae	*Gouania polygama*		135	J	CR
Rhamnaceae	*Zizyphus guatemalensis*		33	J	CR
Thysanopyga gauldi Krüger & Scoble, 1992					
Acanthaceae	*Aphelandra scabra*		1	J	CR
Thysanopyga sp.					
Annonaceae	*Xylopia frutescens*		1	J	CR
Cassymini					
Taeniogramma odrussa Druce, 1892					
Fabaceae (m)	*Calliandra calothyrsis*		1	J	CR
“*Cratoptera*-group”					
Melinodes sp.					
Verbenaceae	*Lippia* sp.			I	CR
Lithinini					
Asestra sp.					
Sapindaceae	*Serjania* sp.			I	CR
Macariini					
Digrammia cyda Druce, 1893					
Fabaceae (m)	*Prosopis glandulosa*			R	Me
Digrammia sp. near *nigricomma* Warren, 1904					
Fabaceae (m)	*Acacia farnesiana*		1	J	
Macaria abydata Guenée, [1858]					
Fabaceae (p)	*Glycine max*			R	Br
Fabaceae (c)	*Parkinsonia aculeata*			R	Me
Fabaceae (c)	*Delonix regia*			R	PR
Macaria approximaria Walker, 1861					
Fabaceae (m)	*Inga punctata*			I	CR
Macaria regulata Fabricius, 1775					
Fabaceae (m)	*Pentaclethra macroloba*			I	CR
Sterculiaceae	*Theobroma cacao*			D	Br
Macaria sp.					
Fabaceae (m)	*Inga sapindoides*			I	CR
”Semiothisa” acepsimaria Schaus, 1923					
Fabaceae (m)	*Enterolobium cyclocarpum*			R	Cu
Fabaceae (m)	*Albizia lebbeck*			R	Cu

“Semiothisa” pallidata Warren, 1897

Fabaceae (m)	*Mimosa pigra*	1	J	CR

Semiothisa sp.

Fabaceae (m)	*Albizia adinocephala*	3	J	CR
Fabaceae (p)	*Dalbergia glabra*	1	J	CR
Fabaceae (m)	*Enterolobium cyclocarpum*	2	J	CR
Fabaceae (m)	*Prosopis juliflora*	2	J	CR
Fabaceae (c)	*Senna pallida*	1	J	CR

Semiothisa sp.

Fabaceae (m)	*Enterolobium cyclocarpum*	2	J	CR
Fabaceae (m)	*Pithecellobium saman*	1	J	CR

Semiothisa sp.

Fabaceae (m)	*Enterolobium cyclocarpum*	1	J	CR

Semiothisa sp.

Fabaceae (m)	*Albizia adinocephala*	1	J	CR

Semiothisa sp.

Fabaceae (m)	*Acacia farnesiana*	2	J	CR
Fabaceae (m)	*Acacia tenuifolia*	2	J	CR
Fabaceae (m)	*Albizia adinocephala*	2	J	CR
Fabaceae (c)	*Caesalpinia exostemma*	2	J	CR
Fabaceae (m)	*Enterolobium cyclocarpum*	8	J	CR
Fabaceae (m)	*Senna pallida*	7	J	CR
Sapindaceae	*Dilodendron costaricensis*	1	J	CR
Sapindaceae	*Thouinidium decandrum*	12	J	CR

Semiothisa sp.

Fabaceae (c)	*Poeppigia procera*		R	Cu

Nacophorini

Betulodes crebraria Guenée, [1858]

Myrtaceae	*Eucalyptus* sp.		D	Br

Cargolia arana Dognin, 1895

Cupressaceae	*Cupressus* sp.		R	Co
Pinaceae	*Pinus patula*		R	Co

Cidariophanes sp.

Rutaceae	*Citrus aurantifolia*		I	CR

Holochroa sp. 1

Bignoniaceae	*Xylophragma seemannianum*	1	J	CR
Connaraceae	*Rourea glabra*	1	J	CR
Erythroxylaceae	*Erythroxylon havanense*	3	J	CR
Fabaceae (m)	*Calliandra rubescens*	1	J	CR
Fabaceae (m)	*Lonchocarpus orotinus*	1	J	CR
Fabaceae (p)	*Myrospermum frutescens*	1	J	CR
Fagaceae	*Quercus oleoides*	1	J	CR
Flacourtiaceae	*Casearia arguta*	1	J	CR
Flacourtiaceae	*Casearia corymbosa*	8	J	CR
Flacourtiaceae	*Casearia tremula*	1	J	CR
Flacourtiaceae	*Zuelania guidonia*	2	J	CR
Hippocrateaceae	*Semialarium mexicanum*	4	J	CR
Rubiaceae	*Calycophyllum candidissimum*	2	J	CR
Rubiaceae	*Genipa americana*	4	J	CR
Rubiaceae	*Guettarda macrosperma*	1	J	CR
Rubiaceae	*Randia monantha*	2	J	CR
Rutaceae	*Essenbeckia berlandieri*	3	J	CR
Verbenaceae	*Rehdera trinervis*	8	J	CR

Ischnopteris cryses Druce, 1893

Aquifoliaceae	*Ilex* sp.		I	CR
Celastraceae	*Perrotettia longistylis*	1	J	CR
Fabaceae (m)	*Inga longispica*	1	J	CR
Rubiaceae	*Hamelia patens*	1	J	CR

Ischnopteris sp.

Euphorbiaceae	*Acalypha diversifolia*	1	J	CR
Fabaceae (p)	*Lonchocarpus guatemalensis*	2	J	CR
Piperaceae	*Piper auritum*	1	J	CR
Sapindaceae	*Cupania glabra*	1	J	CR

Ischnopteris sp.				
Myrtaceae	*Psidium guajava*		I	CR
Thyrintheina arnobia Stoll, 1782		NA		
Aquifoliaceae	*Ilex paraguariensis*		R	Ne
Myrtaceae	*Eucalyptus* sp.		R	Ne
Myrtaceae	*Eucalyptus alba*		D	Br
Myrtaceae	*Eucalyptus grandis*		R	Br
Myrtaceae	*Eucalyptus saligna*		D	Br
Myrtaceae	*Eucalyptus* ssp.		D	Br
Myrtaceae	*Eucalyptus tereticornis*		R	Br
Myrtaceae	*Eucalyptus tereticornis*		D	Br
Rutaceae	*Citrus sinensis*		D	Br
Thyrintheina schadeana Schaus, 1927				
Rubiaceae	*Coffea* sp.		R	Br

Nephodiini

Acronyctodes cautama Schaus, 1901				
Scrophulariaceae	*Schlegelia fuscata*	9	J	CR
Astyochia crane Druce, 1885				
Asteraceae	*Vernonia* sp.		I	CR
Carpella sp.				
Celastraceae	*Crossopetalum parviflorum*	4	J	CR
Fulgurodes aculearia Guenée, [1858]				
Podocarpaceae	*Podocarpus lambertii*		D	Br
Fulgurodes inversaria Guenée, [1858]				
Araucariaceae	*Araucaria* sp.		D	Br
Cupressaceae	*Cupressus sempervirens*		D	Br
Myricaceae	*Myrica tenella*		D	Br
Pinaceae	*Pinus oocarpa*		R	Br
Pinaceae	*Pinus* sp.		D	Br
Podocarpaceae	*Podocarpus lamberti*		D	Br
Podocarpaceae	*Podocarpus* sp.		D	Br
Rosaceae	*Malus sylvestris*		D	Br
Nephodia betala Druce,1892				
Hippocastanaceae	*Billia hippocastanum*	1	J	CR
Nephodia marginata Warren, 1906				
Fabaceae (c)	*Ceratonia siliqua*		R	Ar
Fabaceae (m)	*Prosopis* sp.		R	Ar
Fabaceae (m)	*Psosopis alba*		R	Ar
Nephodia sp.				
Fabaceae (m)	*Inga* sp.		I	CR
Patalene asychisaria Walker, 1860				
Malpighiaceae	*Hiraea reclinata*	1	J	CR
Rubiaceae	*Exostema mexicanum*	2	J	CR
Trigoniaceae	*Trigonia rugosa*	1	J	CR
Patalene ephyrata Guenée, [1858]				
Moraceae	*Ficus carica*		R	Cu
Patalene falcularia Sepp, [1852]				
Asteraceae	*Eupatorium villosum*		R	Cu
Fabaceae (p)	*Sesbania grandiflora*		R	Cu
Patalene hamulata Guenée, [1858]				
Simaroubaceae	*Picramnia comun*	1	J	CR

Ourapterygini

Bassania schreiteri Schaus, 1923				
Cupressaceae	*Cupressus* sp.		R	Co
Pinaceae	unknown		R	Co
Pinaceae	*Pinus patula*		R	Co
Cannagara sp.				
Onagraceae	*Fuchsia paniculata*		I	CR

Drymoea chrysomela Butler & Druce 1872					
Euphorbiaceae	*Croton draco*			I	CR
Euphorbiaceae	*Croton draco*			R	CR
Hygrochroma olivinaria Herrich-Schäffer, 1855					
Piperaceae	*Piper auritum*		4	J	CR
Ira somnolenta Warren, 1904					
Annonaceae	*Rollinia membranacea*		1	J	CR
Asteraceae	*Vernonia* sp.			I	CR
Rosaceae	*Prunus annularis*		1	J	CR
Ira subcostata Walker, 1860					
Celastraceae	*Zinowiewia costaricensis*			I	CR
				D	Br
Leucula festiva Cramer, [1775]					
Araliaceae	*Dendropanax arboreus*			I	CR
Araliaceae	*Hedera helix*			D	Br
Leucula meganira Druce, 1892					
Araliaceae	*Dendropanax arboreus*		1	J	CR
Oxydia apidania Cramer, [1779]					
Aquifoliaceae	*Ilex paraguariensis*			R	Ar
Euphorbiaceae	*Hyeronima alchorneoides*			I	CR
Oxydia augusta Druce, 1892					
Fabaceae (c)	*Senna papillosa*			I	CR
Oxydia bilinea Schaus, 1911					
Fabaceae (p)	*Vigna candida*			I	CR
Oxydia geminata Maassen, 1890					
Cornaceae	*Cornus disciflora*			I	CR
Oxydia hispata Guenée, [1858]					
Bignoniaceae	*Xylophragma seemannianum*		1	J	CR
Clusiaceae	*Vismia baccifera*		1	J	CR
Lauraceae	*Ocotea veraguensis*		1	J	CR
Malpighiaceae	*Mascagania* sp.		1	J	CR
Melastomataceae	*Conostegia xalapensis*		1	J	CR
Piperaceae	unknown		1	J	CR
Solanaceae	*Solanum schlechtendalianum*		1	J	CR
Turneraceae	*Erblichia odorata*		1	J	CR
Verbenaceae	*Stachytarpheta frantzii*		1	J	CR
Oxydia nimbata Guenée, [1858]		NA			
Annonaceae	*Rollinia membranacea*		1	J	CR
Asteraceae	*Vernonia patens*		1	J	CR
Flacourtiaceae	*Casearia corymbosa*		3	J	CR
Fabaceae (p)	*Glycine max*			R	Br
Oxydia platypterata Guenée, [1858]					
Pinaceae	*Pinus patula*			R	Co
Oxydia sp.					
Asteraceae	*Vernonia* sp.			I	CR
Oxydia sp.					
Euphorbiaceae	*Margaritaria nobilis*		1	J	CR
Oxydia sp.					
Malpighiaceae	*Byrsonima crassa*			R	Br
Oxydia sp.					
Flacourtiaceae	unknown			A	Pa
Oxydia? sp.					
Asteraceae	unknown			A	Pa
Oxydia? sp.					
Combretaceae	unknown			A	Pa
Oxydia trychiata Guenée, [1858]					
Cupressaceae	*Cupressus* sp.			R	Co
Pinaceae	*Pinus patula*			R	Co
Oxydia vesulia Cramer, [1779]		NA			
Anacardiaceae	*Mangifera indica*			R	Cu

Anacardiaceae	*Spondias mombin*	2	J	CR
Annonaceae	*Annona glabra*		R	Cu
Asteraceae	*Verbesina gigantea*	2	J	CR
Euphorbiaceae	*Acalypha wilkesiana*		R	PR
Euphorbiaceae	*Ricinus communis*		R	Cu
Fabaceae (p)	*Andira inermis*	1	J	CR
Lauraceae	*Ocotea veraguensis*	6	J	CR
Loranthaceae	*Phoradendron quadrangulare*	2	J	CR
Lythraceae	*Punica granatum*		R	Cu
Piperaceae	*Piper peltatum*		R	Cu
Rosaceae	*Rosa* sp.		R	PR
Rubiaceae	*Cinchona pubescens*		R	PR
Rutaceae	*Citrus sinensis*	2	R	Cu
Rutaceae	*Citrus sinensis*		R	PR
Sapindaceae	*Litchi chinensis*		R	Cu
Sapotaceae	*Manilkara chicle*	1	J	CR

Phyle arcuosaria Herrich-Schäffer, [1855]

Rubiaceae	*Cinchona ledgeriana*		D	Br

Phyle sp.

Myrtaceae	unknown (dababase #13570)	1	J	CR

Simena luctifera Walker, 1856

Acanthaceae	*Justicia* sp.		I	CR

Simopteryx sp.

Solanaceae	*Cestrum* sp. (database #13594)	2	J	CR

Simopteryx torquataria Walker, 1860

Onagraceae	*Fuchsia* sp.		I	CR
Rubiaceae	*Hamelia patens*	3	J	CR
Rubiaceae	*Psychotria* sp. (database #13576)	1	J	CR
Rubiaceae	*Psychotria berteriana*	4	J	CR
Rubiaceae	*Psychotria panamensis*	1	J	CR

Tetracis sp.

Myrtaceae	*Psidium guajava*		I	CR

Palyadini

Argyrotome alba Druce, 1892

Myrsinaceae	*Ardisia revoluta*	13	J	CR

Ophthalmoblysis sp.

Connaraceae	*Connarus* sp. (13724)	1	J	CR

Opisthoxia bella Butler, 1881

Myrsinaceae	unknown (data base #13587)	5	J	CR
Myrsinaceae	unknown (data base #14107)	2	J	CR
Myrsinaceae	*Parathesis* sp. (data base #14132)	1	J	CR

Opisthoxia bolivari Oberthür, 1916

Myrsinaceae	*Ardisia opegrapha*	2	J	CR

Opisthoxia formosante Cramer, [1779]

Myrsinaceae	*Ardisia* sp.		I	CR

Opisthoxia laticlava Warren, 1904

Myrsinaceae	*Parathesis glabra*	2	J	CR

Opisthoxia miletia Druce, 1892

Myrsinaceae	unknown (data base #13587)	1	J	CR

Opisthoxia molpadia Druce, 1892

Myrsinaceae	unknown (data base #13587)	7	J	CR
Myrsinaceae	unknown (data base #14107)	17	J	CR
Myrsinaceae	*Parathesis* sp. (data base #14132)	18	J	

Opisthoxia uncinata Schaus, 1912

Myrsinaceae	*Ardisia compressa*	2	J	CR
Myrsinaceae	*Ardisia revoluta*	22	J	CR

Phrygionis privignaria Guenée, [1858]

Myrsinaceae	*Ardisia revoluta*	28	J	CR

Ennominae genera not assigned to tribe

“Acrotomia” mucia Druce, 1892

Rubiaceae	unknown (data base #13507)	1	J	CR
Rubiaceae	unknown (data base #13588)	2	J	CR
Rubiaceae	*Coussarea austin-smithii*	2	J	CR
Rubiaceae	*Palicourea salicifolia*	1	J	CR
Rubiaceae	*Psychotria berteriana*	2	J	CR
Rubiaceae	*Psychotria correae*	10	J	CR
Rubiaceae	*Psychotria elata*	4	J	CR
Rubiaceae	*Psychotria eurycarpa*	1	J	CR
Rubiaceae	*Psychotria* sp.		I	CR
Rubiaceae	*Psychotria*? sp.	1	J	CR

Acrotomodes sp.

Annonaceae	*Guatteria verrucosa*		I	CR

Cimicodes sp.

Myrtaceae	*Myrcia splendens*	1	J	CR
Monimiaceae	*Siparuna andina*	1	J	CR

Cimicodes sp.

Monimiaceae	*Siparuna* sp.		I	CR

“Cyphoedma” transvolutata Walker, 1860

Annonaceae	*Guatteria verrucosa*	1	J	CR

Erosina hyberniata hyberniata Guenée, [1858]

Solanaceae	*Acnistus arborescens*		I	CR

(?) *Herbita medama* Druce, 1891 or *H. medona* Druce, 1892 (in database *“medana”*)

Anacardiaceae	*Astronium graveolens*	2	J	CR
Araliaceae	*Sciadodendron excelsum*	2	J	CR
Asteraceae	*Koanophyllon albicaule*	1	J	CR
Bignoniaceae	*Amphilohium paniculatum*	1	J	CR
Chrysobalanaceae	*Hirtella racemosa*	1	J	CR
Elaeocarpaceae	*Sloanea terniflora*	1	J	CR
Euphorbiaceae	*Acalypha diversifolia*	1	J	CR
Fabaceae (p)	*Andira inermis*	1	J	CR
Malpighiaceae	*Heteropterys laurifolia*	1	J	CR
Malvaceae	*Hampea appendiculata*	1	J	CR
Melastomataceae	*Miconia argentea*	1	J	CR
Meliaceae	*Cedrela odorata*	2	J	CR
Meliaceae	*Trichilia martiana*	1	J	CR
Rubiaceae	*Exostema mexicanum*	2	J	CR
Sapindaceae	*Cupania guatemalensis*	1	J	CR
Simaroubaceae	*Simarouba amara*	1	J	CR
Turneraceae	*Erblichia odorata*	1	J	CR
Verbenaceae	*Cornutia grandifolia*	1	J	CR

Herbita sp.

Annonaceae	*Rollinia membranacea*	1	J	CR
Lauraceae	*Licaria* sp. (data base #13499)	1	J	CR

Himeromima aulis Druce, 1892

Meliaceae	*Trichilia havanensis*	68	J	CR
Meliaceae	*Trichilia havanensis*		I	CR

Microsema gladiaria Guenée [1858]

Asteraceae	*Senecio brasiliensis*		D	Br
Lamiaceae	*Melissa officinalis*		D	Br

Microxydia orsitaria Guenée, [1858]

Asteraceae	*Baccharis* sp.		I	CR
Fabaceae (m)	*Inga* sp.		R	CR

Microxydia ruficomma Prout, 1910

Fabaceae (m)	*Inga* sp.		I	CR

Nematocampa completa Warren, 1904

Polygonaceae	*Polygonum punctatum*		I	CR

Nepheloleuca politia Cramer, [1777]

NA

Araliaceae	*Oreopanax* sp. (data base #14030)	1	J	CR
Bignoniaceae	*Amphilophium paniculatum*	1	J	CR
Bignoniaceae	unknown	1	J	CR

Bignoniaceae	*Pithecoctinium crucigerum*	1	J	CR
Bignoniaceae	unknown vine (data base # 11809)	1	J	CR
Solanaceae	*Brujmansia arborea*		D	Br
Solanaceae	*Datura fastuosa*		D	Br
Solanaceae	*Datura stramonium*		D	Br
Solanaceae	*Datura suaveolens*		D	Br
Nepheloleuca sp.				
Rubiaceae	*Coffea arabica*		I	CR
“Nephodia” organa Druce, 1893				
Araliaceae	*Oreopanax* sp. (data base #14030)	1	J	CR
Neodora glaucularia Snellen, 1874				
Cupressaceae	*Cupressus lusitanica*		R	Co
Myrtaceae	*Eucalyptus* sp.		R	Co
Pinaceae	*Pinus patula*		R	Co
Pantherodes pardalaria Hübner, 1823				
Bignoniaceae	*Tecoma capensis*		D	Br
Urticaceae	*Boehmeria nivea*		D	Br
Urticaceae	*Urera baccifera*		D	Br
Urticaceae	*Urtica urens*		D	Br
Panterodes? sp.				
Malpighiaceae	unknown		A	Pa
Phyllodonta indeterminata Schaus, 1901				
Meliaceae	*Trichilia trifolia*	1	J	CR
Phyllodonta latrata Guenée, [1858]				
Solanaceae	*Acnistus arborescens*		I	CR
Prochoerodes marciana Druce, 1891				
Connaraceae	*Rourea glabra*	1	J	CR
Lauraceae	*Ocotea veraguensis*	1	J	CR
Melastomataceae	*Conostegia xalapensis*	1	J	CR
Rubiaceae	*Genipa americana*	1	J	CR
Prochoerodes tetragonata Guenee, [1858]				
Ulmaceae	*Celtis tala*		D	Br
Pyrinia helvaria Herrich-Schäffer, 1864				
Melastomataceae	*Mouriri myrtilloides*	1	J	CR
“Sabulodes” arge Druce, 1891				
Asteraceae	*Parthenium hysterophorus*		R	Me
Sabulodes atropesaria Walker, 1860				
Myrtaceae	*Eucalyptus citriodora*		D	Br
Myrtaceae	*Eucalyptus* sp.		D	Br
Sabulodes caberata Guenée, [1858]		NA		
Myrtaceae	*Psidium guajava*		R	Cu
Sabulodes exhonorata Guenée, [1858]				
Myrtaceae	*Eucalyptus* sp.		R	Br
Sabulodes loba Rindge, 1978				
Araliaceae	*Sciadodendron excelsum*	19	J	CR
Elaeocarpaceae	*Sloanea terniflora*	3	J	CR
Meliaceae	*Cedrela odorata*	1	J	CR
Sabulodes sp.				
Cecropiaceae	*Cecropia peltata*		R	PR
Sabulodes sp.				
Myrtaceae	*Psidium guajaba*		I	CR
Sericoptera mahometaria Herrich-Schäffer, 1853				
Fagaceae	*Quercus oleoides*	2	J	CR
Simaroubaceae	*Picrasma excelsa*	1	J	CR
Sicya sp. near *medangula* Dyar, 1918				
Piperaceae	*Piper auritum*	1	J	CR
Phytolaccaceae	*Stegnosperma cubense*	237	J	CR

Sicya sp.					
Rubiaceae	*Exostema mexicanum*		1	J	CR
Spododes sp.					
Myrtaceae	*Psidium guajava*			R	Cu

Larentiinae (20 species)

Euphyini

Disclisioprocta stellata Guenée, [1858]		NA			
Nyctaginaceae	*Mirabilis jalapa*			R	Cu
Nyctaginaceae	*Pisonia aculeata*			R	Cu
Euphyia subguttaria Herrich-Schäffer, 1855					
Fabaceae (c)	*Senna corymbosa*			R	Br
Rubiaceae	*Coffea arabica*			D	Br
Solanaceae	*Cestrum parqui*			D	Br
Hammaptera repandaria Schaus, 1901					
Fabaceae (c)	*Cassia corymbosa*			D	Br
Fabaceae (c)	*Cassia fistula*			D	Br
Solanaceae	*Cestrum nocturnum*			D	Br
Solanaceae	*Cestrum parqui*			D	Br

Eupitheciini

Eois dibapha Schaus, 1912					
Lauraceae				I	CR
Piperaceae	*Dochephora* sp.			I	CR
Piperaceae	*Piper* sp. (data base #13629)		1	J	CR
Eois sp.					
Piperaceae	Piper *sp.*			R	Cu
Eois sp.					
Piperaceae	*Piper* sp. (data base #14069)		3	J	CR
Eupithecia miserulata? Grote, 1863		NA			
Asteraceae	*Parthenium hysterophorus*		2	R	Me
Eupithecia sp.					
Asteraceae	*Mikania trinitania*			R	TT
Eupithecia sp.					
Fabaceae (m)	*Acacia collinsii*		3	J	CR
Erateina staudingeri Snellen, 1878					
Melastomataceae	unknown			I	CR
Hagnagora ephestris Felder & Rogenhofer, 1875					
Clethraceae	*Clethra* sp. (data base #13653)		1	J	CR
Hagnagora mortipax Butler, 1872					
Boraginaceae	*Cordia spinescens*			I	CR
Clethraceae	*Clethra* sp. (data base #13653)		6	J	CR
Clethraceae	*Clethra mexicana*		10	J	CR

Perizomini

Perizoma impromissata Walker, 1882					
Asteraceae	*Cichorium intybus*			D	Br
Asteraceae	*Taraxacum officinale*			D	Br
Basellaceae	*Boussingaultia boselloides*			D	Br
Perizoma sordescens Dognin, 1908					
Chenopodiaceae	*Chenopodium quinoa*			R	Pe
Pseudomennis dioptoides Warren, 1905					
Staphyleaceae	*Turpinia occidentalis*		60	J	CR
Spargania sp.					
Clethraceae	*Clethra mexicana*		2	J	CR

Larentiinae genera not assigned to tribe

Stamnodes? proana Druce 1893 (*Heterusia? proana* Druce 1893, database: *Hagnagora*)					
Boraginaceae	*Cordia spinescens*			I	CR
Triphosa affirmata Guenée, [1858]		NA			
Fabaceae	unknown			R	Br
Fabaceae (p)	*Vicia linearifolia*			R	Br
Fabaceae (p)	*Vicia sativa*			D	Br
“Trocherateina” cachara Schaus, 1901					
Boraginaceae	*Cordia spinescens*			I	CR
“Trocherateina” specularia Walker 1869					
Melastomataceae	*Monochaetum* sp.			I	CR

Geometrinae (18 species)

Hemitheini

Chlorochlamys chloroleucaria Guenée, [1858]		NA			
Asteraceae	*Parthenium hysterophorus*		2	R	Me
Chloropteryx glauciptera Hampson, 1895					
Asteraceae	*Mikania vitifolia*			R	TT
Chloropteryx languescens Warren, 1897					
Asteraceae	*Mikania micrantha*			R	TT

Nemoriini

Chavariella sp.					
Myrtaceae	*Psidium guajava*			R	Cu
Sterculiaceae	*Helicteres guazumaefolia*		1	J	CR
Lissochlora sp.					
Lauraceae	unknown flowers			A	Pa
Nemoria marielosae Pitkin, 1993					
Fagaceae	*Quercus oleoides*		1	J	CR
Nemoria sp.					
Lauraceae	unknown (data base #13487)		2	J	CR
Lauraceae	*Cinnamomum brenesii*		1	J	CR
Phrudocentra centrifugaria Herrich-Schäffer, 1870		NA			
Fabaceae (p)	*Aeschynomene americana*			R	Cu
Myrtaceae	*Eucalyptus*			R	Cu
Myrtaceae	*Eugenia jambos*			R	Cu
Myrtaceae	*Psidium cymosum*			R	Cu
Phrudocentra opaca Butler, 1881					
Loranthaceae	*Phoradendron quadrangulare*		1	J	CR
Phrudocentra pupillata Warren, 1897					
Fabaceae (m)	*Inga vera*		4	J	CR
Phrudocentra sp.					
Mimosaceae	unknown			A	Pa
Anacardiaceae	unknown				

Lophochoristini

Lophochorista calliope Druce, 1892					
Rhamnaceae	*Karwinskia calderoni*		2	J	CR
Oospila confundaria Möschler, 1893					
Fabaceae (m)	*Hymenaea courbaril*		17	J	CR

Synchlorini

Synchlora concinnaria Schaus, 1912 or *S. rufilineata* Warren 1897					
Flacourtiaceae	*Casearia corymbosa*		2	J	CR
Sterculiaceae	*Guazuma ulmifolia*		1	J	CR
Synchlora frondaria Guenée*,* [1858]		NA			
Asteraceae	*Eupatorium villosum*			R	Cu
Asteraceae	*Helianthus annuus*			R	Cu
Asteraceae	*Parthenium hysterophorus*			R	Me
Euphorbiaceae	*Jatropha multifida*			R	PR
Sterculiaceae	*Guazuma ulmifolia*		4	J	CR
Synchlora gerularia Hübner, 1826		NA			
Asteraceae	*Baccharis genistelloides, B. salicina* (translation from Parsons et al. in Scoble 1999)			D	Br
Synchlora indecora Prout, 1916					
Asteraceae	unknown (data base #12914)		12	J	CR
Synchlora sp.					
Mimosaceae	unknown			A	Pa

Sterrhinae (15 species)

Cosymbiini

"Cyclophora" gigantula Warren, 1904					
Podocarpaceae	*Podocarpus lamberti*			D	Br
"Cyclophora" melita Druce, 1892					
Lauraceae	unknown (data base #14090)		10	J	CR
"Cyclophora" nanaria Walker, 1861		NA			
Anacardiaceae	*Schinus molle*			R	Ch
Asteraceae	*Parthenium hysterophorus*		2	R	Me
Oleaceae	*Olea europaea*			R	Ch
"Cyclophora" sp.					
Rhamnaceae	unknown			A	Pa
Leptostales angulata Schaus, 1912					
Rubiaceae	*Alibertia edulis*		3	J	CR
Leptostales penthemaria Dyar, 1913					
Verbenaceae	*Aloysia triphylla*			R	Cu
Pleuroprucha asthenaria Walker, 1861		NA			
Asteraceae	*Helianthus annuus*			R	Cu
Asteraceae	*Parthenium hysterophorus*			R	Me
Gramineae	*Saccharum officinarium*			R	?
Sapotaceae	*Sideroxylon foetidissimum*			R	Cu
Pleuroprucha insularia Guenée, [1858]		NA			
Asteraceae	*Parthenium hysterophorus*		2	R	Me
Semaeopus fulvescens Warren, 1906					
Malpighiaceae	*Hiraea reclinata*		4	J	CR
Tricentrogyna sp.					
Piperaceae	unknown			A	Pa

Sterrhinae genera not assigned to tribe

Anisodes sp.					
Myrtaceae	*Eucalyptus* sp.			R	Cu
Myrtaceae	*Psidium guajava*			R	Cu
Pseudasellodes fenestraria Guenée, [1858]					
Rubiaceae	*Genipa americana*		2	R	Cu
Rubiaceae	*Genipa americana*			R	PR

Pseudasellodes sp.				
Rubiaceae	unknown (data base #14089)	5	J	CR
Smicropus intercepta Walker, 1854				
Malpighiaceae	*Mascagnia sinemariensis*	7	J	CR
Trygodes musivaria Herrich-Schäffer, 1855				
Fabaceae (c)	*Bauhinia forficata*		D	Br
Malvaceae	*Gossypium herbaceum*		D	Br

Oenochrominae (3 species)

Ametris nitocris Cramer, 1780				
Polygonaceae	*Cocoloba venusta*	1	J	CR
Ergavia merops Cramer, 1775				
Polygonaceae	*Triplaris melaenodendron*	8	J	CR
Ergavia sp. 1				
Myrsinaceae	*Ardisia revoluta*	1	J	CR
Polygonaceae	*Triplaris melaenodendron*	52	J	CR

Desmobathrinae (1 species)

Dolichoneura sp. 1				
Sapotaceae	*Manilkara chicle*	2	J	CR

Misspellings or misplaced genera

Entomopteryx sp. (*Erinnyis ello* not available, possibly Hesperiidae)				
Euphorbiaceae	*Euphorbia hypericifolia*		R	PR
Euphorbiaceae	*Euphorbia hyssopifolia*		R	PR
Euphorbiaceae	*Ricinus communis*		RS J	Cu
Renodes curvilune ? (*Remodes* is a synonym of *Sauris* (indopacific))				
Fabaceae (m)	*Inga vera*	1	J	CR
Jodis sp. (*Iodis languescens*, this combination is not available) *Jodis* is indopacific				
Fabaceae (m)	*Acacia tenuifolia*	1	J	CR

Ennominae: genus misidentified (Nearctic or Palaearctic genus)

(Hypomecis) sp.				
Myrsinaceae	*Myrsine floridiana*		I	CR
(Hylaea) sp.				
Rubiaceae	*Psychotria* sp.		I	CR
(Anavitrinella) sp.				
Malvaceae	*Gossypium herbaceum* (leaves)		D	Br

Larentiinae: genus misidentified (Nearctic or Palaearctic genus)

(Cidaria) sp.				
Nyctaginaceae	*Bougainvillea* sp.		D	Br

Appendix 2 List of all 1,010 species and 13,938 specimens collected in a montane rainforest in South Ecuador in the years 1999 and 2000, ordered by subfamily, genus and species. First and second row: sites where moths were sampled, ordered by altitude of the sites (from 1,040 m to 2,677 m above sea level). Coordinates and altitudes of all sites are provided in Chapter 4. **ID** identification number in corresponding database (see Chapter 3). Taxonomy of the subfamily Ennominae follows Pitkin (2002), and follows Parsons et al. (1999) for the rest of Geometridae, where all species authors are listed. Inverted commas were used as by these authors for the “residue” of species belonging to large genera after they have been more restrictively diagnosed. **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. Due to changes during the course of the determination numbering is not complete, or numbers have been replaced (e.g. *Astyochia* sp 03N instead of sp 03). Identification work was carried out in the Zoologische Staatssammlung, Munich, and the Natural History Museum, London. Fifty-two percent of the species and 67% of the specimens were identified at species level (Chapter 3).

ID	Genus	Species	1		2		3		4		5		6		7		8		9		10		11	
			a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b
	DESMOBATHRINAE																							
996	*Ophiogramma*	*coneobiata*	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	ENNOMINAE																							
255	*Acromotodes*	sp cf *subusta*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	3	1	1	1
941	*Acromotodes*	*subusta*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-
938	*Acrosemia*	*vulpecularia*	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
69	*Acrotomia*	*muta*	-	-	-	-	-	-	-	-	-	-	-	-	2	2	2	-	3	1	-	-	-	-
201	*Acrotomodes*	*lichenifera*	-	-	-	-	-	-	-	-	-	-	1	1	1	-	2	1	1	-	-	-	-	-
104	*Aenictes*	*sororcula*	-	-	-	-	-	-	-	2	3	-	-	-	-	-	-	-	-	1	-	-	-	1
997	*Anisoperas*	*rectilinea*	-	2	1	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
292	*"Apiciopsis"*	sp cf *maciza*	-	-	-	-	-	-	-	-	-	-	-	1	-	2	-	-	-	-	-	-	-	-
740	*Aplogompha*	*lafayi*	34	83	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
741	*Aplogompha*	*riofrio*	25	43	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
822	*Aplogompha*	sp cf *aurifera*	6	18	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
304	*Aragua*	*bistonaria*	-	-	-	-	-	-	-	-	-	1	3	-	-	3	4	1	5	11	1	1	-	5
742	*Argyrotome*	*mira*	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
73	*Argyrotome*	*prospectata*	2	1	1	-	23	17	1	-	2	-	2	-	1	2	2	-	1	1	-	-	-	-
221	*Astyochia*	*marginea*	-	-	-	-	2	3	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	1
224	*Astyochia*	sp 01	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
758	*Astyochia*	sp 02	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1032	*Astyochia*	sp 03N	-	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1031	*Astyochia*	sp 04	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
1030	*Astyochia*	sp 05	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
222	*Astyochia*	sp cf *marginea* 01	-	-	-	-	-	1	1	-	3	4	5	3	2	2	-	-	-	-	-	-	-	-
223	*Astyochia*	sp cf *marginea* 02	-	-	-	-	1	5	-	1	-	1	-	1	3	2	-	-	-	-	-	-	-	-
745	*Ballantiophora*	*gibbiferata*	-	8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
55	*Bassania*	*amethystata*	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	1	-	-	1	1	-
53	*Bassania*	*goleta*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
56	*Bassania*	sp cf *amethystata* 01	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	6	2
7	*Bassania*	sp cf *amethystata* 02	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-
57	*Bassania*	sp cf *foingi*	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-
54	*Bassania*	sp cf *goleta*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2	-	5	-	-
254	*"Bassania"*	*crocallinaria*	-	-	-	-	-	2	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-
282	Boarmiini	sp 01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	1
80	*Bonatea*	*duciata*	-	-	-	-	-	-	-	-	4	11	10	3	14	15	2	-	1	3	-	-	-	-
77	*Bonatea*	sp cf *viridilinea* 01	-	-	-	-	-	2	-	-	-	-	1	-	-	-	-	1	7	7	1	3	2	1
78	*Bonatea*	sp cf *viridilinea* 02	-	-	-	-	-	1	1	-	10	-	10	-	5	1	-	1	-	-	-	-	-	-
76	*Bonatea*	*viridilinea*	-	1	2	3	11	3	8	15	-	1	1	-	1	1	-	-	-	-	-	-	-	-
81	*Bonatea*	*viridirufa*	-	-	-	-	-	1	-	-	2	10	16	2	3	7	-	-	1	-	1	1	1	2
857	*Brachyctenistis*	*incongruata*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2	1
273	*Bryoptera*	*basisignata*	1	-	-	-	4	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
267	*Bryoptera*	*canidentata*	-	-	1	1	1	2	-	1	14	9	2	1	8	3	-	-	-	1	-	-	-	-

779	*Bryoptera*	*friaria*	-	1	5	6	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
780	*Bryoptera*	*fulvisquamosa*	-	-	-	2	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
268	*Bryoptera*	sp 01	-	-	5	4	2	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
274	*Bryoptera*	sp 03	-	-	-	-	-	-	1	2	-	1	1	-	-	-	-	-	-	-	-	-	-	-
266	*Bryoptera*	sp cf *deformipennis*	-	1	-	1	5	2	2	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-
774	*Budara*	*partita*	-	-	1	-	-	-	2	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-
800	*Callipseustes*	*pullaria*	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1011	*Callipseustes*	sp 01N	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
338	*Callipseustes*	sp cf *trisecta*	-	-	-	-	3	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
339	*Callipseustes*	*variegata*	-	-	6	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1018	*Canelo*	*albipennis*	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
310	*Canelo*	sp 01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
725	*Canelo*	sp cf *cytereatha*	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
75	*Cargolia*	*arana*	-	-	2	1	8	3	4	16	3	-	-	1	1	2	-	-	-	1	-	1	-	1
74	*Cargolia*	*pruna*	-	-	-	-	-	-	-	-	1	1	6	-	3	1	3	4	-	3	1	2	6	6
821	*Carpella*	*miegii*	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
749	*Certima*	*espuma*	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
936	*Certima*	*esquina*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
95	*Certima*	*lojanata*	-	-	-	1	1	4	-	-	-	-	1	-	1	1	-	1	-	2	-	2	2	3
253	*Certima*	*miligina*	-	-	-	-	-	-	-	1	-	-	1	-	1	1	-	1	-	-	-	-	-	-
133	*Certima*	sp 01N	-	-	-	-	10	11	1	2	-	1	-	-	-	-	-	-	-	3	-	-	-	-
97	*Certima*	sp 02	-	-	-	-	-	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
96	*Certima*	*unicolor*	-	-	-	-	-	-	-	-	1	2	-	-	1	2	-	-	-	-	-	1	1	-
94	*Certima*	*unilineata*	-	-	-	-	-	-	1	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-
718	*Charca*	*canopus*	-	1	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
717	*Charca*	*fulminea*	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-
305	*Charca*	*oppositata*	2	4	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
306	*Charca*	sp 01	-	-	-	-	-	-	-	-	-	-	-	-	1	2	-	-	-	-	-	-	-	1
307	*Charca*	sp 02	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	2	-	-
90	*Cimicodes*	*ruptimacula*	9	7	-	2	-	-	-	1	1	4	3	3	1	1	-	-	-	-	-	-	-	-
294	*Cirsodes*	*acuminata*	-	-	-	-	1	-	2	-	4	7	1	-	-	-	-	-	2	1	-	-	-	-
289	*Cirsodes*	*bella*	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
290	*Cirsodes*	*meridaria*	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
288	*Cirsodes*	*puntiaguada*	-	-	-	-	-	-	-	-	-	-	-	1	1	3	2	3	2	6	6	3	4	9
858	*Cirsodes*	sp 01	-	-	-	-	-	-	-	-	-	1	1	-	3	3	1	1	1	2	-	-	-	-
291	*Cirsodes*	sp 02	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2	6
293	*Cirsodes*	sp 03	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
1040	*Cirsodes*	sp cf *acuminata*	-	-	-	-	-	-	-	-	2	2	2	-	1	1	1	-	-	-	-	-	-	-
126	*Cosmophyga*	*privataria*	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1	-	-	1	-	-	-	-
127	*Cosmophyga*	sp cf *mosticana*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
755	*Cratoptera*	*vestianaria*	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
752	*"Crocallis"*	sp cf *multilinea*	-	1	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
200	*"Cyphoedma"*	*transvolutata*	-	1	-	-	1	2	4	-	3	2	5	3	4	1	-	-	-	-	-	-	-	-
324	Ennominae	sp 01	-	-	-	-	-	-	-	-	-	-	2	5	1	1	-	-	-	1	-	1	-	-
500	Ennominae	sp 02N	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
999	Ennominae	sp 03N	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
320	Ennominae	sp 04N	1	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1004	Ennominae	sp 10	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1005	Ennominae	sp 11	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1006	Ennominae	sp 12	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1010	Ennominae	sp 14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
746	*Epimecis*	*conjugaria*	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
252	*Epimecis*	*diffundaria*	1	1	-	1	1	2	2	-	1	1	-	-	-	1	-	-	-	1	-	-	-	-
911	*Epimecis*	*fraternaria*	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
910	*Epimecis*	*marcida*	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
945	*Erosina*	*hyberniata*	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
380	*Erycinopsis*	*diaphana*	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
723	*Erycinopsis*	sp 01	3	7	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

919	*Eusarca*	*bogotata*	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1
817	*Eusarca*	*colorifera*	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
908	*Eusarca*	*crameraria*	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
179	*Eusarca*	*fractilinearia*	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
751	*Eusarca*	*nemora*	4	7	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
182	*Eusarca*	sp 02	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
183	*Eusarca*	sp 03	-	-	1	1	1	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
184	*Eusarca*	sp 04	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-	1
185	*Eusarca*	sp 05	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
181	*Eusarca*	*venusta*	-	-	-	-	-	-	3	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
314	*Eutomopepla*	*rogenhoferi*	-	2	2	1	1	2	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-
738	*Fulgorodes*	sp 01	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
296	*Furcijuxta*	sp 01	-	-	-	-	-	-	-	-	1	-	-	1	-	1	-	-	-	-	-	-	-	-
295	*Furcijuxta*	sp cf *mathilda*	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
933	*Glena*	*agria*	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
265	*Glena*	*effusa*	1	20	1	1	1	-	1	1	1	-	-	-	2	-	-	-	-	-	-	-	-	-
932	*Glena*	sp 01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
808	*Gypsara*	*exularia*	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
169	*Hemixera*	*fulvida*	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-
86	*Herbita*	*aglausaria flavidisca*	-	-	-	-	-	-	-	1	-	-	-	2	-	-	-	-	-	-	-	-	-	-
85	*Herbita*	*zarina*	-	-	-	-	-	-	-	-	1	-	3	-	-	18	2	3	-	1	-	-	-	-
1012	*Herbita* group 1	*praeditaria*	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
84	*Herbita* group 2	*chiomaria*	1	-	-	-	-	-	-	-	-	2	-	2	5	10	8	7	8	17	3	11	3	1
88	*Herbita* group 3	*decurtaria*	2	4	3	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
82	*Herbita* group 3	*dognini*	1	1	2	2	1	1	-	4	4	3	1	-	2	2	-	-	-	1	-	-	-	-
940	*Herbita* group 3	*opalizans*	-	-	-	-	-	-	-	-	-	-	1	1	-	-	1	-	-	-	-	-	-	-
87	*Herbita* group 3	*tenebrica*	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-
113	*Heteroctenia*	*pectinicornata*	-	-	-	-	-	-	-	-	1	1	11	2	14	18	6	7	5	5	7	4	6	5
70	*Hygrochroma*	*nondina*	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
939	*Hygrochroma*	*olivinaria*	-	-	5	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
731	*Hymenomima*	*semialba*	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
276	*Hymenomima*	sp 01	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
905	*Hymenomima*	sp 02	1	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
720	*Hymenomima*	sp 03N	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
781	*Hymenomima*	sp cf *memor*	-	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
904	*Hymenomima*	*tharpoides*	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
906	*"Hypomecis"*	*pagana*	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
890	*Hypometalla*	*purpurea*	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
83	*Ira*	*somnolenta*	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
730	*Iridopsis*	*anaisaria*	30	62	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
782	*Iridopsis*	*chalcea*	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
748	*Iridopsis*	*fuscolimbaria*	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
257	*Iridopsis*	*gaujoni*	27	100	1	3	4	3	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
260	*Iridopsis*	*huambaria*	4	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
263	*Iridopsis*	*litharia*	-	2	3	1	1	-	1	3	2	1	-	-	-	-	-	-	-	-	1	-	-	-
258	*Iridopsis*	*muscinaria*	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
259	*Iridopsis*	*scolancala*	8	12	-	7	2	1	1	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-
783	*Iridopsis*	sp 04	-	-	-	-	-	-	-	2	1	-	-	-	-	-	-	-	-	-	-	1	-	-
256	*Iridopsis*	sp cf *subnigrata*	-	5	5	2	-	-	-	2	3	-	1	1	3	2	2	-	2	2	3	3	-	1
261	*Iridopsis*	sp cf *tanymetra*	-	-	-	-	-	-	1	-	-	-	-	-	1	-	2	1	-	-	-	1	-	-
262	*Iridopsis*	*subnigrata*	-	-	-	-	-	-	2	1	-	-	1	-	-	-	-	-	-	-	-	-	2	1
747	*"Iridopsis"*	*validaria*	3	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1019	*Ischnopteris*	*bryifera*	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
719	*Ischnopteris*	*callistrepta*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
754	*Ischnopteris*	*chryses*	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
694	*Ischnopteris*	*festa*	-	1	-	-	-	-	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
724	*Ischnopteris*	*festiva*	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
308	*Ischnopteris*	sp cf *chryses*	-	-	-	-	-	2	-	1	9	3	8	1	2	-	-	-	-	-	-	-	-	-

828	*Isochromodes*	*brumosa*	-	1	3	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
108	*Isochromodes*	*crassa*	-	-	-	-	2	-	-	-	17	3	3	2	12	5	2	2	17	20	-	3	2	1
109	*Isochromodes*	*fraterna*	-	1	-	-	1	1	-	6	1	1	-	-	1	1	1	-	-	1	2	-	-	2
103	*Isochromodes*	*palumbata*	-	2	1	-	1	-	2	2	3	2	-	-	-	-	-	-	-	-	-	1	1	4
98	*Isochromodes*	*polvoreata*	-	-	-	-	1	-	-	2	1	1	8	5	11	10	-	-	-	1	-	-	-	-
102	*Isochromodes*	sp 01	-	-	1	-	-	-	1	-	-	-	-	1	2	-	-	-	-	-	-	-	-	-
149	*Isochromodes*	sp 02N	-	1	-	1	-	-	-	-	3	-	2	-	3	4	-	-	-	1	-	-	-	-
668	*Isochromodes*	sp 03N	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	3	-	2
105	*Isochromodes*	sp 04	-	-	1	-	-	-	2	2	2	1	-	-	-	-	-	-	-	-	-	-	-	-
106	*Isochromodes*	sp 05	-	-	-	-	-	-	-	1	-	4	-	1	1	1	-	-	-	-	1	1	2	-
107	*Isochromodes*	sp 06	-	-	-	-	-	-	-	-	1	2	1	-	2	8	3	-	1	3	-	-	-	-
32	*Isochromodes*	sp 07N	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
110	*Isochromodes*	sp 09	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
111	*Isochromodes*	sp 10	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
112	*Isochromodes*	sp 11	1	17	2	1	-	-	3	1	2	1	11	1	3	12	-	1	4	2	-	-	-	-
115	*Isochromodes*	sp 14	-	-	-	-	-	-	-	-	1	-	6	-	1	1	-	-	-	-	-	-	-	-
116	*Isochromodes*	sp 15	-	-	-	-	-	-	-	-	-	-	1	1	1	1	-	-	-	-	-	-	-	-
117	*Isochromodes*	sp 16	-	-	-	-	-	-	-	2	-	1	-	-	1	-	-	-	-	-	-	-	-	-
118	*Isochromodes*	sp 17	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	2	1	-	-
693	*Isochromodes*	sp 24	-	3	6	4	-	-	5	-	1	1	7	-	3	6	-	-	6	-	-	-	-	1
829	*Isochromodes*	sp 26	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
1002	*Isochromodes*	sp cf *analiplaga*	-	-	-	-	1	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	1	-
101	*Isochromodes*	sp cf *duplicata*	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	1	-	1	-	-
99	*"Isochromodes"*	*atristicta*	-	-	-	-	-	-	1	2	1	-	1	1	-	-	-	-	-	-	-	-	-	-
119	*"Isochromodes"*	*nigripunctata*	-	-	-	-	-	-	1	1	1	-	-	-	1	-	1	-	-	-	-	-	-	-
992	*"Isochromodes"*	sp 19	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1
993	*"Isochromodes"*	sp 20	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
743	*Leuciris*	*fimbriaria*	5	18	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
744	*Leuciris*	*institata*	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
300	*Leuculopsis*	*pulverulenta*	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	8	6	1	1	-	1
301	*Leuculopsis*	sp cf *pulverulenta* 01	-	-	-	-	-	-	-	-	1	-	4	-	5	2	4	1	1	2	1	1	-	2
302	*Leuculopsis*	sp cf *pulverulenta* 02	-	-	-	-	-	-	-	-	-	-	3	-	3	2	-	-	-	-	-	-	-	-
157	*Lobopola*	*cimarrona*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	3	3	-	-	-	-
639	*Lobopola*	sp 03	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
684	*Lobopola*	sp 04	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
218	*Locha*	sp cf *panopea*	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
191	*Lomographa*	*"inaequata"*	-	-	-	-	-	-	-	-	-	-	2	-	1	5	-	-	-	-	-	-	-	-
690	*Lomographa*	*albifrons*	-	-	-	-	2	3	-	2	-	-	3	2	3	2	-	-	-	2	-	-	-	-
187	*Lomographa*	*bicineata*	-	-	-	-	1	1	-	2	3	3	5	1	8	21	4	2	5	4	-	-	-	-
190	*Lomographa*	*chartularia*	-	-	-	-	1	-	2	2	-	7	16	20	35	9	2	-	3	4	-	-	-	-
193	*Lomographa*	*nubimargo*	-	-	-	-	-	-	-	-	-	-	-	1	9	15	6	4	5	10	-	-	-	-
691	*Lomographa*	sp 01N	-	-	-	-	-	-	-	1	1	-	1	1	5	6	1	1	-	-	-	-	-	-
613	*Lomographa*	sp 02N	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
929	*Lomographa*	sp 03	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
930	*Lomographa*	sp 04	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
856	*Lomographa*	sp 05N	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	3	6
188	*Lomographa*	sp cf *proximata* 01	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	4	-	2	-	-	1	1
189	*Lomographa*	sp cf *proximata* 02	-	-	-	-	-	-	-	-	1	-	-	-	1	2	1	-	-	-	-	-	-	-
192	*Lomographa*	*tributaria*	-	4	2	2	5	6	4	5	6	1	8	-	9	27	4	4	4	5	5	6	3	4
763	*Macaria*	*(tenniscripta)*	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
685	*Macaria*	*bejucoaria*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
784	*Macaria*	*cardinea*	17	10	10	9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
768	*Macaria*	*lydia*	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
173	*Macaria*	*ostia*	1	5	16	11	1	1	4	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-
729	*Macaria*	*postnigra*	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
655	*Macaria*	*regulata*	1	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
176	*Macaria*	sp 01	1	1	-	-	-	-	1	-	3	-	-	-	2	1	1	-	1	-	-	-	-	-
767	*Macaria*	sp 01	-	4	3	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

764	*Macaria*	sp 03	1	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
612	*Macaria*	sp 04N	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
927	*Macaria*	sp 09	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
172	*Macaria*	sp cf *bejucoaria*	-	-	-	-	-	-	1	2	3	5	10	6	9	6	4	1	1	1	1	-	-	-
174	*Macaria*	sp cf *indentata*	-	-	-	-	-	-	-	1	2	-	-	-	-	-	-	-	1	-	-	-	-	-
859	*Mallomus*	sp 01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	3
860	*Mallomus*	sp 02	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1	2	3	1	2
937	*Mallomus*	sp cf *colopholeuca*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
790	*Mallomus*	*synopsioides*	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
923	*Melanolophia*	*conta*	3	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
269	*Melanolophia*	*reducta meridiana*	-	-	-	-	-	1	-	2	-	-	-	-	-	-	2	-	2	2	-	-	-	-
271	*Melanolophia*	sp 01	-	-	-	-	-	-	-	-	-	-	-	-	1	2	-	1	1	2	5	4	7	10
765	*Melanolophia*	*sp cf flexilinea*	2	5	6	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
270	*Melanolophia*	*trisurca*	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-
199	*"Melanolophia"*	*atigrada*	-	-	-	-	-	-	1	-	-	1	-	-	7	-	3	-	2	-	-	-	-	-
220	*Melanoscia*	*oreades*	-	-	-	-	-	1	-	1	-	3	2	2	2	-	1	-	1	2	1	1	-	-
219	*Melanoscia*	*thiaucourti*	-	-	-	-	-	-	-	-	-	-	-	2	4	3	-	-	-	1	1	-	-	-
164	*Melinodes*	*apricaria*	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
331	*Melinodes*	*saeta*	-	-	-	-	3	1	1	6	-	-	-	-	1	-	-	-	-	-	-	-	-	-
163	*Melinodes*	sp cf *subapicata*	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
160	*Melinodes*	*subapicata*	-	-	-	-	-	-	-	1	-	1	1	4	-	-	1	1	2	-	1	-	-	-
753	*Melinodes*	*subspurcata*	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
161	*"Melinodes"*	*fulvitincta*	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-
916	*"Melinodes"*	*ignea*	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-
732	*"Melinodes"*	sp 04	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
918	*"Melinodes"*	sp 05	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
186	*Mesedra*	*confinis*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	4	5	4	3	6	11
177	*Mesedra*	*munda*	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-
180	*Mesedra*	sp 01	1	1	3	3	1	-	3	4	8	3	5	9	19	-	3	-	2	8	-	-	3	1
687	*Mesedra*	sp cf *confinis*	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
178	*Mesedra*	sp cf *confinis* 03N	-	-	-	-	-	-	-	-	-	3	-	-	-	1	1	-	-	-	-	-	-	-
159	*Microxydia*	*colorata*	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
329	*Microxydia*	*fulvicollis*	-	-	-	-	-	-	1	1	-	-	-	-	-	9	4	12	5	11	2	-	-	2
330	*Microxydia*	sp 01	-	-	-	-	-	-	1	-	1	-	-	-	1	8	1	1	-	1	-	-	-	-
695	*Microxydia*	sp cf *ruficomma*	-	-	1	1	9	8	5	8	3	1	2	1	-	1	-	-	-	-	-	-	-	-
805	*Microxydia*	*strigosa strigosa*	-	-	8	2	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
838	*Mimosema*	*sobrina*	2	4	-	-	2	3	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
129	*Mimosema*	sp cf *sobrina* 01	-	-	-	-	-	-	-	2	-	2	-	-	-	6	2	-	3	1	2	1	-	-
114	*Mimosema*	sp cf *sobrina* 02	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
922	*Mychonia*	sp 04	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	5	-	8
931	*Mychonia*	sp 05	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
166	*Mychonia*	sp cf *violacea*	-	-	-	-	1	2	-	2	1	-	3	2	3	13	1	4	-	1	2	-	-	-
168	*Mychonia*	*tepida*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	1	-	1	-	-
921	*Mychonia*	*violacea*	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
722	*Myrmecophantes*	*albifascia*	3	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1017	Nacophorini	sp 02	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
802	*Narragodes*	sp cf *lilacina*	-	-	2	3	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
303	*Nazca*	*indentata*	-	-	-	-	1	-	1	1	-	3	20	6	38	24	28	11	30	31	3	2	1	1
801	*Nazca*	*zofra*	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
170	*Neazata*	*fragilis*	-	-	-	-	-	1	1	-	2	1	6	-	8	2	1	-	-	1	-	-	-	-
727	*Nematocampa*	*angulifera*	21	11	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
130	*Nematocampa*	sp cf *falsa*	-	-	-	-	3	1	3	9	5	3	-	-	-	-	-	-	-	-	-	-	-	-
796	*"Nematocampa"*	sp 01	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
332	*"Nematocampa"*	sp cf *confusa*	-	-	-	-	1	1	2	-	20	3	13	16	5	13	-	-	-	-	-	-	-	-
903	*"Nematocampa"*	*straminea*	2	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
143	*Neobapta*	*camptogrammata*	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	1	1	-	1	-	-	1
145	*Neobapta*	*costata*	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-
144	*Neobapta*	*perrubra*	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	1	-	2	1	1	-	-

981	*Neobapta*	*recessa*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
142	*Neobapta*	sp cf *recessa* 01	-	-	-	-	-	-	-	-	-	-	-	1	-	3	2	2	-	-	-	1	1	-
998	*Neobapta*	sp cf *recessa* 03	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	2
141	*Neobapta*	*violacearia*	-	-	-	-	-	-	1	1	-	-	-	-	1	-	1	-	-	-	1	-	-	-
131	*"Neobapta"*	*leprosata*	-	-	-	-	-	-	-	1	-	-	1	-	4	8	6	9	13	21	-	-	-	-
287	*Neodora*	*costinotata*	-	-	-	-	-	-	-	-	-	-	-	1	-	3	1	1	-	1	-	-	-	-
286	*Neodora*	*glaucularia*	-	-	-	-	-	1	1	1	3	1	-	1	-	7	3	1	1	1	-	-	-	-
950	*Nephodia*	*aethiopissa*	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
810	*Nephodia*	*clara*	-	-	4	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
772	*Nephodia*	*claudaria*	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1034	*Nephodia*	*coenulenta*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	2	1
214	*Nephodia*	*exclamationis*	-	-	-	-	1	-	-	-	-	-	-	-	3	1	-	-	-	1	1	1	-	1
847	*Nephodia*	*manchata*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	5	2	5
849	*Nephodia*	*nudata*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	2	1
205	*Nephodia*	*pania*	-	-	1	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-
207	*Nephodia*	*pellucenta*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	7	6	4	4	-	-
809	*Nephodia*	*pieria*	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
895	*Nephodia*	*rotundata*	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
206	*Nephodia*	*sororcula*	-	-	-	-	5	2	-	-	1	1	7	4	10	1	1	-	-	1	-	-	-	-
842	*Nephodia*	sp 01N	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
846	*Nephodia*	sp 02N	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	3
209	*Nephodia*	sp 03	-	-	-	-	-	-	2	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-
210	*Nephodia*	sp 04	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	1	-	-	-	-	1
211	*Nephodia*	sp 05	-	-	-	-	-	-	-	-	-	-	2	-	1	2	-	-	-	2	2	2	-	1
215	*Nephodia*	sp 09	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
771	*Nephodia*	sp 14	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
807	*Nephodia*	sp 18	4	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
848	*Nephodia*	sp 20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	3	2
1021	*Nephodia*	sp 21	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
1022	*Nephodia*	sp 22	2	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1023	*Nephodia*	sp 23	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
1024	*Nephodia*	sp 24	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1027	*Nephodia*	sp 27	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1028	*Nephodia*	sp 28	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
299	*Nephodia*	sp cf *astyochiodes*	-	-	-	-	-	1	-	-	6	5	4	-	2	2	-	-	-	1	-	-	-	-
204	*Nephodia*	sp cf *cissoessa*	-	-	3	2	-	-	-	3	-	1	-	-	1	-	-	-	-	-	-	-	-	-
216	*Nephodia*	sp cf *incoloraria*	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
212	*Nephodia*	sp cf *interposita*	-	-	-	-	-	1	-	-	-	-	1	-	-	-	3	-	-	1	-	-	-	-
769	*Nephodia*	sp cf *orcipennata*	2	11	1	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
203	*Nephodia*	sp cf *pecalba*	-	-	-	-	-	-	-	-	2	3	1	4	5	2	1	1	-	2	-	-	-	-
770	*Nephodia*	*trisecta*	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
688	*Nephodia*	*turpis*	-	-	-	-	1	-	-	-	-	-	1	1	-	-	-	-	-	1	-	-	-	-
773	*Nephodia*	*vestigiata*	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
213	*"Nephodia"*	*fumosata*	-	2	7	2	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
208	*"Nephodia"*	*panacea*	-	-	3	-	-	-	-	-	-	-	1	-	4	1	-	-	-	-	1	-	2	-
735	*"Nephodia"*	*philomela*	5	17	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
284	*Odysia*	sp 01	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-
272	*"Odysia"*	sp cf *excuvaria*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	-	2
278	*"Odysia"*	*venusta*	1	6	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
147	*Oenoptila* group 1	*anagogaria*	-	-	-	-	-	-	1	2	2	-	-	1	1	3	3	1	2	4	-	-	-	-
155	*Oenoptila* group 1	*binigrata*	-	-	-	-	-	-	-	-	-	-	-	5	3	-	-	-	-	-	-	-	-	-
608	*Oenoptila* group 1	*nigriplaga*	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	1	1	-	-	-	-
156	*Oenoptila* group 1	*purpurea*	-	-	-	-	-	-	1	1	-	-	-	-	1	-	1	-	-	1	1	-	-	-
994	*Oenoptila* group 1	sp cf *purpurea* 01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	4
675	*Oenoptila* group 1	sp cf *purpurea* 02	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-
231	*Opisthoxia*	*archidiaria*	-	-	-	-	1	1	1	1	2	2	3	2	2	-	1	-	-	-	-	-	-	-
233	*Opisthoxia*	*branickiaria*	-	-	-	-	-	-	1	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-
234	*Opisthoxia*	*descimoni*	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-	1	-	2	-	-	-	-

228	*Opisthoxia*	*metargyria*	-	1	-	-	-	-	-	2	-	-	-	-	-	1	-	-	-	-	-	-	-	-
823	*Opisthoxia*	*pepita*	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
236	*Opisthoxia*	sp 01	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-
235	*Opisthoxia*	sp cf *(astyocharia)*	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
762	*Opisthoxia*	sp cf *archidiaria*	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
232	*Opisthoxia*	sp cf *danaeata*	-	-	-	-	1	-	1	-	2	1	1	-	1	1	-	-	-	2	-	-	-	-
64	*Oxydia*	*agliata*	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
59	*Oxydia*	*augusta*	-	-	-	-	-	5	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	1
1013	*Oxydia*	*distichata*	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
60	*Oxydia*	*geminata*	-	-	5	1	-	-	-	1	-	-	1	2	3	3	-	1	1	1	-	-	1	-
67	*Oxydia*	*herbertina*	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
171	*Oxydia*	*masthala*	-	15	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
65	*Oxydia*	*mexicata*	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
61	*Oxydia*	*olivata*	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
71	*Oxydia*	*optima*	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-
72	*Oxydia*	*scriptipennaria*	3	2	7	5	2	3	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1
546	*Oxydia*	sp 01N	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
826	*Oxydia*	sp 02	4	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
673	*Oxydia*	sp 03N	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1014	*Oxydia*	sp 06	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
66	*Oxydia*	sp cf *insolita*	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1	-	1	1	-	1
62	*Oxydia*	sp cf *olivata*	1	-	-	-	-	1	1	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-
775	*Oxydia*	sp cf *rotara*	3	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
68	*Oxydia*	*subdecorata*	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
63	*Oxydia*	*translinquens*	-	1	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
58	*Oxydia*	*trychiata*	-	15	21	14	6	1	12	4	12	15	11	3	20	9	-	-	3	4	-	-	-	-
79	*Oyxdia*	sp 04N	1	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
297	*Pantherodes*	*colubraria viperaria*	-	1	2	2	3	1	1	2	-	-	1	-	-	-	-	-	-	-	1	-	1	-
298	*Pantherodes*	*conglomerata*	1	1	2	1	4	1	3	4	-	-	-	-	-	1	-	1	-	-	-	-	-	-
644	*Paragonia*	*cruraria*	-	2	11	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1007	*Patalene*	*asina*	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
312	*Patalene*	*flavibasis*	-	-	-	-	-	-	-	-	1	1	1	-	7	6	1	1	1	3	-	-	-	-
313	*Patalene*	*hamulata*	-	-	-	-	2	1	-	1	-	2	14	1	5	13	1	4	2	6	-	-	-	1
785	*Patalene*	*pholata*	-	-	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
649	*Patalene*	sp cf *hamulata* 01	-	-	-	-	-	-	-	-	-	-	1	-	-	3	2	-	-	-	-	-	-	-
9	*Patalene*	sp cf *hamulata* 02	-	-	-	-	1	-	-	-	1	-	2	-	1	12	1	3	1	4	-	-	-	-
726	*Penthophlebia*	*altaba*	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
162	*Periclina*	*rumiaria*	-	1	-	-	-	-	2	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
165	*Periclina*	*sp cf merana*	-	-	1	-	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
154	*Perissopteryx*	*nigricomata*	-	2	-	1	1	-	-	2	-	-	-	2	-	-	-	-	-	-	1	3	1	-
912	*Perissopteryx*	*raveni*	-	1	6	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
158	*Perissopteryx*	sp 01	-	-	-	-	-	-	-	-	-	-	-	-	1	4	-	-	1	4	-	-	-	-
10	*Perissopteryx*	sp 02	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
19	*Perissopteryx*	sp 03	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1001	*Perissopteryx*	sp cf *distincta*	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
947	*Pero*	*algerna*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
239	*Pero*	*buckleyi*	-	-	3	2	-	1	2	3	3	-	-	1	2	-	4	-	-	-	-	-	-	-
250	*Pero*	*castanea*	-	-	-	-	1	-	-	-	-	-	-	1	-	1	-	-	-	1	-	-	-	-
248	*Pero*	*caustomeris*	-	-	-	-	-	-	-	-	1	-	-	-	-	2	-	-	-	-	1	-	-	1
241	*Pero*	*gamuza*	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	2	1	3	1	2	1	6
249	*Pero*	*homodoxa*	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
251	*Pero*	*maculicosta*	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
831	*Pero*	*mathanaria*	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
942	*Pero*	*mathilda*	4	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
943	*Pero*	*mnasilaria*	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
245	*Pero*	*periculosaria*	-	-	-	-	-	-	-	-	-	-	-	1	2	-	-	-	-	-	-	1	-	1
247	*Pero*	*pincha*	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	2
237	*Pero*	*plenilunata*	-	-	-	-	2	1	7	3	2	3	2	3	-	-	-	-	-	-	-	-	-	-

832	*Pero*	*plenilunata*	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
240	*Pero*	*pretensa*	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	1	1	-	3	-	-
834	*Pero*	*rapta*	1	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
246	*Pero*	*scitaria*	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	2	-	-	1	-
792	*Pero*	sp 03	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
833	*Pero*	sp 08	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1
835	*Pero*	sp 10	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
244	*Pero*	*speciosata*	-	-	1	-	2	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
791	*Pero*	*spectrata*	-	-	1	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
238	*Pero*	*stuposaria* group 01	-	-	-	-	-	-	-	-	2	-	1	-	2	1	1	1	3	3	1	-	-	-
242	*Pero*	*tabitha*	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
243	*Pero*	*trena*	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-
794	*Pero*	*yahua*	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
120	*Perusia*	sp 01	-	-	-	-	-	1	1	-	-	-	-	4	3	10	1	-	2	2	-	-	-	-
134	*Perusia*	sp 03N	-	1	-	-	-	-	-	-	-	-	1	-	2	1	1	1	-	1	1	3	2	3
123	*Perusia*	sp 04	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-
135	*Perusia*	sp 05N	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
136	*Perusia*	sp 06N	-	-	-	-	-	-	-	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-
328	*Perusia*	*verticata*	1	1	1	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
327	*Perusia*	*viridis*	-	-	-	-	-	-	-	-	-	-	-	-	4	2	3	-	9	8	6	1	4	5
915	*Perusia*	*zoma*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	2	-	-
139	*"Petelia"*	*interrupta*	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	3	-	-	-	-
140	*"Petelia"*	*nummifera*	-	1	-	-	1	1	1	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-
124	*"Petelia"*	*plagiata*	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
132	*"Petelia"*	sp 01	-	-	-	-	-	1	2	-	-	10	6	3	3	3	2	1	-	-	-	-	1	-
121	*"Petelia"*	sp 02N	-	-	-	-	-	-	1	1	-	1	2	-	-	-	-	-	-	-	-	-	-	-
1003	*"Petelia"*	sp 03N	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
148	*"Petelia"*	sp 07	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-
150	*"Petelia"*	sp 09	-	-	-	-	-	-	-	-	1	-	1	-	-	1	-	-	2	-	-	-	-	-
151	*"Petelia"*	sp 10	-	-	-	-	-	-	1	-	-	1	-	-	2	-	-	-	-	-	-	-	-	-
152	*"Petelia"*	sp 11	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-
153	*"Petelia"*	sp 12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
995	*"Petelia""*	sp 12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	1
146	*"Petelia"*	sp cf *anagonaria*	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	2	3	6	-	2	1
138	*"Petelia"*	sp cf *plagiata*	-	-	-	-	-	-	-	-	-	1	-	-	1	-	1	-	-	1	5	3	4	4
716	*Pherotesia*	*coiffaiti*	1	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
925	*Pherotesia*	sp 01	-	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
197	*Pherotesia*	*subjecta*	-	-	-	-	-	1	-	-	3	3	5	2	4	3	5	-	-	1	-	-	-	-
198	*Pherotesia*	*suffumosa*	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	3	-	-	-	2
226	*Phrygionis*	*flavilimes*	-	-	-	-	-	-	-	1	2	-	-	-	2	10	3	3	-	4	-	-	-	-
227	*Phrygionis*	*platinata platinata*	-	-	-	-	-	-	1	4	4	7	-	-	-	-	-	-	-	-	-	-	-	-
225	*Phrygionis*	*polita*	-	-	-	-	2	5	-	3	3	-	-	-	1	-	-	-	-	-	-	-	-	-
737	*Phrygionis*	*privignaria*	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
128	*Phyle*	*transglauca*	-	2	1	1	-	-	-	-	-	-	-	-	1	2	-	-	1	3	4	1	1	1
326	*Phyle*	*versatile*	-	-	-	-	-	-	-	-	-	-	9	6	-	4	1	1	-	-	-	-	-	-
49	*Phyllodonta*	*caninata*	-	-	-	-	1	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
51	*Phyllodonta*	*cataphracta*	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-
45	*Phyllodonta*	*flabellaria*	-	-	-	-	-	1	-	-	-	2	1	1	-	2	1	1	-	-	-	-	-	-
1015	*Phyllodonta*	*flexilinea*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
50	*Phyllodonta*	*obscura*	-	-	-	-	-	-	-	-	4	1	4	-	-	4	9	4	4	9	1	-	-	-
47	*Phyllodonta*	*semicava*	-	-	-	-	-	-	-	-	1	3	3	4	8	4	6	-	4	8	-	-	-	-
46	*Phyllodonta*	sp cf *flabellaria* 01	-	-	-	-	-	1	1	-	-	3	15	3	8	11	4	2	6	9	2	-	-	-
137	*Phyllodonta*	sp cf *latrata*	-	-	-	-	2	-	-	-	-	-	-	-	-	-	1	-	-	1	1	3	-	-
48	*Phyllodonta*	*succedens*	3	1	-	1	2	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
337	*Physocleora*	*bella*	-	1	3	3	1	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
335	*Physocleora*	*enana*	3	5	8	1	-	-	-	1	1	2	6	-	1	1	-	-	-	1	-	-	-	-
336	*Physocleora*	*flaviplaga*	-	-	-	-	2	-	1	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-
840	*Physocleora*	*grossica*	4	6	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

279	*Physocleora*	*latimedia*	-	1	-	-	-	-	-	-	-	1	-	1	2	1	-	1	-	-	-	-	-	-
333	*Physocleora*	*pulverata*	-	4	5	-	8	9	90	85	39	21	29	21	22	24	4	-	4	6	2	1	1	3
281	*Physocleora*	sp 01	-	-	-	-	-	-	1	2	5	2	6	11	1	3	-	1	1	2	-	-	-	-
334	*Physocleora*	sp 01	-	-	2	3	1	2	18	26	1	2	-	1	1	-	-	-	-	-	-	-	-	-
275	*Physocleora*	sp 02N	-	-	1	-	2	1	3	9	1	-	-	-	-	-	-	-	-	-	-	-	-	-
283	*Physocleora*	sp 03	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
285	*Physocleora*	sp 05	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
885	*Physocleora*	sp 05	1	1	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
886	*Physocleora*	sp 06	-	4	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
887	*Physocleora*	sp 07	-	4	66	16	1	-	-	1	-	2	2	-	1	1	-	-	-	-	-	-	-	-
888	*Physocleora*	sp 08	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
907	*Physocleora*	sp 10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	3
280	*Physocleora*	sp cf *accessilinea*	-	-	-	-	1	-	1	3	1	-	-	-	2	-	-	-	-	-	-	-	-	-
230	*Pityeja*	*histrionaria*	-	-	-	-	-	-	1	-	-	1	5	1	3	3	-	-	1	2	-	-	-	-
229	*Pityeja*	*nazada*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
909	*Polla*	*aristaria*	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
946	*Postazuayia*	*stigmatalis*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
89	*Prochoerodes*	*cristata*	-	-	-	-	-	3	1	4	3	11	6	1	5	17	1	-	-	-	-	-	-	-
1009	*Psilosetia*	*pura*	-	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
734	*Pyrinia*	*abditaria*	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
323	*Pyrinia*	*coearia*	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
317	*Pyrinia*	*megara*	1	3	1	-	-	-	-	1	-	1	-	-	2	-	-	-	2	-	2	1	1	3
316	*Pyrinia*	sp 01	-	-	-	-	-	2	-	1	-	-	1	-	-	2	-	-	1	1	-	-	-	-
839	*Pyrinia*	sp 02N	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
318	*Pyrinia*	sp 03	-	-	2	1	-	-	-	1	1	-	-	-	-	-	-	-	1	-	-	-	-	-
319	*Pyrinia*	sp 04	-	-	1	-	1	2	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
322	*Pyrinia*	sp 07	-	-	-	-	2	1	-	-	1	-	-	-	-	-	-	-	-	1	-	-	-	-
1008	*Pyrinia*	sp 10	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
315	*Pyrinia*	sp cf *sanitaria*	-	-	2	-	-	-	-	-	-	1	-	-	1	1	-	-	-	-	-	-	-	-
733	*Pyrinia*	*vanidosa*	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
309	*Rucana*	*brunneoviridis*	-	1	-	-	-	1	2	5	-	-	1	-	-	-	-	-	-	-	-	-	-	-
311	*Rucana*	sp cf *brunneoviridis*	-	-	-	-	1	1	1	4	7	4	8	-	-	-	-	-	-	2	-	-	-	-
759	*Sabulodes*	*boarmidaria*	1	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
92	*Sabulodes*	*boliviaria*	-	-	-	-	-	-	-	-	1	1	2	1	11	2	1	-	1	4	-	-	-	-
93	*Sabulodes*	*caberata oberthuri*	-	-	-	-	-	-	-	3	2	1	-	-	1	-	-	-	-	-	-	-	-	-
750	*Sabulodes*	*ornatissima*	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
944	*Sabulodes*	*prolata*	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
122	*Sabulodes*	sp cf *carbina*	-	-	-	1	2	-	10	-	9	5	1	-	2	1	-	-	-	-	-	-	-	-
990	*Sabulodes*	sp cf *carbina* 02	-	-	-	-	-	-	-	-	-	-	1	-	2	4	-	-	1	-	11	7	3	6
991	*Sabulodes*	sp cf *carbina* 03	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
125	*Sabulodes*	*thermidora*	-	1	-	-	35	39	2	7	8	1	3	-	7	3	7	1	-	4	-	-	-	2
934	*"Sabulodes"*	*mima*	1	-	-	-	-	-	1	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-
1016	*Salasaca*	*spinea*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
175	*Semiothisa*	*radiata*	-	-	-	-	-	-	-	1	-	-	-	-	2	-	-	-	-	-	-	-	-	-
766	*Semiothisa*	sp cf *quadriseriata*	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
202	*Sericoptera*	*mahometaria*	6	3	-	-	1	1	-	1	-	-	-	-	-	-	-	-	1	-	-	-	-	-
689	*Sicya*	*directaria*	-	1	-	-	1	1	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-
91	*Sphacelodes*	*vulneraria*	3	-	2	-	-	-	-	-	-	-	-	-	2	-	6	-	-	-	-	-	-	-
277	*Stenalcidia*	*castaneata*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
217	*Tarma*	*theodora*	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
917	*Tetragonodes*	*asphales*	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
913	*"Thysanopyga"*	sp cf *casperia*	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
920	*Trotogonia*	*agelaea*	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	GEOMETRINAE																							
370	*Cathydata*	*batina*	-	1	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-
721	*Chavarriella*	*fallax*	-	-	4	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
965	*Chavarriella*	*lafayaria*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
364	*Chavarriella*	*psittacina*	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-

960	*Chloropteryx*	*dealbata*	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
358	*Chloropteryx*	*opalaria*	-	-	5	2	14	18	14	21	15	3	2	-	2	-	-	-	-	-	-	-	-	-
959	*Chloropteryx*	*punctilinea*	1	3	-	-	-	-	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-
786	*Chloropteryx*	*stigmatica*	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
343	*Hyalochlora*	*nadia*	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	1	-	-	-	-
368	*Hydata*	*projiciens*	-	-	-	-	-	1	-	-	1	-	-	-	-	-	2	-	2	-	-	-	-	-
958	*Hydata*	*propinqua*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	2
778	*Hydata*	sp cf *elegans*	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
369	*Hydata*	*stigmatica*	-	-	-	2	-	-	-	1	2	-	1	-	1	-	1	-	-	-	-	-	-	-
692	*Hydata*	*subfenestraria*	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-
761	*Lissochlora*	*cecilia*	-	3	1	-	-	2	2	1	6	1	2	1	7	3	1	1	-	3	-	-	-	1
354	*Lissochlora*	*diarita*	-	1	3	1	-	-	1	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-
827	*Lissochlora*	*hena*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
348	*Lissochlora*	*jenna*	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	2	-	1	-	1	1
352	*Lissochlora*	*latuta*	1	6	3	2	3	5	7	6	9	3	23	7	25	3	20	6	10	13	3	3	16	14
351	*Lissochlora*	*pectinifera*	1	11	4	1	-	1	1	4	1	-	3	2	16	4	6	2	4	8	-	-	-	-
852	*Lissochlora*	sp 01N	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
963	*Lissochlora*	sp cf *rufipicta*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
371	*Neagathia*	*corruptata*	-	2	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
355	*Nemoria*	*aturia*	-	-	2	-	-	2	1	2	2	-	1	-	7	3	7	1	8	8	6	1	1	1
962	*Nemoria*	*conspersa*	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
869	*Nemoria*	*dentilinea dentilinea*	-	2	6	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
757	*Nemoria*	*erina*	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
340	*Nemoria*	*heterograpta*	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-
346	*Nemoria*	*imitans*	3	-	2	4	1	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
345	*Nemoria*	*nigrisquama*	-	-	-	-	4	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
964	*Nemoria*	*roseilinearia*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
356	*Nemoria*	*scriptaria*	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
349	*Nemoria*	*sellata*	-	-	1	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-
819	*Nemoria*	sp 01N	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
353	*Nemoria*	sp 02	-	-	-	-	1	2	-	-	1	1	1	2	3	2	-	-	-	-	-	-	-	-
777	*Nemoria*	sp 04	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
988	*Nemoria*	sp 06	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
776	*Nemoria*	sp cf *conspersa*	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
363	*Oospila*	*asmura*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
362	*Oospila*	*concinna*	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-
957	*Oospila*	*confundaria*	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
367	*Oospila*	*depressa*	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-
344	*Oospila*	*micularia*	-	1	-	-	1	2	2	2	3	3	1	-	-	-	-	-	-	-	-	-	-	-
366	*Oospila*	sp cf *congener*	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
365	*Oospila*	sp cf *holochroa*	-	-	-	-	1	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
948	*Phrudocentra*	*opaca*	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
360	*Phrudocentra*	*subaurata*	-	-	-	-	-	-	-	1	-	-	-	-	4	-	1	-	-	2	1	-	-	-
361	*Phrudocentra*	*trimaculata*	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
949	*Phrudocentra*	*vagilinea*	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
341	*Poecilochlora*	*minor*	-	-	-	-	-	1	-	1	-	1	-	-	5	-	1	-	-	-	-	-	-	-
342	*Rhodochlora*	*roseipalpis*	-	-	-	-	1	1	-	-	-	-	1	3	6	3	1	-	1	-	2	-	-	1
347	*Synchlora*	*amplimaculata*	2	1	-	1	2	-	-	1	-	1	6	2	4	2	1	1	1	1	-	-	-	-
350	*Synchlora*	*decorata*	1	2	6	2	-	-	-	-	-	-	-	-	1	2	-	-	-	-	-	-	-	-
756	*Synchlora*	sp cf *decorata* 01	1	2	1	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
611	*Synchlora*	sp cf *decorata* 02	-	-	-	-	3	2	1	1	1	-	-	-	2	1	-	-	1	2	1	1	1	-
372	*Tachychlora*	*flavidisca*	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-
359	*Telotheta*	*muscipunctata*	-	-	2	4	2	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	LARENTIINAE																							
438	*Brabirodes*	*cerevia*	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-
428	*Callipia*	*constantinaria*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-
429	*Callipia*	*parrhasiata*	-	-	-	-	-	-	-	-	-	-	1	-	-	2	-	-	3	2	-	-	-	1
985	*Callipia*	*rosetta*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-

483	*Cirrhorhema*	*androconiata*	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
458	*Deinoptila*	*penicula*	-	-	-	-	-	-	-	-	-	-	1	-	2	12	-	1	3	-	-	1	-	1
459	*Deinoptila*	sp 01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	2	1	-	1	5
449	*Distroneura*	*pastaza*	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
439	*Dyspteris*	*breviataria*	-	2	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
375	*Eois*	*adimaria*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
391	*Eois*	*amarillada*	-	1	-	-	-	-	-	-	-	-	-	-	4	1	-	-	-	-	-	-	-	-
376	*Eois*	*angulata*	-	2	2	1	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
799	*Eois*	*antiopata*	-	-	2	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
397	*Eois*	*azafranata*	-	-	-	-	2	-	-	1	-	1	10	16	66	30	53	54	35	55	7	8	5	10
401	*Eois*	*basaliata*	1	2	-	-	2	4	-	4	1	-	-	-	-	-	-	-	-	-	-	-	-	-
710	*Eois*	*binaria*	4	10	5	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
374	*Eois*	*borrata*	2	3	-	-	1	2	1	1	-	1	5	2	29	2	16	3	3	4	-	-	-	-
385	*Eois*	*burla*	-	-	-	-	4	2	-	2	5	1	2	4	7	1	10	1	4	2	1	2	-	1
417	*Eois*	*canariata*	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
386	*Eois*	*cancellata*	-	-	-	1	-	1	-	-	1	-	9	5	10	2	4	1	1	3	-	-	-	2
389	*Eois*	*carrasca*	-	-	-	1	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-
426	*Eois*	*catana*	-	6	1	-	-	1	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
392	*Eois*	*chasca*	-	-	2	3	1	2	3	1	2	5	1	3	3	1	3	-	-	1	-	-	-	-
1029	*Eois*	*chrysocraspedata*	-	-	-	-	2	-	-	3	1	-	-	-	-	-	-	-	-	-	-	-	-	-
403	*Eois*	*ciocolatina*	-	2	4	1	5	2	6	11	-	-	-	-	-	-	-	-	-	-	-	-	-	-
407	*Eois*	*cobardata*	-	-	-	-	-	-	-	-	-	-	-	-	5	-	9	2	2	5	1	-	1	1
914	*Eois*	*contraversa*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
423	*Eois*	*dorisaria*	-	1	-	-	1	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-
798	*Eois*	*fasciata*	-	-	4	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
394	*Eois*	*fucosa*	-	-	19	8	3	1	2	7	-	-	-	-	-	2	-	-	1	-	-	-	1	1
396	*Eois*	*golosata*	-	-	1	-	-	-	4	5	10	3	7	9	55	9	37	4	17	10	4	1	2	1
390	*Eois*	*haematodes*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	3	-	1	1	-	-	-
739	*Eois*	*isographata*	1	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
384	*Eois*	*lucivittata*	-	4	2	3	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
413	*Eois*	*mediostrigata*	-	-	3	2	2	1	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
395	*Eois*	*necula*	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-
388	*Eois*	*nigrosticta*	-	1	-	-	1	-	-	1	-	1	-	1	-	-	1	1	2	7	-	-	-	-
416	*Eois*	*olivacea*	-	4	3	5	-	1	4	9	-	-	-	-	1	-	-	-	-	-	-	2	-	-
424	*Eois*	*paraviolascens*	-	-	5	4	3	-	2	4	1	-	-	-	-	1	1	-	-	-	1	-	-	-
696	*Eois*	*paulona*	1	-	-	1	2	-	2	3	3	-	2	-	1	2	-	-	1	1	2	2	-	1
383	*Eois*	*planetaria*	-	-	-	-	1	-	2	-	-	-	-	1	1	-	-	-	-	-	1	-	-	1
837	*Eois*	*restrictata*	2	8	1	-	1	-	3	2	3	2	1	2	1	1	1	-	-	-	-	-	-	1
377	*Eois*	*sagittaria*	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-
382	*Eois*	sp *(thiaucourti)*	-	-	-	-	-	-	-	-	-	3	3	2	1	3	2	-	3	1	-	1	-	-
456	*Eois*	sp 01N	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
803	*Eois*	sp 02N	-	4	7	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
30	*Eois*	sp 03N	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
405	*Eois*	sp 05	-	-	-	-	-	-	1	-	-	1	2	-	-	1	-	-	1	-	-	-	-	-
406	*Eois*	sp 06	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	3	6	5	11	9
408	*Eois*	sp 08	-	2	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
409	*Eois*	sp 09	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
420	*Eois*	sp 14	-	-	-	-	-	-	3	-	-	-	13	-	1	-	1	-	-	-	-	-	-	-
421	*Eois*	sp 15	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
427	*Eois*	sp 16	-	-	-	-	-	-	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
707	*Eois*	sp 17	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
708	*Eois*	sp 18	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
706	*Eois*	sp 19	-	-	-	-	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
709	*Eois*	sp 20	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
797	*Eois*	sp 21	-	1	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
816	*Eois*	sp 24	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
818	*Eois*	sp 26	1	1	1	1	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
968	*Eois*	sp 27	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-

836	*Eois*	sp 28	2	7	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
820	*Eois*	sp 30	-	5	6	3	-	-	1	1	-	-	-	-	-	1	-	-	-	-	-	1	-	-
415	*Eois*	sp 31	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
851	*Eois*	sp 32	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1
853	*Eois*	sp 34	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	8
854	*Eois*	sp 35	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	5
855	*Eois*	sp 36	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	1
975	*Eois*	sp 37	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	2
889	*Eois*	sp 38	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1	-	-
976	*Eois*	sp 40	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
977	*Eois*	sp 41	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
978	*Eois*	sp 42	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
399	*Eois*	sp cf *adimaria*	-	-	-	-	-	-	1	-	1	-	-	3	27	6	15	1	10	17	3	-	1	-
425	*Eois*	sp cf *catana*	-	-	1	-	1	-	-	2	-	-	1	-	-	1	-	-	-	-	-	-	-	-
398	*Eois*	sp cf *golosata*	-	-	-	-	4	2	-	3	4	8	4	2	4	-	8	1	5	4	-	-	-	-
402	*Eois*	sp cf *inflammata*	-	-	-	-	-	1	-	-	-	1	1	-	2	-	-	1	-	-	-	1	-	1
410	*Eois*	sp cf *lunifera* 01	-	-	-	-	-	-	-	-	-	-	3	-	11	1	-	1	-	2	-	-	-	-
411	*Eois*	sp cf *lunifera* 02	-	2	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
412	*Eois*	sp cf *lunifera* 03	-	-	1	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
419	*Eois*	sp cf *odalis*	-	-	-	-	1	-	-	-	-	2	-	-	1	-	-	-	-	-	-	-	-	-
381	*Eois*	sp cf *olivacea* 01	-	-	-	-	1	-	1	3	-	-	-	-	-	-	1	-	1	-	-	-	1	-
404	*Eois*	sp cf *plumbeofusa*	1	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-
379	*Eois*	sp cf *sagittaria* 01	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	1	-	-	2	-	-
378	*Eois*	sp cf *singularia*	-	-	1	-	1	5	1	1	-	-	1	-	1	-	-	-	-	1	-	2	1	-
387	*Eois*	*subcroceraria*	-	-	5	3	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	1
418	*Eois*	*tegularia* 01	-	-	-	-	1	1	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
961	*Eois*	*tegularia* 02	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
414	*Eois*	*trillista*	-	1	-	-	1	1	1	1	1	-	-	-	-	-	5	1	8	6	1	1	1	-
967	*Eois*	*veniliata*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-
422	*Eois*	*xanthoperata*	3	8	1	1	-	-	1	-	1	1	-	1	4	-	2	-	-	-	-	1	-	-
400	*Eois*	*yvata*	-	-	-	-	-	-	-	-	-	-	2	-	3	1	4	3	3	5	1	1	2	1
966	*Eois*	*zorra*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
680	*Erebochlora*	*simulator*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3
461	*Ersephila*	sp cf *prema*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-
484	*Euphyia*	*acerbata*	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	1	1	-	2	-	-
480	*Euphyia*	*alboscripta*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	2	1
697	*Euphyia*	*balteata*	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-	1	-	-	-	-
457	*Euphyia*	*cinerascens*	-	-	2	-	1	1	4	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
952	*Euphyia*	*infundibulata*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-
830	*Euphyia*	*porraceata*	6	15	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
633	*Euphyia*	*psyra*	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
466	*Euphyia*	*rojiza*	-	-	-	-	-	-	-	1	-	2	2	1	1	2	1	-	-	3	1	-	2	5
462	*Euphyia*	sp 01	-	-	-	-	1	-	-	1	2	-	-	1	4	-	6	-	1	3	2	1	2	3
463	*Euphyia*	sp 02	-	-	-	-	-	-	-	-	-	-	-	-	1	1	3	-	2	8	-	1	-	-
464	*Euphyia*	sp 03	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
465	*Euphyia*	sp 04	-	-	-	-	-	-	-	4	-	-	-	-	-	1	-	-	-	-	-	-	-	1
453	*Euphyia*	sp 05N	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
472	*Euphyia*	sp 08	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
473	*Euphyia*	sp 09	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
787	*Euphyia*	sp 12	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
494	*Euphyia*	sp cf *acerbata* 01	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	4	2	2	6
841	*Euphyia*	sp cf *acerbata* 02	-	-	-	-	-	-	-	-	1	1	-	-	-	2	-	-	-	-	-	-	-	-
953	*Euphyia*	sp cf *pontina*	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
460	*Euphyia*	*subguttaria*	11	11	20	15	1	-	-	-	1	-	-	-	-	-	1	-	-	-	2	2	5	3
452	*Euphyia*	*tujillaria*	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
813	*Euphyia*	*violetta*	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
954	*Euphyia*	*zalmoxis*	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
471	*Euphyia*	*zara*	-	-	-	-	-	-	-	1	-	-	-	-	-	-	3	-	-	-	-	1	-	-

703	*Eupithecia*	*acragas*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2	-	2	1
577	*Eupithecia*	*albirasa*	-	-	-	-	1	-	-	-	-	-	-	1	3	13	4	1	11	10	3	2	2	1
623	*Eupithecia*	*anita*	-	1	10	14	1	-	-	-	1	-	-	1	1	-	-	-	-	-	-	-	-	-
705	*Eupithecia*	*bullata*	-	-	-	1	-	-	-	2	-	1	-	1	1	1	-	-	-	1	-	-	-	-
554	*Eupithecia*	*casta*	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-
572	*Eupithecia*	*contexta*	-	-	-	-	-	1	-	1	1	1	1	5	9	10	-	4	5	2	1	-	-	2
647	*Eupithecia*	*cuneilineata*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1	-	-	-
566	*Eupithecia*	*cunina*	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-
652	*Eupithecia*	*cupreata*	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	1	1	-	-	-	-	-
567	*Eupithecia*	*descimoni*	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	1	4	1	-	-
559	*Eupithecia*	*disformata*	-	-	-	-	1	1	-	1	-	-	-	2	5	7	2	9	12	8	1	1	-	-
575	*Eupithecia*	*drastica*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-
556	*Eupithecia*	*duena*	1	-	-	-	2	-	-	-	-	-	1	-	4	-	3	2	4	3	9	5	6	14
557	*Eupithecia*	*galepsa*	-	-	-	-	1	-	-	-	-	1	-	-	1	-	-	-	1	3	-	-	1	3
679	*Eupithecia*	*hilaris*	-	-	-	-	-	-	-	-	-	-	1	-	-	6	-	7	-	6	-	-	-	-
569	*Eupithecia*	*hormiga*	-	-	-	-	3	1	-	-	-	-	2	-	2	5	-	-	1	2	1	1	2	-
564	*Eupithecia*	*junctifascia*	-	1	-	-	-	-	-	-	-	1	-	-	1	1	1	1	4	7	-	-	-	-
563	*Eupithecia*	*lachaumei*	-	-	-	-	-	-	-	2	-	-	-	-	1	1	-	-	-	-	-	-	-	-
661	*Eupithecia*	*nigrithorax*	1	2	-	-	-	-	-	1	1	-	-	-	1	-	-	-	-	-	-	-	-	-
614	*Eupithecia*	*ochrosoma*	-	-	-	1	4	1	2	2	2	-	5	1	3	3	1	1	3	-	2	-	-	-
648	*Eupithecia*	*pallidicosta*	-	-	-	-	1	-	-	-	1	2	4	8	8	15	6	4	1	4	-	-	-	-
561	*Eupithecia*	*penicilla*	-	-	-	-	-	-	-	2	2	-	2	4	1	7	1	-	6	-	-	-	-	-
550	*Eupithecia*	*rubellicincta*	-	-	-	-	8	1	3	13	3	2	15	3	17	16	15	4	13	41	25	18	6	13
555	*Eupithecia*	*sobrina*	-	-	-	-	-	-	-	1	-	-	-	-	2	-	-	-	-	-	4	2	1	2
576	*Eupithecia*	sp 01N	-	-	-	-	-	-	-	-	-	-	-	-	1	8	1	6	1	10	5	1	11	7
578	*Eupithecia*	sp 02	-	-	-	-	1	2	-	-	-	-	4	3	6	1	1	-	5	3	8	-	5	7
579	*Eupithecia*	sp 03	-	-	-	-	-	-	-	-	-	1	-	-	1	1	-	-	-	2	-	-	-	-
580	*Eupithecia*	sp 04	-	-	-	-	1	-	-	5	-	-	-	-	1	1	-	-	-	-	-	-	-	-
581	*Eupithecia*	sp 05	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	1	-
582	*Eupithecia*	sp 06	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	2	5	1
583	*Eupithecia*	sp 07	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	4	2	-	-
584	*Eupithecia*	sp 08	-	-	-	-	2	1	-	-	-	-	-	2	3	18	-	1	3	1	2	-	-	-
585	*Eupithecia*	sp 09	-	-	-	-	-	1	1	-	-	-	1	-	3	-	-	1	2	1	1	-	-	-
586	*Eupithecia*	sp 10	-	-	-	-	5	-	1	-	1	1	1	-	1	4	-	-	2	-	-	-	-	-
587	*Eupithecia*	sp 11	-	-	-	-	-	-	-	-	-	-	-	1	5	1	5	2	10	9	21	7	15	26
588	*Eupithecia*	sp 12	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
589	*Eupithecia*	sp 13	-	-	-	-	-	-	-	-	1	1	3	-	-	2	1	-	-	-	-	-	-	-
590	*Eupithecia*	sp 14	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
591	*Eupithecia*	sp 15	-	-	-	-	-	-	-	-	-	-	1	-	5	1	1	-	11	5	-	2	-	-
592	*Eupithecia*	sp 16	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	2	3	5
593	*Eupithecia*	sp 17	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
594	*Eupithecia*	sp 18	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-
596	*Eupithecia*	sp 20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	2
597	*Eupithecia*	sp 21	1	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
598	*Eupithecia*	sp 22	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	13	8	4	7
599	*Eupithecia*	sp 23	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1
600	*Eupithecia*	sp 24	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	5	-
601	*Eupithecia*	sp 25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	3	11
602	*Eupithecia*	sp 26	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
603	*Eupithecia*	sp 27	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	3	-
604	*Eupithecia*	sp 28	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
605	*Eupithecia*	sp 29	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
606	*Eupithecia*	sp 30	3	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
607	*Eupithecia*	sp 31	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
609	*Eupithecia*	sp 32	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
610	*Eupithecia*	sp 33	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
651	*Eupithecia*	sp 34N	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
615	*Eupithecia*	sp 38	-	-	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

616	*Eupithecia*	sp 39	-	-	2	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
617	*Eupithecia*	sp 40	9	4	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
618	*Eupithecia*	sp 41	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
619	*Eupithecia*	sp 42	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
620	*Eupithecia*	sp 43	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	1
621	*Eupithecia*	sp 44	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
622	*Eupithecia*	sp 45	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	1	-	1	-	-
624	*Eupithecia*	sp 47	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-
625	*Eupithecia*	sp 48	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-
626	*Eupithecia*	sp 49	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1
628	*Eupithecia*	sp 51	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
629	*Eupithecia*	sp 52	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2	1	-	3	-	-	8	1
631	*Eupithecia*	sp 54	-	-	-	-	-	-	-	1	1	-	-	-	-	2	1	-	-	1	-	-	-	-
632	*Eupithecia*	sp 55	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-
635	*Eupithecia*	sp 58	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
636	*Eupithecia*	sp 59	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
638	*Eupithecia*	sp 61	-	1	6	6	1	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-
640	*Eupithecia*	sp 62	-	-	-	-	1	-	1	-	-	1	-	-	3	-	-	-	-	-	1	-	-	-
642	*Eupithecia*	sp 64	-	-	-	-	-	-	-	-	1	-	-	1	5	2	4	1	8	6	13	11	25	31
643	*Eupithecia*	sp 65	-	-	-	-	-	-	-	-	-	-	-	1	2	4	5	3	6	11	6	1	6	4
645	*Eupithecia*	sp 67	-	-	-	-	6	1	2	10	-	-	1	-	1	2	-	-	1	-	-	-	-	-
646	*Eupithecia*	sp 68	-	3	-	-	6	9	2	4	3	-	3	-	1	1	-	1	-	-	1	-	3	-
650	*Eupithecia*	sp 72	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
653	*Eupithecia*	sp 75	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	8	8	4	18
654	*Eupithecia*	sp 76	-	-	-	-	4	1	1	5	1	-	1	1	1	1	-	-	-	1	-	-	-	-
656	*Eupithecia*	sp 78	-	-	-	-	3	-	-	1	5	-	-	-	1	3	-	-	1	-	-	-	-	-
657	*Eupithecia*	sp 79	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
658	*Eupithecia*	sp 80	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	2	-	-	-	-
659	*Eupithecia*	sp 81	-	1	-	-	1	-	-	-	3	5	2	-	3	2	-	-	1	-	7	4	1	1
660	*Eupithecia*	sp 82	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1	3	3
662	*Eupithecia*	sp 84	-	-	-	-	-	-	-	-	1	-	-	-	-	3	1	-	2	2	6	1	2	1
663	*Eupithecia*	sp 85	-	-	-	-	-	-	2	1	1	2	-	-	1	-	-	-	-	-	-	1	-	-
664	*Eupithecia*	sp 86	-	-	5	3	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
665	*Eupithecia*	sp 87	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
666	*Eupithecia*	sp 88	-	-	-	-	1	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-
669	*Eupithecia*	sp 91	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	4	1	8	4	-	2
670	*Eupithecia*	sp 92	-	-	-	-	1	-	-	-	-	1	3	2	-	6	-	-	-	-	-	-	-	-
671	*Eupithecia*	sp 93	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	3	1	-	-
672	*Eupithecia*	sp 94	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
674	*Eupithecia*	sp 96	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
677	*Eupithecia*	sp 99	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
678	*Eupithecia*	sp 100	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-
989	*Eupithecia*	sp 102	-	-	-	-	-	-	-	-	-	-	-	-	1	3	-	-	-	-	-	-	-	-
681	*Eupithecia*	sp 103	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
682	*Eupithecia*	sp 104	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	2	3	8
683	*Eupithecia*	sp 105	-	-	-	-	-	-	1	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-
571	*Eupithecia*	sp 106	-	-	-	-	-	-	-	-	-	1	-	2	3	5	-	-	-	-	-	-	-	-
870	*Eupithecia*	sp 107	-	-	-	-	-	-	-	-	-	-	-	2	-	1	-	-	-	-	-	-	-	-
871	*Eupithecia*	sp 108	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	1	-	2
872	*Eupithecia*	sp 109	-	-	-	-	-	-	-	-	-	-	4	-	-	1	-	-	-	-	-	-	-	-
874	*Eupithecia*	sp 111	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
875	*Eupithecia*	sp 112	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	4	8	5
876	*Eupithecia*	sp 113	-	-	-	-	-	-	-	-	-	-	1	1	6	7	3	1	5	2	3	1	3	3
877	*Eupithecia*	sp 114	-	-	1	-	-	-	-	-	-	-	1	-	3	1	-	1	3	2	-	1	-	-
878	*Eupithecia*	sp 115	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
879	*Eupithecia*	sp 116	-	-	-	-	-	-	-	-	1	-	2	-	1	3	2	4	2	5	2	-	7	2
891	*Eupithecia*	sp 119	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
892	*Eupithecia*	sp 120	-	-	1	-	2	-	-	3	1	-	-	-	1	-	-	-	-	-	-	-	-	-

893	*Eupithecia*	sp 121	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	3	2	2	-
896	*Eupithecia*	sp 124	-	-	-	-	-	-	-	-	-	-	-	-	3	3	-	-	-	-	-	-	-	-
897	*Eupithecia*	sp 125	-	-	-	-	1	-	2	-	1	1	8	2	5	2	-	-	1	1	2	-	-	-
898	*Eupithecia*	sp 126	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	2	1
899	*Eupithecia*	sp 127	-	-	-	-	-	-	-	1	1	-	-	-	3	1	-	-	8	3	4	1	1	2
900	*Eupithecia*	sp 128	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	5	7	3	10	5
901	*Eupithecia*	sp 129	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	2	-	1	-	2
902	*Eupithecia*	sp 130	-	-	-	-	1	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
641	*Eupithecia*	sp cf *albivirata*	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	1	2	-	-	-	-
573	*Eupithecia*	sp cf *contexta* 01	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-
574	*Eupithecia*	sp cf *contexta* 02	-	-	-	-	-	-	-	-	-	-	-	-	2	3	1	2	1	-	-	-	-	-
560	*Eupithecia*	sp cf *disformata*	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
565	*Eupithecia*	sp cf *junctifascia*	-	-	-	-	-	-	-	1	-	-	1	-	-	1	-	-	-	-	-	-	-	-
562	*Eupithecia*	sp cf *penicilla*	-	-	-	-	-	-	-	1	-	-	-	1	1	6	-	1	-	-	-	-	-	-
551	*Eupithecia*	sp cf *rubellicincta* 01	-	-	-	-	1	-	-	1	-	-	1	1	2	7	1	4	11	8	-	-	-	-
552	*Eupithecia*	sp cf *rubellicincta* 02	-	-	-	-	-	1	-	-	-	-	-	1	2	4	1	3	2	9	-	-	-	-
553	*Eupithecia*	sp cf *rubellicincta* 03	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
702	*Eupithecia*	sp cf *rubellicincta* 04	-	-	-	-	6	1	-	-	-	-	1	-	1	1	-	-	-	1	4	3	7	2
637	*Eupithecia*	*tenera*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	2
558	*Eupithecia*	*triangulifera*	-	-	-	-	-	-	-	-	-	-	2	1	1	4	1	-	1	6	-	-	-	1
568	*Eupithecia*	*trigenuata*	-	-	-	-	-	-	-	1	-	-	3	3	1	5	-	6	3	2	2	-	-	-
570	*Eupithecia*	*versiplaga*	-	-	1	-	-	-	-	-	-	-	2	-	-	3	1	-	-	1	5	-	2	2
667	*Eupithecia*	*yangana*	-	-	-	-	8	5	1	1	2	1	2	-	2	3	2	1	3	2	9	3	11	4
430	*Graphidipus*	*flaviceps*	-	-	-	1	-	1	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
431	*Graphidipus*	*graphidiparia*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
432	*Graphidipus*	*puncticulata*	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
435	*Hagnagora*	*anicata*	-	-	-	-	-	-	-	1	-	1	1	1	5	1	-	-	3	1	4	4	2	3
434	*Hagnagora*	*croceitincta*	-	-	-	-	-	-	-	1	1	1	2	-	1	3	-	-	-	-	1	-	-	-
433	*Hagnagora*	*ephestris*	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	1	1	2	-
436	*Hagnagora*	*mortipax mortipax*	-	-	1	2	1	-	-	-	11	1	-	-	-	1	-	-	-	-	-	-	-	-
468	*Hammaptera*	*praderia*	-	-	-	-	1	-	5	9	4	2	-	-	-	-	-	-	-	-	-	-	-	-
986	*Hammaptera*	*probataria*	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
956	*Hammaptera*	*repandaria*	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
477	*Hydriomena*	*multangulata*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-
474	*Hydriomena*	*polyphonata*	-	-	-	-	-	-	-	-	1	1	-	-	-	1	-	-	-	-	-	-	-	-
479	*Hydriomena*	*prelatata*	-	-	-	-	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
478	*Hydriomena*	sp 03	-	1	2	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	2	2	7
788	*Hydriomena*	sp 05	-	-	1	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
476	*Hydriomena*	sp cf *algosa*	-	-	-	-	1	-	1	-	-	-	1	1	-	2	-	-	1	1	3	9	19	28
475	*Hydriomena*	sp cf *cydra*	-	-	2	-	2	-	-	3	-	-	-	-	1	-	2	-	-	3	-	-	1	-
445	Larentiinae	sp 01	1	-	-	-	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
450	Larentiinae	sp 02N	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
482	Larentiinae	sp 08	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
495	Larentiinae	sp 10	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
812	Larentiinae	sp 12	-	-	2	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
815	Larentiinae	sp 15	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
811	Larentiinae	sp 16	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
983	Larentiinae	sp 24	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
194	*Leucoctenorrhoe*	*quadrilinea*	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
715	*Obila*	*floccosaria*	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
951	*Obila*	*umbrinata*	3	1	-	-	2	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
442	*Orthonama*	*dicymanta*	-	-	-	-	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
441	*Orthonama*	*effluata*	-	1	2	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
984	*Perizoma*	*arcillata*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
492	*Perizoma*	*basiplaga*	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-	1	1	2	3	2	3	6
537	*Perizoma*	*cinerolimitata*	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
486	*Perizoma*	*emmelesiata*	-	-	-	1	20	7	-	-	1	-	1	-	1	-	-	-	-	1	-	-	1	4
493	*Perizoma*	*fallax*	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	9	3	8	1	3	2	4

485	*Perizoma*	*interlauta*	-	-	-	-	-	-	-	-	-	-	-	-	2	-	1	1	1	3	1	1	-	-
491	*Perizoma*	sp 01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	3	2	3	1
519	*Perizoma*	sp 06	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-
973	*Perizoma*	sp 07	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-
487	*Perizoma*	*zenobia*	-	-	-	-	11	6	1	2	7	2	4	-	7	1	-	2	8	8	2	7	1	3
711	*Priapodes*	sp cf *longipalpata*	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
516	*Psaliodes*	*albistriga*	-	-	-	-	-	-	-	-	-	1	-	1	-	-	2	-	1	1	-	-	-	-
979	*Psaliodes*	*analiplaga*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
862	*Psaliodes*	*annuligera*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
549	*Psaliodes*	*biconalis*	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	1	-	1	-
496	*Psaliodes*	*catenifera*	1	-	2	2	2	1	1	-	11	5	1	-	3	1	-	1	-	1	5	5	-	1
539	*Psaliodes*	*cedaza*	-	-	-	-	1	-	1	1	6	7	11	1	7	25	19	7	22	35	41	18	7	11
538	*Psaliodes*	*confusa*	-	-	-	1	-	-	4	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
532	*Psaliodes*	*crassinota*	-	-	-	-	-	1	1	2	-	1	1	2	-	8	-	1	-	-	-	-	-	-
489	*Psaliodes*	*cronia*	-	-	4	2	2	1	-	-	2	2	6	3	13	2	5	-	3	2	-	1	-	-
545	*Psaliodes*	*cupreipennis*	-	-	-	-	2	1	1	2	5	1	2	-	2	1	-	-	1	-	-	-	-	-
523	*Psaliodes*	*cynthia*	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
531	*Psaliodes*	*detractata*	-	-	-	-	-	-	-	1	1	1	3	-	2	6	-	4	1	5	2	-	1	3
806	*Psaliodes*	*fractilinea*	-	-	-	-	-	-	-	-	-	-	1	-	1	1	-	-	-	-	-	-	-	-
100	*Psaliodes*	*infantula*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	1	-	2
488	*Psaliodes*	*inundulata*	-	-	1	-	-	1	4	5	6	1	5	-	2	3	3	-	-	1	-	-	-	-
542	*Psaliodes*	*liebra*	-	-	-	-	-	1	-	-	-	-	-	-	-	1	1	3	-	1	4	4	2	3
863	*Psaliodes*	*lignosata*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
528	*Psaliodes*	*lisera*	-	-	-	-	-	-	-	-	-	-	2	-	-	5	-	-	1	-	-	-	-	-
506	*Psaliodes*	*magnipalpata*	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	1	-	1	3	2	1	-
509	*Psaliodes*	*miniata*	-	1	-	-	-	2	-	-	5	2	6	2	1	5	1	1	2	-	-	1	-	1
699	*Psaliodes*	*nexilinea*	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
698	*Psaliodes*	*nictitans*	-	-	-	1	-	1	-	1	1	-	5	2	13	16	10	2	6	4	1	1	-	-
541	*Psaliodes*	*perfuscata*	-	-	-	-	1	-	-	-	2	3	3	2	6	4	15	4	17	18	4	5	4	9
498	*Psaliodes*	*rica*	-	1	-	-	-	-	-	-	-	1	1	-	-	7	2	2	-	1	-	-	-	-
881	*Psaliodes*	*samaniegoi*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1
503	*Psaliodes*	*semirasa*	-	-	-	-	-	-	1	1	8	-	-	-	-	-	-	-	-	-	-	-	-	-
864	*Psaliodes*	*simplex*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
627	*Psaliodes*	sp 01N	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-
1026	*Psaliodes*	sp 02N	-	-	-	-	-	-	-	1	-	-	1	1	1	-	-	-	-	-	-	-	-	-
508	*Psaliodes*	sp 03N	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	4	1
501	*Psaliodes*	sp 06	-	-	-	-	1	1	-	1	2	2	3	2	2	8	2	1	5	3	-	-	-	-
502	*Psaliodes*	sp 07	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-
504	*Psaliodes*	sp 09	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	4	4	8	3	3
505	*Psaliodes*	sp 10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	3	1	-	-	-
507	*Psaliodes*	sp 12	-	-	1	-	1	-	-	-	-	-	-	-	-	1	-	1	-	1	1	3	1	1
510	*Psaliodes*	sp 15	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
511	*Psaliodes*	sp 16	-	-	-	-	-	-	-	2	-	-	-	-	1	-	-	-	-	-	-	-	-	-
514	*Psaliodes*	sp 19	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3
515	*Psaliodes*	sp 20	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-
517	*Psaliodes*	sp 22	-	-	1	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
518	*Psaliodes*	sp 23	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
520	*Psaliodes*	sp 25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	7	4	-	4
521	*Psaliodes*	sp 26	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
522	*Psaliodes*	sp 27	-	-	-	-	-	-	-	-	-	-	-	1	-	1	1	-	-	-	-	-	-	-
524	*Psaliodes*	sp 29	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
525	*Psaliodes*	sp 30	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-
526	*Psaliodes*	sp 31	-	-	-	-	-	1	-	2	-	-	-	-	2	-	3	-	-	-	-	1	-	-
527	*Psaliodes*	sp 32	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	1	2	-	-	1	-
530	*Psaliodes*	sp 35	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	1	1	1	1
700	*Psaliodes*	sp 38	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
865	*Psaliodes*	sp 45	1	-	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
866	*Psaliodes*	sp 46	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1

867	*Psaliodes*	sp 47	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1
868	*Psaliodes*	sp 48	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
982	*Psaliodes*	sp 50	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
540	*Psaliodes*	sp cf *cedaza* 02	-	-	2	-	1	-	1	6	2	3	2	-	1	-	-	-	-	-	-	-	-	-
543	*Psaliodes*	sp cf *cedaza* 05	-	-	-	-	-	-	-	-	-	-	-	1	-	2	4	-	2	4	6	1	-	1
544	*Psaliodes*	sp cf *cedaza* 06	-	-	-	-	-	-	-	6	5	8	-	2	7	1	1	1	-	-	2	-	-	-
547	*Psaliodes*	sp cf *cedaza* 09	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
548	*Psaliodes*	sp cf *cedaza* 10	-	-	-	-	-	-	-	-	-	-	-	1	1	-	5	1	6	5	2	3	1	4
535	*Psaliodes*	sp cf *crassinota* 04	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	2	5	5
536	*Psaliodes*	sp cf *crassinota* 05	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
490	*Psaliodes*	sp cf *cronia*	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
529	*Psaliodes*	sp cf *disrupta*	-	-	-	-	-	-	-	-	-	-	1	1	-	7	1	-	-	-	-	-	-	-
499	*Psaliodes*	sp cf *endotrichiata*	-	-	-	-	-	-	-	-	-	1	1	-	5	4	11	5	21	11	5	3	2	5
534	*Psaliodes*	sp cf *paleata*	-	1	-	-	3	2	5	2	20	-	-	-	1	2	1	-	2	-	2	-	-	-
497	*Psaliodes*	sp cf *tripita*	-	-	-	-	8	2	-	4	2	-	-	-	2	-	-	-	-	-	-	-	-	-
533	*Psaliodes*	*trilunata*	-	-	-	-	-	-	-	-	1	2	-	2	-	2	-	2	3	1	19	9	5	6
980	*Psaliodes*	*tripartita*	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
701	*Psaliodes*	*tripita*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	1	-	-
444	*Ptychorrhoe*	*blosyrata confirmata*	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
437	*Rhinura*	*populonia*	-	-	2	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1020	*Rhopalodes*	*ligereza*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
443	*Rhopalodes*	sp 01	-	-	-	-	-	-	-	-	1	-	1	-	5	6	2	3	4	1	2	1	-	3
712	*Rhopalodes*	sp cf *concinna*	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
513	*Smileuma*	*plagifracta*	-	-	-	-	-	-	1	1	-	-	-	-	2	1	-	1	1	-	2	3	1	1
448	*Spargania*	*cultata*	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
470	*Spargania*	*cultata*	-	-	-	-	-	-	3	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
454	*Spargania*	*flavolimbarioides*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
883	*Spargania*	*leucocyma*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-
451	*Spargania*	*narangilla*	-	-	-	1	-	-	2	4	2	2	2	3	-	-	-	-	-	-	-	-	-	-
469	*Spargania*	sp 03	-	-	2	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
455	*Spargania*	sp 06	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-
789	*Spargania*	sp 11	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
850	*Spargania*	sp 12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	1
884	*Spargania*	sp 14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
467	*Spargania*	sp cf *intensa*	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-
325	*Trichorrhages*	*pizzarena*	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
447	*Trichozoma*	*picaria*	-	-	2	-	2	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
440	*Triphosa*	*affirmata*	-	-	-	-	-	-	1	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-
446	*Triphosa*	*pallidivittata*	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
481	*Triphosa*	sp 01N	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
	OENOCHROMINAE																							
824	*Ergavia*	*roseivena*	4	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
196	*Racasta*	*rhodosticta*	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1	-	-	-	-
195	*Racasta*	*spatiaria*	-	1	1	-	-	-	-	-	-	-	-	-	2	4	2	-	-	1	1	-	-	1
	STERRHINAE																							
29	*Cyclophora*	*acutaria*	-	-	-	-	1	3	3	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
28	*Cyclophora*	*coecaria*	1	-	3	3	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
972	*Cyclophora*	sp 01	3	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
6	*"Cyclophora"*	*ferruginata*	-	-	-	-	-	-	-	-	-	-	3	3	-	1	-	-	-	-	-	-	-	-
15	*"Cyclophora"*	*gigantula gigantula*	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	1	-	-	-
13	*"Cyclophora"*	*globaria*	-	-	-	-	-	1	1	-	-	-	2	2	-	-	1	-	-	-	1	-	1	3
8	*"Cyclophora"*	*gracilinea*	-	-	-	-	-	-	1	-	1	2	4	-	7	5	-	1	1	-	-	-	1	4
5	*"Cyclophora"*	*griseomixta*	-	-	-	-	-	-	-	-	-	-	-	1	3	-	-	-	-	-	-	-	-	-
11	*"Cyclophora"*	*lancearia*	-	-	-	-	-	-	-	-	-	1	-	1	1	-	-	-	-	1	-	-	-	-
18	*"Cyclophora"*	*megista*	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
16	*"Cyclophora"*	*rhodostigma*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	1	-
14	*"Cyclophora"*	*seposita*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-

1	*"Cyclophora"*	sp 01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
2	*"Cyclophora"*	sp 02	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
3	*"Cyclophora"*	sp 03	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
843	*"Cyclophora"*	sp 06	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
844	*"Cyclophora"*	sp 07	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1	3
845	*"Cyclophora"*	sp 08	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1	1	1
4	*"Cyclophora"*	sp cf *scintillans*	-	-	-	-	-	-	-	-	-	-	1	1	2	1	2	2	2	-	-	-	-	1
12	*"Cyclophora"*	*sypharia*	-	1	-	-	-	-	-	-	1	1	-	2	1	-	1	-	-	1	-	-	-	-
17	*"Cyclophora"*	*torsivena*	-	1	-	1	1	-	3	-	1	2	4	-	2	2	1	-	-	-	-	-	-	-
44	*Dithecodes*	*distracta*	-	6	11	8	2	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
36	*Idaea*	*arhostioides*	-	1	-	1	2	-	1	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-
40	*Idaea*	*fimbriata*	-	-	2	-	-	-	1	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-
41	*Idaea*	*quadrirubata*	-	1	2	-	2	2	-	-	-	-	-	-	1	-	-	-	-	-	4	-	1	-
34	*Idaea*	*recrinita*	-	2	3	-	1	4	7	7	24	11	57	22	58	60	29	15	36	43	2	1	-	-
969	*Idaea*	sp 01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	5	1	3
35	*Idaea*	sp 02	-	-	-	-	1	1	22	4	15	3	4	3	-	1	-	-	-	-	-	-	-	-
970	*Idaea*	sp 03	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	1
971	*Idaea*	sp 04	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2	1
31	*Idaea*	sp 05	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
634	*Idaea*	sp 06N	-	1	2	1	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-
37	*Idaea*	sp cf *abnormipennis*	-	3	1	-	1	-	1	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-
676	*Idaea*	sp cf *caudata*	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
38	*Lobocleta*	*costalis*	1	3	5	1	-	2	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
373	*Odontoptila*	sp 01	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
736	*Odontoptila*	sp 02	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
25	*Scopula*	sp 01	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
26	*Scopula*	sp 02	-	1	-	-	1	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-
321	*Scopula*	sp 03	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
27	*Scopula*	*subquadrata*	-	-	2	1	3	5	1	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-
20	*Semaeopus*	*calavera*	1	2	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
23	*Semaeopus*	*dentilinea*	-	1	-	-	-	-	-	2	-	-	-	3	3	-	1	-	-	1	-	-	-	-
1000	*Semaeopus*	*hypoderis*	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
22	*Semaeopus*	*ladrilla*	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	1	-	1	-	1	-
713	*Semaeopus*	*redundata*	-	-	30	19	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
24	*Semaeopus*	sp 01	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-
1035	*Semaeopus*	sp 07	1	2	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
728	*Semaeopus*	sp cf *hypoderis*	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
21	*Semaeopus*	*verbena*	-	-	-	-	-	-	-	-	-	-	-	-	2	-	1	-	-	1	-	-	-	-
1036	Sterrhinae	sp 05	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1037	Sterrhinae	sp 06	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1038	Sterrhinae	sp 07	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1039	Sterrhinae	sp 08	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
714	*Tricentra*	*gavisata*	-	2	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
43	*Tricentra*	sp 01	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	2	-	-	-	-	-
804	*Tricentra*	sp 03	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
42	*Tricentrogyna*	*collustrata*	-	-	-	1	2	3	-	1	2	-	-	-	-	-	1	1	-	1	-	-	-	-
39	*Tricentrogyna*	*nigricosta*	1	-	3	2	-	1	-	-	4	-	-	1	-	-	-	-	-	-	-	-	-	-

Appendix 3 List of the most abundant species (total number of specimens caught ≥50), sorted by their altitudinal ranges. First and second row: sites where moths were sampled, ordered by altitude of the sites (from 1,040 m to 2,677 m above sea level), see Chapter 4. Elevational levels where species were recorded are shaded dark grey. Light grey: no records within the elevational range of the species. Printed in **bold** is each site with the highest number of specimens. Further explanations: see Appendix 2.

			1		2		3		4		5		6		7		8		9		10		11	
ID	Genus	Species	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b
730	*Iridopsis*	*anaisaria*	30	**62**																				
741	*Aplogompha*	*riofrio*	25	**43**																				
740	*Aplogompha*	*lafayi*	34	83		1																		
257	*Iridopsis*	*gaujoni*	27	**100**	1	3	4	3							1									
887	*Physocleora*	sp 07		4	**66**	16	1			1		2	2		1	1								
374	*Eois*	*borrata*	2	3			1	2	1	1		1	5	2	**29**	2	16	3	3	4				
351	*Lissochlora*	*pectinifera*	1	11	4	1		1	1	4	1		3	2	**16**	4	6	2	4	8				
112	*Isochromodes*	sp 11	1	**17**	2	1			3	1	2	1	11	1	3	12		1	4	2				
58	*Oxydia*	*trychiata*		15	**21**	14	6	1	12	4	12	15	11	3	20	9			3	4				
34	*Idaea*	*recrinita*		2	3		1	4	7	7	24	11	57	22	58	**60**	29	15	36	43	2	1		
180	*Mesedra*	sp 01	1	1	3	3	1		3	4	**23**	3	5	9	19		3		2	8			3	1
460	*Euphyia*	*subguttaria*	11	11	**20**	15	1				1						1				2	2	5	3
84	*Herbita*	*chiomaria*	1									2		2	5	10	8	7	8	**17**	3	11	3	1
556	*Eupithecia*	*duena*	1				2						1		4		3	2	4	3	9	5	6	**14**
352	*Lissochlora*	*latuta*	1	6	3	2	3	5	7	6	9	3	23	7	**25**	3	20	6	10	13	3	3	16	14
125	*Sabulodes*	*thermidora*		1			35	**39**	2	7	8	1	3		7	3	7	1		4				2
192	*Lomographa*	*tributaria*		4	2	2	5	6	4	5	6	1	8		9	**27**	4	4	4	5	5	6	3	4
333	*Physocleora*	*pulverata*		4	5		8	9	**90**	85	39	21	29	21	22	24	4		4	6	2	1	1	3
358	*Chloropteryx*	*opalaria*			5	2	14	18	14	**21**	15	3	2		2									
334	*Physocleora*	sp 01			2	3	1	2	18	**26**	1	2		1	1									
698	*Psaliodes*	*nictitans*				1		1		1	1		5	2	13	**16**	10	2	6	4	1	1		
396	*Eois*	*golosata*			1				4	5	10	3	7	9	**55**	9	37	4	17	10	4	1	2	1
355	*Nemoria*	*aturia*			2			2	1	2	2		1		7	3	7	1	**8**	**8**	6	1	1	1
332	*Nematocampa*	sp cf *confusa*					1	1	2		**20**	3	13	16	5	13								
35	*Idaea*	sp 02					1	1	**22**	4	15	3	4	3		1								
89	*Prochoerodes*	*cristata*						3	1	4	3	11	6	1	5	**17**	1							
187	*Lomopgrapha*	*bicineata*					1	1		2	3	3	5	1	8	**21**	4	2	5	4				
648	*Eupithecia*	*pallidicosta*					1				1	2	4	8	8	**15**	6	4	1	4				
190	*Lomopgrapha*	*chartularia*					1		2	2		7	16	20	**35**	9	2		3	4				
46	*Phyllodonta*	sp cf *flabellaria* 01						1	1			3	**15**	3	8	11	4	2	6	9	2			
559	*Eupithecia*	*disformata*					1	1		1				2	5	7	2	9	**12**	8	1	1		
577	*Eupithecia*	*albirasa*					1							1	3	**13**	4	1	11	10	3	2	2	1
313	*Patalene*	*hamulata*					2	1		1		2	**14**	1	5	13	1	4	2	6				1
487	*Perizoma*	*zenobia*					**11**	6	1	2	7	2	4		7	1		2	8	8	2	7	1	3
539	*Psaliodes*	*cedaza*					1		1	1	6	7	11	1	7	25	19	7	22	35	**41**	18	7	11
550	*Eupithecia*	*rubellicincta*					8	1	3	13	3	2	15	3	17	16	15	4	13	**41**	25	18	6	13
541	*Psaliodes*	*perfuscata*					1				2	3	3	2	6	4	15	4	17	**18**	4	5	4	9
108	*Isochromodes*	*crassa*					2				17	3	3	2	12	5	2	2	17	**20**		3	2	1
667	*Eupithecia*	*yangana*					8	5	1	1	2	1	2		2	3	2	1	3	2	9	3	**11**	4
397	*Eois*	*azafranata*					2			1		1	10	16	**66**	30	53	54	35	55	7	8	5	10
303	*Cidariophanes*	*indentata*					1		1	1		3	20	6	38	24	28	11	30	**31**	3	2	1	1
476	*Hydriomena*	*sp cf algosa*					1		1				1	1		2			1	1	3	9	19	**28**
131	*Oenoptila*	*leprosata*								1			1		4	8	6	9	13	**21**				
172	*Macaria*	sp cf *bejucoaria*							1	2	3	5	**10**	6	9	6	4	1	1	1	1			
399	*Eois*	sp cf *adimaria*							1		1			3	**27**	6	15	1	10	17	3		1	
80	*Bonatea*	*duciata*									4	11	10	3	14	**15**	2		1	3				
113	*Heteroctenia*	*pectinicornata*									1	1	11	2	14	**18**	6	7	5	5	7	4	6	5
533	*Psaliodes*	*trilunata*									1	2		2		2		2	3	1	19	9	5	6
605	*Eupithecia*	sp 29									1			1	5	2	4	1	8	6	13	11	25	**31**
499	*Psaliodes*	sp cf *endotrichiata*										1	1		5	4	11	5	**21**	11	5	3	2	5
193	*Lomographa*	*nubimargo*												1	9	**15**	6	4	5	10				
678	*Eupithecia*	sp 100												1	5	1	5	2	10	9	21	7	15	**26**
576	*Eupithecia*	sp 01N													1	8	1	6	1	**10**	5	1	11	7

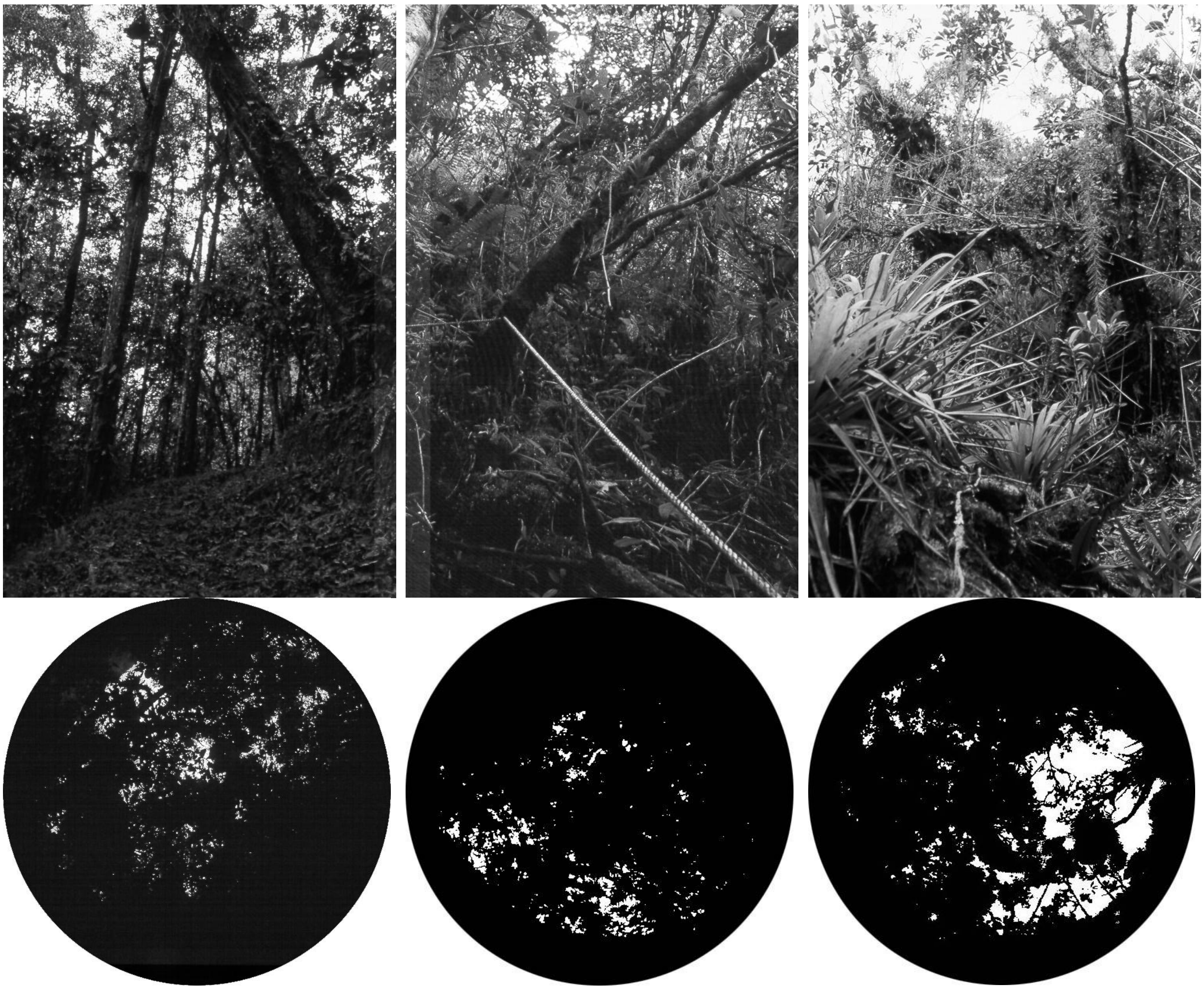
Appendix 4 Observed diurnal species of Geometridae in the study area in South Ecuador. A total of 49 specimens representing 25 species were recorded in 1999 and 2000. Only one of the listed species was also recorded in light-traps: the ennomine moth *Erycinopsis diaphana*. Similar to the patterns observed in night-active species (Chapter 4), Ennominae tend to dominate at the lower altitudes, whereas Larentiinae (in particular *Erateina* species) dominate at medium to high altitudes. D. Bartsch and C.L. Häuser collected a part of the moths, and J. Wojtusiak helped to identify the *Erateina* species. Real elevational ranges and flight periods are expected to be considerably larger than those observed.

Species	n	Observed range (m)	Observed in months
Ennominae (11 species)			
Eudule ficulnea Druce	2	1,550-1,900	x, xii
Eudule orilochina Druce	2	1,550-1,900	x, xii
Eubaphe tritonia Druce	3	1,850-1,900	x, xii
Siosta bifasciata Latreille	1	1,000-1,200	xii
Siosta acera Boisduval	1	1,200	x
Devarodes sp. 01	2	1,800-2,000	xi
Ennominae sp. 01	1	1,880-2,000	xi
Ennominae sp. 02	1	1,000-1,200	xii
Erycinopsis diaphana Felder	2	1,850-1,880	xi, xii
Erycinopsis sp. 01	1	1,000-1,200	xii
Erycinopsis sp. 02	4	1,000-1,200	xii
Larentiinae (13 species)			
Heterusia conna Druce	1	1,880-2,000	xi
Heterusia sp. 01	2	1,000-1,200	xii
Heterusia sp. 02	1	1,000-1,200	xii
Stamnodes sp. near *gandialis* Prout	2	1,830-1,850	x, xii
Erateina siliquata Guenée	9	1,800-1,850	ix, x, xii
Erateina medama Druce	1	1,900	x
Erateina radiaria Herrich-Schäffer	2	1,800-1,900	ix, x
Erateina sp. near *siliquata* Guenée	1	1,880	xi
Erateina artabates Druce	2	1,890	x
Erateina zoraidina Bastelberger	1	2,165	vi
Erateina sp. near *zoradina* Bastelberger	1	1,880	xi
Erateina melanocera Bastelberger	2	1,880-1,990	vi, xi
Erateina drucei Thierry-Mieg	1	1,800	xi
Sterrhinae (1 species)			
Smicropus ochra Druce	3	1,000-1,200	xii

Appendix 5 Short structural characterisation of sampling sites. Visible sky is a measure that reflects canopy closure, and was calculated from hemispherical photographs using the HemiView program (Delta-T Devices 1999). Values are available only for 19 out of 22 sites because of technical problems when photographs were taken. Average values (from five photographs each) tend to be low at most of the lower sites and rise with altitude. However, some of the lower sites are characterised by higher average values of visible sky. This is due to anthropogenic disturbance (sites 1a, 1b, 2a, 4a and 4b), or due to closeness of sites to natural gaps (the rivulet Rio San Francisco). Localities: **B** Bombuscaro, **S** road between Loja and Zamora, **T1**, **T2** transect paths in the area of the Estación Científica San Francisco.

Site #	Locality	Altitude (m)	Visible Sky	SD	Closest plot Paulsch (2002)	Altitude (m)	Forest structure according to Paulsch (2002)
1a	B	1,040	0.08	0.05	-	-	-
1b	B	1,040	0.07	0.03	-	-	-
2a	S	1,380	0.22	0.16	-	-	-
2b	S	1,380	0.06	0.01	-	-	-
3a	T1	1,800	0.17	0.16	-	-	-
3b	T2	1,800	0.21	0.08	-	-	-
4a	T2	1,850	0.08	0.01	N25	1,830	Primary ravine forest at higher altitudes
4b	T1	1,875	0.09	0.05	N110	1,840	Primary ravine forest at lower altitudes
5a	T1	2,005	0.04	0.01	N68	1,970	Ravine forest under human influence
5b	T2	2,005	0.05	0.01	N108	2,040	Primary ravine forest at lower altitudes
6a	T1	2,112	0.07	0.03	N137	2,080	Mesophyll ridge forest
6b	T2	2,113	0.05	0.01	N82	2,100	Macrophyll ridge forest
7a	T2	2,180	0.07	0.02	N83	2,170	Microphyll ridge forest
7b	T1	2,212	0.13	0.07	N138	2,180	Microphyll ridge forest
8a	T2	2,290	0.17	0.08	N113	2,230	Microphyll ridge forest
8b	T1	2,308	0.13	0.07	N86	2,310	Microphyll ridge forest
9a	T1	2,375	0.28	0.13	N116	2,240	Microphyll ridge forest
9b	T2	2,387	0.38	0.04	N87	2,380	Microphyll ridge forest
10a	T1	2,524	-	-	N88	2,450	Microphyll ridge forest
10b	T1	2,558	-	-	N90	2,500	Microphyll ridge forest
11a	T1	2,671	0.76	0.18	N89	2,600	Microphyll ridge forest
11b	T1	2,677	-	-	N135	2,650	Microphyll ridge forest

Habitat photographs and hemispherical photographs of three selected sites at different altitudes taken in November 2000: sites 1a (1,040 m), 5a (2,005 m), 7a (2,180 m). Exact geographical positions are provided in Chapter 4, Table 1. Along the elevational gradient, structure and composition of the vegetation change significantly. The hemispherical photographs document that canopy closure decreases (see Table above). The leaves of trees become smaller as altitude increases (Paulsch 2002), and the tree crown height decreases with altitude: while tree crowns in forests at the lowest altitudes reach heights of 25 m (D. Piechowski pers. comm.), trees in the Microphyll ridge forest reach only heights of 10-15 m (Paulsch 2002). The floristical composition also changes significantly. The diversity of tree and liana species decreases (Homeier in prep., Matezki in prep.), while the diversity of epiphytic plants such as Orchidaceae and Bromeliaceae is very high throughout the whole gradient (Werner 2002). A single tree species becomes dominant at sites in Microphyll ridge forest (Cyrillaceae: *Purdiaea nutans*).



Erklärung

Hiermit erkläre ich, dass ich die vorliegende Arbeit selbstständig verfasst und keine anderen als die von mir angegebenen Quellen und Hilfsmittel benutzt habe.

Ferner erkläre ich, dass ich nicht anderweitig versucht habe, mit oder ohne Erfolg eine Dissertation einzureichen oder mich der Doktorprüfung zu unterziehen.

Bayreuth, den 10. April 2002