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No genetic differentiation among populations up to 300 km apart in three species of carrion beetles

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Abstract

1. Habitat fragmentation and loss globally threatens biodiversity and ecosystem functioning. Fragmentation disrupts gene flow and isolates populations, endangering species persistence. Dispersal ability is critical for species to maintain gene flow among populations and colonising new habitats. However, most species' dispersal abilities are unknown, raising the question of whether species are dispersal or habitat limited.
2. Carrion beetles recycle animal necromass, an important ecosystem function. In theory, species depending on ephemeral resources such as carrion have good dispersal abilities to colonise new habitat patches regularly. However, little is known about the dispersal capacity of carrion beetles.
3. To infer such dispersal abilities, we investigated the population genetic structure of three common carrion beetles (Coleoptera: Staphylinidae: Silphinae): *Nicrophorus vespilloides* Herbst, *Necrodes littoralis* Linnaeus and *Oiceoptoma thoracicum* Linnaeus. We sampled individuals using liver-baited pitfall traps and laid out carcasses in 47 sites in four regions in southern Germany. The distances between sampling sites ranged from 100 m to 320 km. We used microsatellite markers to assess population genetic structure and gene flow at local and regional spatial scales. Markers were newly developed for *N. littoralis* and *O. thoracicum*. Pairwise F_{ST}, AMOVA and

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DAPC analyses revealed no significant population genetic structure within all three species, indicating no limitation in gene flow, even over long distances.

4. Our data suggest excellent dispersal abilities in all three species without critical spatial limitation at the regional scale of our study. This implies that carrion management should focus more on habitat amount rather than spatial arrangements for the conservation of carrion insects.

KEYWORDS

carrion decomposition, microsatellite analysis, *Necrodes littoralis*, necromass, *Nicrophorus vespilloides*, *Oiceoptoma thoracicum*

INTRODUCTION

One of the main human-induced biodiversity threats is habitat fragmentation, the related habitat isolation and loss of habitat amount (Díaz et al., 2019; Fahrig, 2019; Fahrig et al., 2019; Pimm et al., 2014). A key trait of organisms that allows them to deal with habitat fragmentation and habitat isolation is dispersal (Thomas, 2000). Dispersal maintains gene flow among distant habitats and allows the colonisation of new habitats. Therefore, dispersal affects population dynamics, extinction risk and species distributions (Hanski et al., 1994).

Dispersal may be influenced by landscape configuration, habitat preferences and resource use (Finand et al., 2024; Reyes et al., 2023; Travis et al., 2013). Species living in long-lasting and stable habitats are often associated with low dispersal abilities and propensity, whereas species in short-lived, ephemeral habitats should have better dispersal abilities and thus longer dispersal distances (Denno et al., 1996; Feldhaar & Schauer, 2018; Southwood, 1962). Furthermore, the amount of available habitat and the habitat requirements affect how far individuals of a species must disperse (Marten et al., 2006). If a species is specialised in a certain type of habitat, which is also rare, isolated or short-lived, this species should have good dispersal abilities (Barbaro & van Halder, 2009; Büchi & Vuilleumier, 2016; Feldhaar & Schauer, 2018; Samways & Lu, 2007).

Dispersal distances of up to several dozens of kilometres were recorded for some bark beetles (Scolytinae) (Chase et al., 2017; Meurisse & Pawson, 2017; Nilsen, 1984), which often use fresh deadwood of various tree species that is often ephemeral and scattered in space (Raffa, 1993). For true bugs (Hemiptera) and jewel beetles (Buprestidae) long-distance dispersal flights are reported for those species using the bark of deadwood or freshly burnt stumps (Gossner & Damken, 2018; Schmitz & Bousack, 2012; Seibold et al., 2014). Furthermore, for house flies (Muscidae), visiting exposed carrion, dispersal distances can reach up to 7 km (Nazni et al., 2005). Even longer distances (up to 63.5 km) have been detected for blowflies (Braack & Retief, 1989). Still, studies about dispersal distances of species inhabiting ephemeral habitats are rare.

One important ecosystem function is the decomposition of necromass (Benbow et al., 2019; von Hoermann et al., 2023) – dead organic material such as deadwood, dung or carrion. Carrion decomposition is a critical factor in the nutrient cycle of any ecosystem, achieved mainly through microbes, invertebrates and vertebrates (Barton & Bump, 2019). It allows nutrients and energy of deceased animals to re-enter the nutrient pool of the ecosystem (Reimchen et al., 2003). Carrion is a nutrient-rich resource for a multitude of necrophilous insects, facultative and obligate scavengers, but it also has long-term effects on soil, soil microbiome, plants, mammals, birds and fungal communities (Barton et al., 2013; Benbow et al., 2019; Elbroch et al., 2017). The spread of diseases is limited through the rapid consumption of carcasses, which prevents soil and water contamination (Buechley & Şekercioğlu, 2016; Le Sage et al., 2019; Ogada et al., 2012). Compared to leaf litter or deadwood, carrion has higher contents of macronutrients, for example, nitrogen and phosphorus, and decomposes much faster, leading to a faster availability of nutrients but also a spatially and temporally more limited resource (Carter et al., 2007; Moore et al., 2004; Parmenter & MacMahon, 2009).

In addition to the effects on nutrient cycles, carrion provides a resource pulse, creating a biodiversity hotspot (Olea et al., 2019; Stiegler et al., 2020; von Hoermann et al., 2021, 2023) for bacteria, fungi, arthropods, birds and mammals (Barton et al., 2013; Barton & Bump, 2019; Carter et al., 2008). As the process of decomposition is continuous, carrion can offer heterogeneous resources to species specialised on early, medium and late stages of decomposition (Barton et al., 2013; Büchner et al., 2024). Carrion-associated arthropods can be direct consumers of the carcasses or indirectly feed on eggs and larvae of other decomposers on the carcasses (Barton & Bump, 2019). For example, in predatory beetles such as staphylinids, large masses of maggots on large vertebrate carcasses (=high carcass biomass) are the preferred feeding sites (Lee Goff, 2009). Large carcasses are especially important for biodiversity, as they can harbour more diverse communities of arthropods than smaller ones (Büchner et al., 2024; Schoenly & Reid, 1983; Wierer et al., 2024). Aside from dipterans (Anderson et al., 2019; Benbow et al., 2019), the most dominant arthropod decomposers of carcasses are carrion beetles (Coleoptera: Staphylinidae: Silphinae) (Anderson et al., 2019; Matuszewski et al., 2014). Despite their importance for decomposition, only a little is known about the effects of habitat fragmentation on the population structure of carrion beetles. Carrion beetles, especially those inhabiting forests, face habitat changes in this ecosystem in several ways. Firstly, carcasses of large vertebrates have become less common as the number of top predators, leaving remains of their prey, dropped significantly in the last centuries (Bump et al., 2009; Estes et al., 2011), a trend which is currently reversed in many areas of

Europe (Cimatti et al., 2021). Over the last centuries, the number of large body-sized vertebrates has mostly been controlled by humans, especially through hunting, where the carcasses of the game are removed from the environment, and only residues from big game hunting remain (Coulson et al., 2004; Mateo-Tomás et al., 2015; Ueno et al., 2010). Secondly, the forest habitat itself becomes more fragmented (Haddad et al., 2015). This can happen within forests through intensive forest management practices (Gascon et al., 2000), leading to isolated habitat patches with long distances in between or through landscape changes, where whole forest sites are converted to agriculture or urbanised areas (Potapov et al., 2017). These long inter-patch distances often act as dispersal barriers that can only be bridged by species with good dispersal abilities (Feldhaar & Schauer, 2018; Shepherd & Brantley, 2005).

Carrion-breeding insects frequently exhibit little to no population genetic substructure, even across fragmented landscapes or varying degrees of habitat specialisation, likely due to their high dispersal capabilities. This trend is observed across multiple taxa, including the endangered American burying beetle (*Nicrophorus americanus* Olivier), which, despite its conservation concern, shows relatively weak genetic differentiation across its range, suggesting substantial gene flow among populations (Szalanski et al., 2000). Similarly, studies on blowfly species such as *Phormia regina* Meigen and *Lucilia sericata* Meigen have consistently found low levels of population structure, even when sampling across large spatial scales (Picard & Wells, 2010, 2014). Recent work on invasive blowflies further supports this pattern: species such as *Chrysomya latifrons* Malloch, show no evidence of population genetic structure despite inhabiting highly fragmented rainforest habitats (Butterworth, Benbow, & Barton, 2023; Butterworth, Wallman, et al., 2023), and other invasive blowflies demonstrate rapid genetic mixing following colonisation and low genetic differentiation (Croft, Matheson, Butterworth, et al., 2024; Croft, Matheson, Flemming, et al., 2024). Together, these studies highlight how the strong dispersal ability of carrion-breeding insects plays a dominant role in shaping their genetic structure, often overriding the expected effects of habitat and/or ecological specialisation or fragmentation. However, not all carrion-breeding species exhibit low population genetic structure. Pascoal and Kilner (2017) found significant genetic differentiation among populations of the burying beetle *Nicrophorus vespilloides* even at local spatial scales, suggesting limited gene flow. Their findings indicate that despite the beetle's mobility, local environmental or behavioural factors may restrict dispersal and contribute to fine-scale genetic structure.

Here, we aim to infer the dispersal abilities of three different carrion beetle species with different habitat requirements using genetic population structure based on microsatellite loci as an indirect measurement of dispersal ability. We investigated (a) *Nicrophorus vespilloides*, a forest species specialised on small carcasses for reproduction (Eggert & Müller, 1997; von Hoermann et al., 2016), (b) *Necrodes littoralis*, a habitat generalist found in forest and grassland habitats preferring large carcasses for breeding (Büchner et al., 2024; Matuszewski et al., 2014), and (c) *Oiceoptoma thoracicum*, showing a high affinity to forest habitats using all sizes of carcasses (Colijn & Heijerman, 2020; Matuszewski et al., 2013), but higher abundances in large carcasses (Büchner et al., 2024).

Habitat specialists tend to show greater population genetic structure because they rely on specific, often fragmented habitats. This limits their movement between populations, reducing gene flow and increasing isolation. As a result, genetic drift and local adaptation cause populations to become more genetically distinct from each other. In contrast, generalists are less restricted by habitat factors and maintain more genetic mixing, leading to less structure (Eckert et al., 2008; Funk et al., 2012; Slatkin, 1987). Given the spatially scattered and ephemeral nature of carcasses as a resource required for larval development of the three carrion-breeding beetle species, we expect proficient dispersal abilities in all three species. However, we expect that genetic substructuring would be more pronounced in the two habitat specialist species *Nicrophorus vespilloides* and *Oiceoptoma thoracicum*, which are disproportionately affected by forest habitat fragmentation and reduction in comparison to *Necrodes littoralis*.

MATERIALS AND METHODS

Study area and sampling

Carrion beetle samples were collected between June and August 2021 at 47 sites in Bavaria, Germany (Figure 1, for coordinates of sampling locations and number of individuals genotyped, see Appendix S1) spanning an area of approx. 300,000 km^2. Sampling concentrated on four regions, with sampling sites within regions being closer together than samples among regions (northern sampling site: 5 traps with distances among traps: minimum 8 km, maximum 100 km; southern sampling site: 1 trap; south-eastern sampling site: distance among 2 traps: 5 km; eastern sampling site: distances among 39 traps: minimum 100 m, maximum 60 km). The largest distance between sampling sites was 320 km. The sampling locations in the north and east of Bavaria are characterised by higher forest cover (Steigerwald and Bavarian Forest). The area between the northern and eastern sampling locations and the southern and southeastern sampling locations has less forest cover, and forests are more fragmented (see Figure 1). For sample collection, a combination of pitfall traps with liver as bait and/or whole cadavers of roe deer, red deer or wild boar were used for high sampling efficiency. Samples were conserved in pure Ethanol (99.8%) for further genetic analysis. We analysed a minimum of 5 individuals per species at each sampling location (trap) to enable robust population genetic analyses (for the number of genotyped individuals per sampling location see Appendix S1).

Study organisms

For this study, three common European carrion beetles (Coleoptera: Staphylinidae: Silphinae) were chosen: *Nicrophorus vespilloides*, *Necrodes littoralis* and *Oiceoptoma thoracicum*. *Nicrophorus vespilloides*

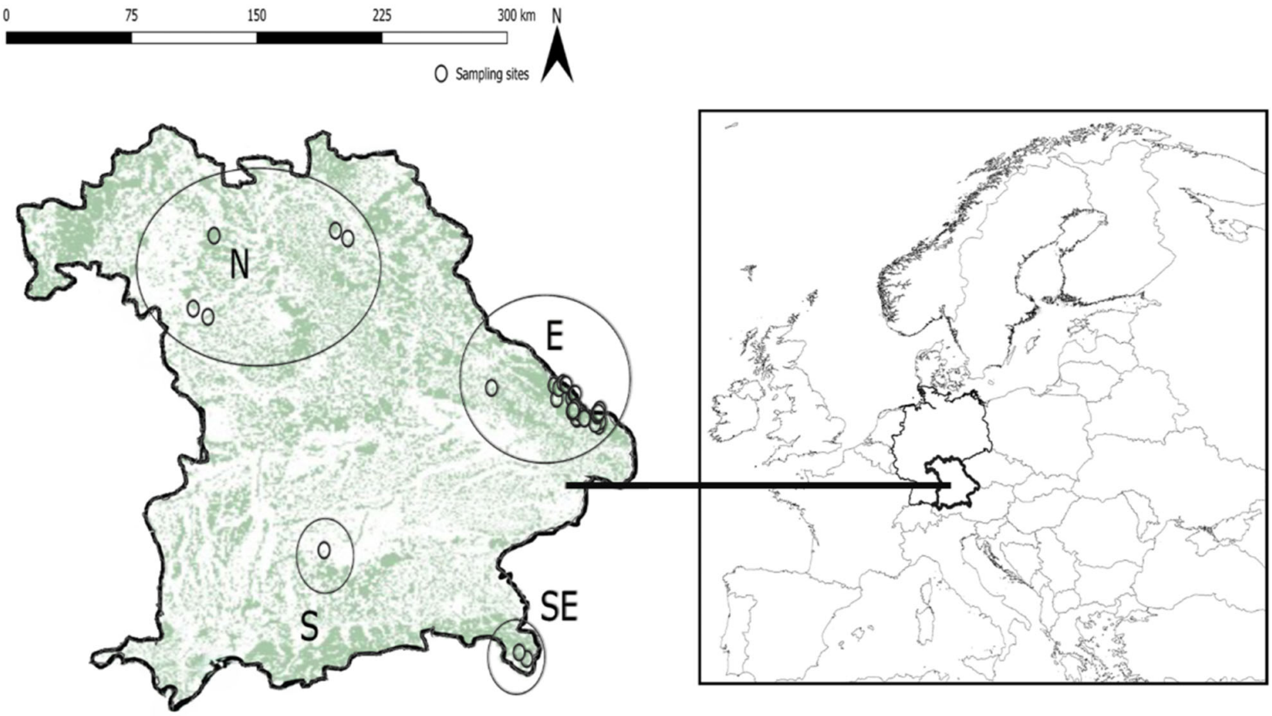

FIGURE 1 Sampling sites of carrion beetles across Bavaria (Germany). Circles represent sampling sites. N = northern region, S = southern region, E = eastern region, SE = south-eastern region. Data source forest coverage: DLM250 (Digitales Landschaftsmodell digital landscape model 1:250,000).

is a medium-sized carrion beetle (9–19 mm body length), found across Europe, Palearctic Asia and North America (Colijn & Heijerman, 2020). Larval development from hatching to adult takes about 25 days, depending on temperature (Potticary et al., 2024; Scott, 1998; S. Steiger, personal communication) and adult lifespan is up to 60 days (De Gasperin et al., 2015). Generation time is about 50 days, and generations can overlap (S. Steiger personal communication). This taxon commonly lives in forest habitats, especially dry coniferous forests (Dekeirsschieter et al., 2011). *N. vespilloides* is well known for its parental care, which is very rare in beetles (Brandmayr, 1992). For their reproduction, fresh and small vertebrate carcasses, for example, from rodents and birds, are preferred, as they can be buried easier and will be defended against other individuals of the same genus (Scott, 1998). Small carcasses are buried and formed into a brood ball, which serves as both a food source and nursery for the larvae (Potticary et al., 2024).

Necrodes littoralis is a larger carrion beetle with a body length of 15–25 mm, found across central Europe (Colijn & Heijerman, 2020; Dekeirsschieter et al., 2011). The developmental time of *N. littoralis* is strongly temperature dependent, ranging from 23 to 89 days (Gruszka & Matuszewski, 2022). It is a habitat generalist and can be found in forest and agricultural habitats (Dekeirsschieter et al., 2011). These beetles prefer larger carcasses (Büchner et al., 2024), for example, pig carcasses, and are found primarily on early to advanced stages of decomposition of the carcasses (Charabidze et al., 2016; Colijn & Heijerman, 2020). Following mating, females begin oviposition in the soil adjacent to and beneath the carrion. The hatched larvae feed on decomposing organic material and are also capable of preying on Dipteran larvae (Charabidze et al., 2016).

Oiceoptoma thoracicum shows a strong linkage to forest habitats across Europe, as forests provide lower temperatures and lower temperature fluctuations compared to open habitats, especially during summer (Matuszewski et al., 2013). It is a medium-sized beetle (12–17 mm body length) and shows no strong preference for a specific size of carcass (Colijn & Heijerman, 2020). Its developmental time is about 30 days (Qubaiová et al., 2022). *O. thoracicum* colonises carcasses chiefly in advanced decay stages (Kočárek, 2003; Müller et al., 2024) and is also more abundant in larger carcasses (Büchner et al., 2024). Adult individuals exhibit a diverse saprophagous feeding ecology, consuming carrion, dung and fungi (Dekeirsschieter et al., 2011). Larvae instead display a necrophagous feeding strategy (Kočárek, 2003).

Molecular methods

DNA was extracted from 4 to 6 legs per individual using the Puregene DNA Purification Kit (Qiagen) according to the manufacturer's recommendations. For *Nicrophorus vespilloides*, six polymorphic loci (Table 1) established by Pascoal and Kilner (2017) were used (other loci developed by Pascoal & Kilner, 2017 were run by us but could not be scored unambiguously). For *Necrodes littoralis* and *Oiceoptoma thoracicum*, microsatellite markers had to be established. Therefore, AllGenetics (A Coruña, Spain; https://www.allgenetics.eu/) was contracted to establish microsatellite-enriched libraries and to design primers. In total, 32 primer pairs of *N. littoralis* and 47 primer pairs of *O. thoracicum* were tested for their suitability for microsatellite analysis. After testing the suggested primer pairs, eight polymorphic primers for *N. littoralis* and *O. thoracicum* remained. However, after testing for the frequency of null alleles using the R package 'PopGenreport' (Adamack & Gruber, 2014) six loci remained per species that were used for further genetic analysis. A detailed description of PCR conditions is provided in the Appendix S2.

TABLE 1 Microsatellite loci and genetic diversity of *Nicrophorus vespilloides*.

Locus	Number individuals	Forward primer	Reverse primer	Repeat motif	Amplicon range size (bp)	Number alleles	H_E	H_O	p_{HWE}	F_{IS}
Nvesp_A	456	CTACGGCGTGCAGAATTACC	AACTCTCTGGTGTCGACGTC	AAC	111–174	22	0.8265	0.8143	>0.05	0.0147
Nvesp_D	456	TACGTGCGGTAATGAGGCG	ACGCCCTGCTCCCTATTTAG	AAC	164–206	15	0.8286	0.7452	<0.05	0.1007
Nvesp_F	456	TAAAGGGTTGGGAGGTTGGC	CACGATCCATACACGTGCAC	AC	183–233	18	0.8171	0.7769	>0.05	0.0493
Nvesp_I	456	CTGATCACCGGAACCCTCTC	GAATTCCCGGGTTTATGCCG	AG	281–309	16	0.5790	0.5092	<0.05	0.1206
Nvesp_E	456	ATGGATGGATGGAGAGTGGC	TTGATGGTTTCGAAAGGGCG	AC	175–211	16	0.8405	0.6693	<0.05	0.2037
Nvesp_H	456	TCGTAGATGTCTCGTGCCTG	CAGTTTGAAGGTGGTGGCTG	AG	259–303	23	0.8754	0.8205	<0.05	0.0627

Abbreviations: F_{IS}, inbreeding coefficient; H_E, expected heterozygosity; H_O, observed heterozygosity; p_{HWE}, *p*-value calculated against Hardy–Weinberg Equilibrium (HWE).

Analysis of genetic diversity

For all genetic analyses, we excluded individuals with missing genotypic information as well as sampling locations with less than five individuals per species. Hardy–Weinberg Equilibrium (HWE) over all populations per locus, number of alleles (*A*), expected (H_E) and observed (H_O) heterozygosity, inbreeding coefficient (F_{IS}) for each locus was calculated using the R package 'hierfstat' v 0.5-11 (Goudet, 2005). We calculated pairwise F_{ST} values (regarding every sampling location as separate population) using the R package 'hierfstat', using the 'WC84' (Weir & Cockerham, 1984) method for calculating the genetic distance. To test for linkage disequilibrium between microsatellite loci the index of association was used (IA, Brown et al., 1980) and additionally the index $\bar{r}$ d (Agapow & Burt, 2001), which accounts for the number of loci and is thus less biased. All calculations were performed using the R package 'poppr' v2.9.4 (Kamvar et al., 2015).

Analysis of genetic structure

We used the program STRUCTURE v.2.3.4 (Pritchard et al., 2000) to infer genetic substructure and potential subpopulations (*K*) based on differences in allele frequencies and likelihood analysis. Here, we also chose a two-step approach analysing the data with or without a priori information on the sampling location to evaluate the influence on the number of calculated genetic clusters. We carried out five independent runs for all three investigated species for a maximum of $K = 5$ using admixture models with 10^6 Markov chain Monte Carlo (MCMC) iterations, discarding the first 10^4 iterations as burn-in. To find the most likely number of genetic clusters, we used the Method of Evanno (2005) implemented in the R package 'pophelper' v.2.3.1 (Francis, 2017).

We used the discriminant analysis of principal components (DAPC), a method not based on assumptions of HWE equilibrium and defined genetic models (Jombart et al., 2010), to find genetic clusters and maximise differences between them (Jombart et al., 2010). DAPC was conducted using the R package 'adegenet' v.2.1.10 (Jombart & Ahmed, 2011). In the first DAPC analysis, sampling locations were used as predefined groups. In a second step, the find.clusters() function was used to determine the optimal number of groups (*K*), validated by the lowest BIC value. To find the optimal number of PCs to retain for both analyses, the opti.a.score() function was used. The number of replicates to be carried out at each level of PC retention was set to 1000. Individuals sampled from the same sampling location (same trap) were assigned to the same genetic cluster.

AMOVA was used to estimate genetic variability within and among populations at the level of sampling locations (every sampling location, meaning every trap, regarded as a separate subpopulation) and additionally at the regional level between the northern, eastern, south-eastern and southern populations (individuals from different sampling locations per region combined, see Figure 1) as the large geographical distances between the regions may hinder gene flow. AMOVA was conducted using the R package 'poppr' v2.9.4 (Kamvar et al., 2015) with 999 pairwise permutations.

The importance of isolation by distance was inferred by testing the relationship between genetic distances and geographic distances using the mantel randtest from the 'ade4' package (Dray & Dufour, 2007).

RESULTS

Genetic diversity

We found evidence of null alleles in all loci of every species, with the highest frequency of null alleles in the locus Nvesp_E (median frequency = 0.12) of *Nicrophorus vespilloides*, Nli_020 (median frequency = 0.41) of *Necrodes littoralis* and Oth_259 (median frequency = 0.05) of *Oiceoptoma thoracicum*.

456 specimens of *Nicrophorus vespilloides* originating from 28 locations were genotyped, with a mean of 16.3 ± 7.5 (SD) individuals and a minimum of five individuals to a maximum of 43 individuals per sampling location. In *Nicrophorus vespilloides*, the number of alleles per locus ranged from 15 (Nvesp_D) to 22 (Nvesp_A). The expected heterozygosity (H_E) ranged from 0.58 to 0.87, and observed heterozygosity (H_O) ranged from 0.50 to 0.82. The loci Nvesp_D ($\chi^2 = 185$, df = 105, $p < 0.001$), Nvesp_I ($\chi^2 = 1068$, df = 120, $p < 0.001$), Nvesp_E ($\chi^2 = 692$, df = 120, $p < 0.001$) and Nvesp_H ($\chi^2 = 314$, df = 253, $p < 0.001$) showed significant departure from HWE, when calculated over all populations (Table 1). The inbreeding coefficient F_{IS} per locus (Table 1) ranged from 0.015 (Nvesp_A) to 0.204 (Nvesp_E) (over all loci 0.091) and the pairwise F_{ST} ranged from 0 to 0.041 (mean ± SD, 0.005 ± 0.007) (Appendix S3). We found no significant linkage disequilibrium in all pairwise comparisons of the microsatellite loci (for details see Appendix S4).

484 specimens of *Necrodes littoralis* originating from 34 locations were genotyped, with a mean of 14.24 ± 5.65(SD) and a minimum of five individuals to a maximum of 29 individuals per sampling location. In *Necrodes littoralis* the number of alleles per locus ranged from 10 (Nli_290) to 26 (Nli_260). H_E ranged from 0.69 to 0.85 and H_O ranged from 0.28 to 0.86. The loci Nli_020 ($\chi^2 = 1479$, df = 45, $p < 0.001$), Nli_290 ($\chi^2 = 564$, df = 45, $p < 0.001$) and Nli_427 ($\chi^2 = 596$, df = 105, $p < 0.001$) showed significant departure from HWE; when calculated over all populations (Table 2). The inbreeding coefficient F_{IS} per locus (Table 2) ranged from − 0.015 (Nli_210) to 0.608 (Nli_020) (over all loci 0.0.154) and the pairwise F_{ST} ranged from 0 to 0.087 (mean ± SD, 0.007 ± 0.016) (Appendix S5). We detected significant linkage disequilibrium only between the loci Nli_290 and Nli_427 ($I_A = 0.030$, $p(I_A) = 0.034$; $\bar{r}_d = 0.030$, p $(\bar{r}_d) = 0.033$) (for details see Appendix S6).

412 specimens of *Oiceoptoma thoracicum* originating from 25 sampling locations were genotyped, with a mean of 16.48 ± 7.86(SD) and a minimum of five individuals to a maximum of 46 individuals per sampling location. In *Oiceoptoma thoracicum*, the number of alleles ranged from 10 (Oth_293) to 30 (Oth_226). H_E ranged from 0.59 to 0.88 and H_O ranged from 0.54 to 0.85. The loci Oth_149 ($\chi^2 = 221$, df = 136, $p < 0.01$) and Oth_259 ($\chi^2 = 498$, df = 55, $p < 0.001$) showed significant departure from HWE when calculated over all populations (Table 3). The inbreeding coefficient F_{IS} ranged from (Table 3) from − 0.013 (Oth_063) to 0.112 (Oth_149) (over all loci 0.036) and the pairwise F_{ST} ranged from 0 to 0.036 (mean ± SD, 0.001 ± 0.001) (Appendix S7). All genetic diversity metrics on sampling location level can be found in the Appendix (see Appendices S8–S10).

We detected no significant linkage disequilibrium in any of the pairwise comparisons of the microsatellite loci (for details see Appendix S11).

Genetic structure

For all three species, the STRUCTURE analysis revealed no clear results for the estimates of most likely numbers of clusters based on the criteria of Evanno's *K*. Moreover, the visual inspection of STRUCTURE plots showed no clear genetic clustering for $k > 1$ (Appendices S12–S14). These results indicate no genetic differentiation of all three species investigated.

The DAPC scatterplots for a priori defined groups (Figure 2a–c) of all three species showed a strong overlap of almost all genetic clusters (groups of individuals sampled from the same trap), indicating strong genetic similarity in the ordination space, and therefore no or only very weak substructuring (Figure 2a for *Nicrophorus vespilloides*, Figure 2b for *Necrodes littoralis*, Figure 2c for *Oiceoptoma thoracicum*). The same is true for the de novo clustering without providing a priori grouping information (Appendices S15–S20). The optimal number of PC's retained for the analysis and their optimal *K* for without a priori defined groups was for (a) *N. vespilloides* is 12 PC's and $K = 11$ with lowest BIC = 375.23, (b) for *N. littoralis* is 8 PC's and $K = 14$ with lowest BIC = 351.23 and (c) for *O. thoracicum* is 15 PC's and $K = 10$ with lowest BIC = 292.90.

For all three species, the AMOVA revealed that – above the level of genetic variation within an individual – genetic variation was highest among individuals sampled from the same trap. Evidence for genetic substructuring at this level was significant ($p > 0.05$) for all three species (*Nicrophorus vespilloides*: explained genetic variation 9.07%, *Necrodes littoralis*: explained genetic variation 15.12%, $p < 0.01$, *Oiceoptoma thoracicum*: explained genetic variation 3.47%, $p < 0.01$). Only a non-significant ($p > 0.05$) portion of genetic variance

TABLE 2 Microsatellite loci and genetic diversity of *Necrodes littoralis*.

Locus	Number individuals	Forward primer	Reverse primer	Repeat motif	Amplicon range size (bp)	Number alleles	H_E	H_O	p_{HWE}	F_{IS}
Nli_20	635	CAGGCACGTGTATCTACTCCC	GTGCAATGGATGTATGACCG	AT	140–216	10	0.7039	0.2756	<0.05	0.6084
Nli_063	635	CGCCCAATTCCCTTTACAT	TCGCGCATGAGAATTAAGAA	AC	135–185	21	0.8457	0.8572	0.05	−0.0136
Nli_210	635	GCCAAGTGTGAATTGTGGAG	CATTGTTCTACCATCAAATTACCG	AT	120–166	17	0.7327	0.7435	>0.05	−0.0148
Nli_260	635	AAATGATGGGTGTTACTGGG	TAAATTGCCAAGGTTGTGTAAA	AC	225–285	26	0.7905	0.7327	>0.05	0.0732
Nli_290	635	CGTTTACAACCCGTCATTGTT	TTCAATGTAAATATACAATCACAAGCA	AG	135–153	10	0.6881	0.4510	<0.05	0.3445
Nli_427	635	AGATTCGAGATTGCGCGG	ATACGAAGATTCCGGCCATA	AG	177–219	15	0.7390	0.7489	<0.05	−0.0135

Note: All primers from Pascoal and Kilner (2017).

Abbreviations: F_{IS}, inbreeding coefficient; H_E, expected heterozygosity; H_O, observed heterozygosity; p_{HWE}, p-value calculated against Hardy–Weinberg Equilibrium (HWE).

was explained by differences among regions (north, east and south-east; southern region was excluded from AMOVA due to low numbers of individuals) with −0.01% in *Nicrophorus vespilloides*, −0.19% in *Necrodes littoralis* and −0.28% in *Oiceoptoma thoracicum*. The genetic variance explained by population within the same region was not significant ($p > 0.05$) for all tested species (explained genetic variation in *Nicrophorus vespilloides*: 0.21%, *Necrodes littoralis*: 0.22%, *Oiceoptoma thoracicum*: 0.31%) (Appendix S21).

None of the three species showed evidence of isolation by distance (*Nicrophorus vespilloides*: simulated p-value = 0.9; *Necrodes littoralis*: simulated p-value = 0.3; *Oiceoptoma thoracicum*: simulated p-value = 0.98).

DISCUSSION

In our study, none of the three carrion beetle species *Nicrophorus vespilloides*, *Necrodes littoralis* and *Oiceoptoma thoracicum* showed genetic substructuring. Even the large distances between populations of the investigated carrion beetles (up to approximately 320 km) did not lead to any substructuring. On average, all three species showed very low F_{ST} values. The AMOVA revealed that the largest percentage of genetic variation is explained by the differences among individuals within the same trap and not by individuals caught in different traps within the same region or among regions. We found deviations from HWE in some loci of all species. Deviations from HWE can indicate genetic differentiation of populations or can be explained by inbreeding, as related individuals can bias allele frequencies (Cox & Kraft, 2006; Wang & Shete, 2012). The mixing of individuals from different breeding units within the same trap may also result in deviations from HWE. Additionally, null alleles can result in deviations from HWE (Wu et al., 2019), for which we found evidence in some loci in all three species. However, after reducing the number of loci from eight to six loci by excluding the loci with the highest frequency of null alleles, there was still no evidence for genetic population structuring, which should become more pronounced by removing loci containing null alleles (Wu et al., 2019). Thus, it is unlikely that the deviations from HWE originated from genetic structuring on the level of (sub-) populations. This is also supported by the DAPC analysis, which is not based on similarity of multilocus genotypes (Jombart et al., 2010) and is thus robust against violations of HWE. The DAPC analysis, with or without a priori information on sampling location, indicated no substructuring of the populations in all three species, as all populations largely overlapped in the DAPC space. Including a priori information on sampling location did not result in better resolution of subpopulations according to sampling locations. Only *N. littoralis* showed some clustering in the DAPC space when giving a priori information. However, considering all other analyses, there is evidence for no or only weak genetic substructuring for *N. littoralis*. Also, using the Bayesian clustering method of STRUCTURE, we found no evidence for genetic substructure in all three species, neither with a priori information nor without.

TABLE 3 Microsatellite loci and genetic diversity of *Oiceoptoma thoracicum*.

Locus	Number individuals	Forward primer	Reverse primer	Repeat motif	Amplicon range size (bp)	Number alleles	H_E	H_O	p_{HWE}	F_{IS}
Oth_063	412	ATTCGCGTGGTATTGGAAAC	GACCCTCCTGTCAGGGTTAG	AC	126–168	19	0.851	0.839	>0.05	−0.013
Oth_149	412	TTGAAATCTTATATGGGCGCT	CATCCCATCGAGGAACTATCA	CCG	73–139	17	0.502	0.578	<0.05	0.112
Oth_226	412	TCAAGCCGAACAAATCCAG	TCTTGTTTGTCAAGTCCTGTATGTC	AT	149–213	30	0.837	0.883	>0.05	0.049
Oth_259	412	AGCCACTGGTCTCTTATCGCT	CAATGTAGTAAACGTACCAATTTGA	AAC	90–123	11	0.612	0.653	<0.05	0.073
Oth_293	412	AAGTCGCCCTTCTGCCTAAT	CCTGAAGAACCGGTGAAGGT	AC	112–132	10	0.743	0.736	>0.05	−0.009
Oth_430	412	CCGCACACATCAATTCAACT	AACCGTCGATCACCGAAAGAG	AC	124–192	25	0.782	0.804	>0.05	0.029

Abbreviations: F_{IS}, inbreeding coefficient; H_E, expected heterozygosity; H_O, observed heterozygosity; p_{HWE}, *p*-value calculated against Hardy–Weinberg Equilibrium (HWE).

Our expectation was to find higher levels of substructuring in more specialised species, with respect to habitat preference (*Nicrophorus vespilloides* and *Oiceoptoma thoracicum* being highly specialised towards forest habitats), as the forest habitats are more fragmented between northern and eastern, and southern sampling sites. However, we did not find evidence of substructuring in the population.

All three species are common (Colijn & Heijerman, 2020) and thus likely have large population sizes within our study area. This is also supported by the large number of individuals trapped in this study. Larger populations are generally less affected by genetic drift and the loss of alleles, which would cause genetic differentiation. Additionally, in larger populations, more individuals will disperse. Therefore, the reduction of genetic diversity is slowed down (Hedrick & Miller, 1992) and we might not find evidence for genetic substructuring. Genetic variability might be conserved in populations, even without gene flow and migration between populations, if the effective population size is large enough. This would therefore lead to no genetic substructure even when populations are not in continuous gene flow (Hedrick, 2009).

Finding no genetic substructure might be caused by large populations with high effective population sizes, continuous gene flow through migration events, good dispersal abilities or a combination thereof. In this study, we cannot distinguish between these factors, as we have no direct measures of population size, and dispersal ability is measured indirectly by analysing genetic structure of the species. So it might be that the lack of genetic substructure is due to large population sizes alone or in combination with good dispersal ability. However, there is strong evidence that carrion beetles have good dispersal abilities.

General theory predicts that species using ephemeral habitats or resources must have good dispersal abilities to sustain viable populations compared to species living in long-lasting habitats (Denno et al., 1996; Southwood, 1962). For carrion beetles of the tribe Nicrophorini, good dispersal abilities are necessary, as the availability of small carcasses as brood balls for their offspring is temporarily and spatially highly variable due to competition and fast decomposition (Charabidze et al., 2016).

The successful colonisation of new habitats requires two factors. Firstly, the habitat or resource amount and quality must be sufficient (habitat limitation) and secondly, it must be within reachable distances (dispersal limitation). Both factors can be fulfilled by being physically able to disperse long distances or having a dense matrix of suitable resources and habitat, where long-distance dispersal is unnecessary. Carrion beetles olfactorily specialised in perceiving odour bouquets of a certain kind of carcass (e.g. size, species, decomposition stage, von Hoermann et al., 2016; Trumbo & Steiger, 2020) can rapidly find carrion even at large distances (Evans et al., 2020). In direct observations, using a flight mill set up *Nicrophorus vespilloides* showed flight distances of up to 26 km (Attisano & Kilner, 2015). Thus, there seems to be no physical or physiological (von Hoermann et al., 2013) dispersal limitation. However, direct observations of physical dispersal ability are still lacking for most carrion beetles. In our core study region in the Bavarian Forest, we recaptured a marked *Necrodes littoralis* at a

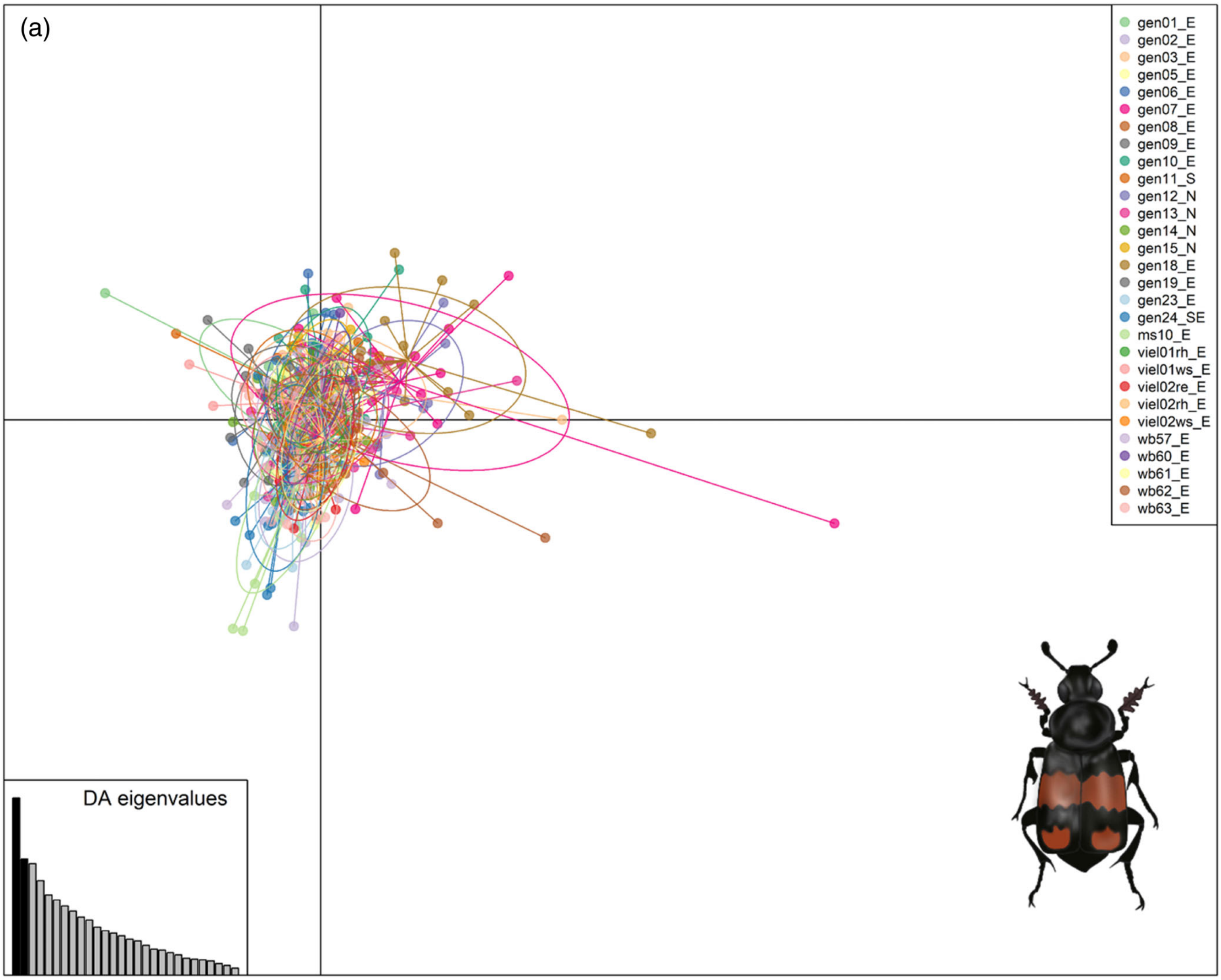

FIGURE 2 Discriminant analysis of principal components (DAPC) of (a) *Nicrophorus vespilloides*, (b) *Necrodes littoralis* and (c) *Oiceoptoma thoracicum* with sampling location (same trap) as a priori grouping (represented by coloured ellipses; dots represent individuals) were assigned to the same genetic cluster. The scatterplot shows the first two principal components of the DAPC. Each colour represents a sampling location (see Table S1). Legend is coded as Sampling location_Geographical region (N = North, E = East, S = South, SE = Southeast). Eigenvalues of the principal components are displayed in the inset.

distance of 34 km from its release site after a few days (C. von Hoermann, personal communication). In our study, we were unable to distinguish which of the two factors – good dispersal abilities or high resource density – might be the leading cause for the absence of genetic substructuring, as we do not know the densities of carcasses between the sampling locations. Thus, we assume good dispersal abilities of all three investigated species and a dense matrix of sufficiently sized habitats and resources, supporting large populations. Increased numbers of carcasses of different sizes supporting larger populations might occur due to a drastic increase of wild ungulate populations all over Europe during the last decades, such as roe deer or red deer (Burbaitė & Csányi, 2010; Hothorn et al., 2015; Linnell et al., 2019; von Hoermann et al., 2018). Concurrently, there is also a potential increase in the abundance of smaller carcasses, such as those of mice, particularly during mast events of trees, such as oaks or beech trees, which happens more regularly nowadays (Imholt et al., 2017). Due to the increased number of seeds during mast years, the number of resources for smaller vertebrates increases. This leads to more individuals and eventually to smaller carcasses.

In contrast to our study, Pascoal and Kilner (2017) reported significant genetic substructuring of populations of *Nicrophorus vespilloides* within a range of less than 20 km between populations in the UK. Their study was conducted in a farmland-dominated area, with small forest remnants; potentially resulting in a generally smaller population size compared to the population sizes in our study. For congeneric species, habitat fragmentation, for example, through deforestation, has been shown to negatively affect the abundance and reproductive success of burying beetles (Gibbs & Stanton, 2001; Trumbo & Bloch, 2000), and even driving some species to become endangered (Anderson, 1982; Creighton et al., 2009).

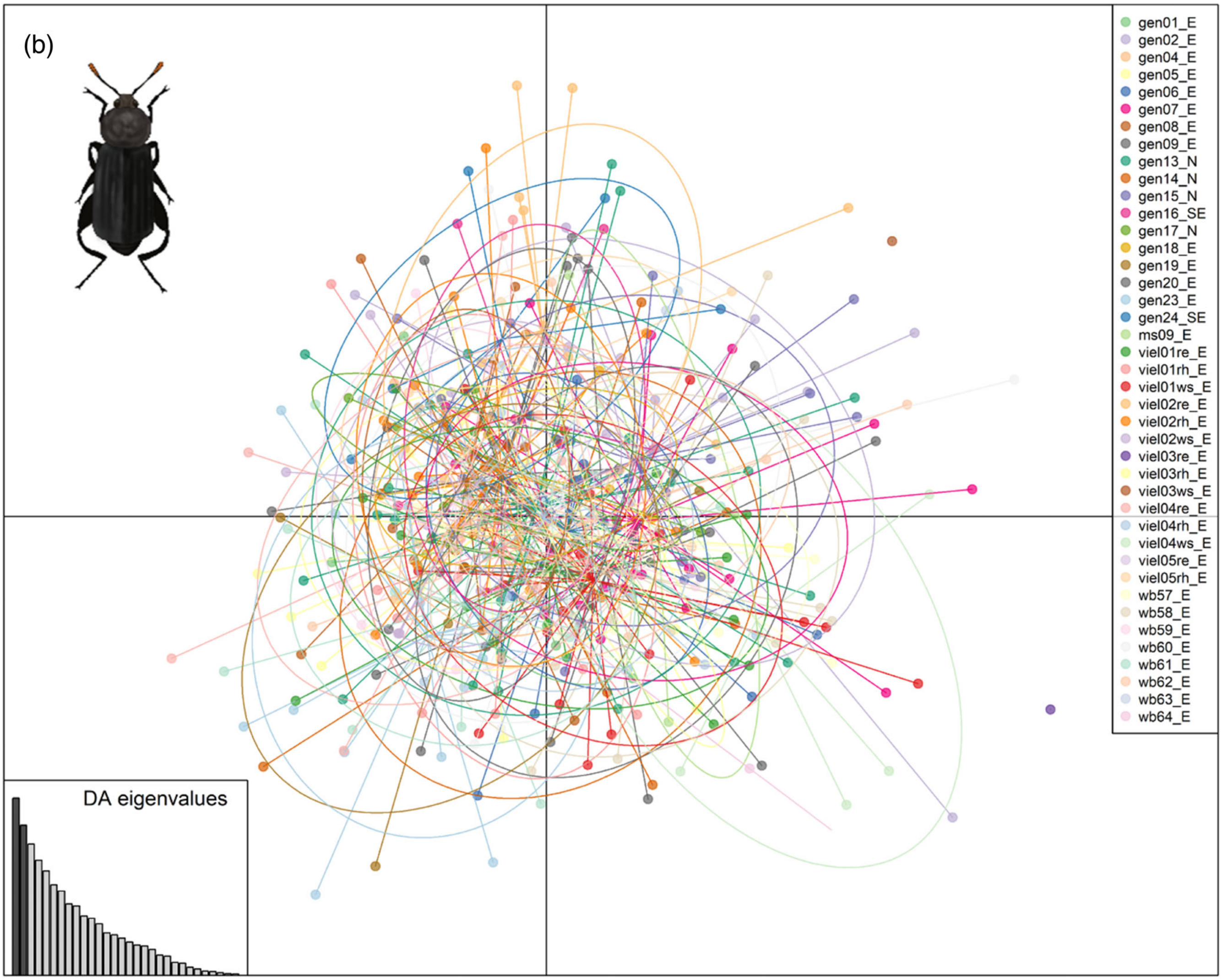

FIGURE 2 (Continued)

Carrion beetles are part of the necrobiome, defined as the community of all organisms decomposing any auto – or heterotrophic-derived necromass (Benbow et al., 2019). One component of the necromass is deadwood. Saproxylic organisms, defined as dependent on dead wood in at least one stage of their lifecycle (Speight, 1989), face similar conditions regarding the spatiotemporal availability of their resources. Certain types of dead wood are also ephemeral resources in space and time, like carrion (Butterworth, Benbow, et al., 2023; Butterworth, Wallman, et al., 2023). The spatiotemporal variability of ephemeral resources has the potential to apply selective pressure towards wing morphology and shape dispersal syndromes (Butterworth, Benbow, et al., 2023; Butterworth, Wallman, et al., 2023; Meresman et al., 2020). Consequently, we find saproxylic organisms that show a great variety of dispersal distances. For saproxylic insects, dispersal distances, measured either directly by mark-recapture, flight mill or field experiments, or indirectly by using population genetic measurements, reach from a few meters to several kilometres (for an overview, see Feldhaar & Schauer, 2018; Komonen & Müller, 2018). Highest distances measured with direct methods were found in *Monachamus galloprovincialis OLIVIER* (Cerambycide) and *Hylobius abietis LINNAEUS* (Curculionidae), with 63 km and up to 80 km, respectively (David et al., 2014; Solbreck, 1980). Genetic measures revealed no genetic substructuring at distances over 600 km in *Rosalia alpina* LINNAEUS (Cerambycidae) (Drag et al., 2015). For pioneer species that use fresh stages of decaying wood, even larger dispersal distances have been reported (Komonen & Müller, 2018). Better dispersal abilities of pioneer species are biologically functional as early decay stages are available for a shorter period than later stages of decay (Stokland et al., 2012). Furthermore, pyrophilous species, for example, species dependent on freshly burnt wood, are suggested to have good dispersal capabilities (Ranius et al., 2014). Freshly burnt wood is only available for a short period, and fire events are often kilometres apart (Saint-Germain et al., 2008). Schmitz and Bousack (2012) reported the attraction of a jewel beetle species from a distance of 80 to 130 km, the nearest coniferous forest where these species occur, to an oil tank fire.

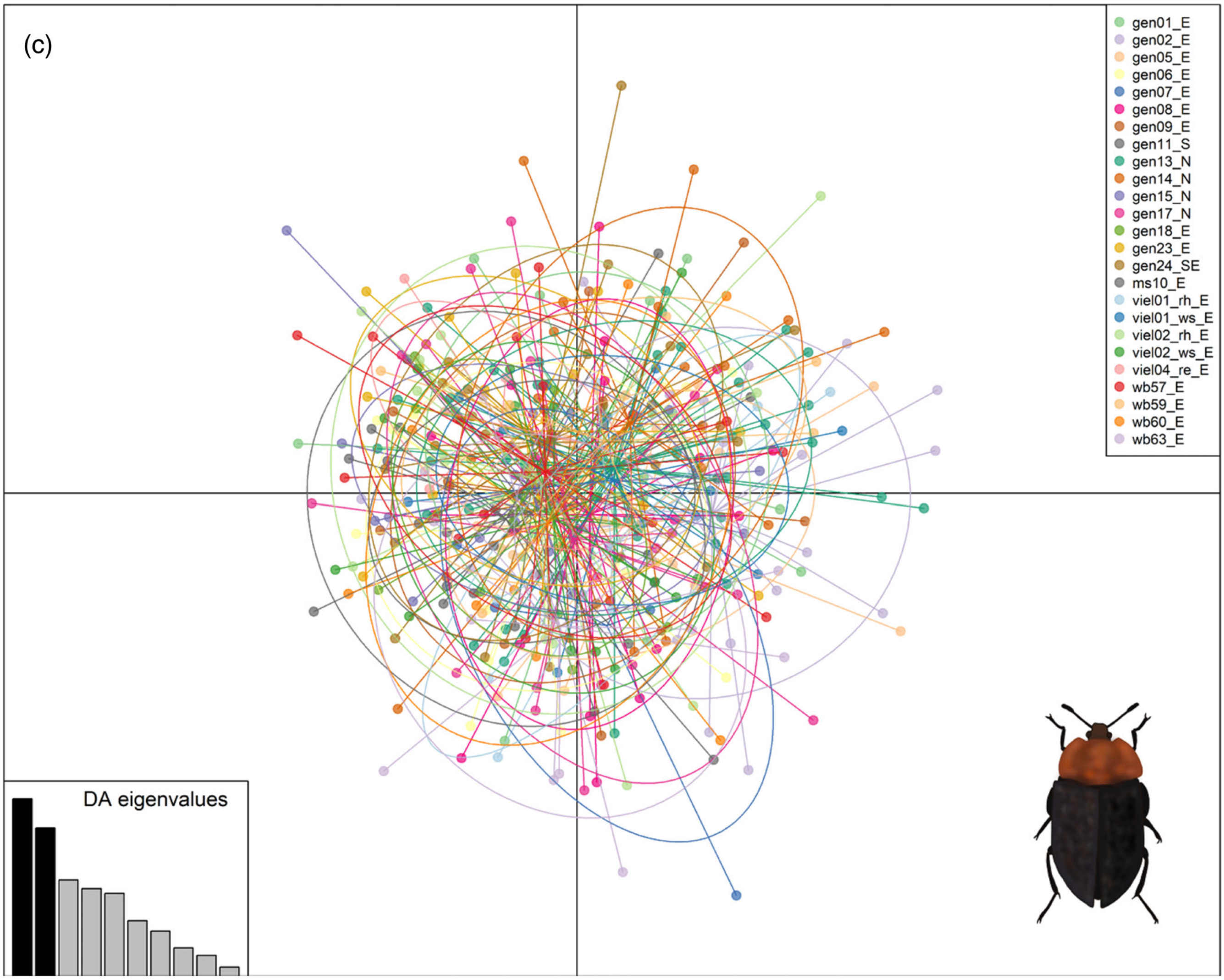

FIGURE 2 (Continued)

Studies on dispersal abilities are important for conservation measures to detect possible threshold habitat sizes and connectivity to maintain viable populations through continuous gene flow. Dispersal syndromes are driven by multiple biotic and abiotic factors (Kubisch et al., 2014) and the dispersal abilities of an organism can be shaped by – among other factors– habitat and resource use. While ongoing fragmentation and habitat loss can lead to dispersal limitations even among common species (Sydenham et al., 2017), these factors will affect small populations more strongly, resulting in population substructure. The study of Pascoal and Kilner (2017) on *Nicrophorus vespilloides* revealed that species with potentially good dispersal abilities show population genetic substructuring and eventually isolation of populations. As the effects of the interplay of habitat fragmentation, population size and the utilisation of an ephemeral resource are still not clear, comparative analyses of a range of species with potentially different dispersal abilities and population sizes but similar resource and habitat use are required to disentangle these factors.

AUTHOR CONTRIBUTIONS

Bastian Schauer: Writing – review and editing; writing – original draft; formal analysis; validation; methodology; data curation; visualization. **Marvin Dutschke:** Methodology; data curation; writing – review and editing; investigation. **Marco Heurich:** Investigation; methodology; writing – review and editing. **Christian von Hoermann:** Investigation; methodology; writing – review and editing. **Jens Schlüter:** Investigation; methodology; writing – review and editing. **Tomáš Lackner:** Investigation; methodology; writing – review and editing. **Annika Busse:** Investigation; methodology; writing – review and editing. **Sandra Steiger:** Investigation; methodology; writing – review and editing. **Roland Brandl:** Investigation; methodology; writing – review and editing. **Jörg Müller:** Conceptualization; methodology; investigation; supervision; funding acquisition; writing – review and editing; writing – original draft; project administration. **Heike Feldhaar:** Writing – original draft; writing – review and editing; conceptualization; methodology; validation; investigation; supervision.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

DATA AVAILABILITY STATEMENT

The datasets generated during and/or analysed during the current study are available at Figshare. https://doi.org/10.6084/m9.figshare.28943864.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1. Supporting Information.

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