Functional traits drive ground beetle community structures in Central European forests: implications for conservation

Dorothea Nolte^{1*}, Andreas Schuldt^{2,3}, Martin M. Gossner^{4,5}, Werner Ulrich⁶ and Thorsten Assmann¹

¹ Leuphana University Lüneburg, Institute of Ecology, Scharnhorststrasse 1, 21335 Lüneburg, Germany,
Thorsten Assmann - assmann@uni.leuphana.de

*Corresponding author: dorothea.nolte@uni.leuphana.de, phone: +49 (0)4131 677 2902

² German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e,
04103 Leipzig, Germany, andreas.schuldt@idiv.de

³ Martin-Luther-University Halle-Wittenberg, Institute of Biology/Geobotany and Botanical Garden,
Am Kirchtor 1, 06108 Halle, Germany

⁴ Swiss Federal Research Institute WSL, Forest Entomology, Zürcherstrasse 111, 8903 Birmensdorf,
Switzerland, martin.gossner@wsl.ch

⁵ Technical University Munich, Terrestrial Ecology Research Group, Department of Ecology and
Ecosystem Management, 85354 Freising, Germany

⁶ Nicolaus Copernicus University Toruń, Ecology and Biogeography, Faculty of Biology and
Environmental Protection, Lwowska 1, 87-100 Toruń, Poland, ulrichw@umk.pl

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Abstract

Community metrics describing the structuring of ecological communities, such as nestedness and the potential linkages between functional traits and the occurrence of species, might hold important information for biodiversity conservation. The order in which species are ranked in nested communities, as well as species traits determining community composition, can help pinpoint species vulnerable to extinction. However, these patterns remain understudied for many taxa of conservation concern and across larger spatial scales. We used a large dataset of ground beetle communities in Central European forests to test for nestedness, variation in species composition, and whether species traits can explain species composition patterns. We found only weak evidence of nestedness of ground beetle communities. However, community compositions across regions were remarkably similar. Species traits explained over half the variance in the overall occurrence ranks of ground beetle species. Wing dimorphism, breeding in both spring and autumn, and hibernation as both larval instars and as imago coincided with increasing occurrence probability, probably due to the greater flexibility of such species to adapt to fluctuating environmental conditions. In contrast, predominantly granivorous species or those with smaller geographical ranges had small occurrence ranks. These results emphasise the importance of investigating the relationships between species traits and occurrence ranks to better understand the mechanisms which shape community composition, and these relationships should be taken into consideration in conservation contexts. Our results provide a basis for the development of more effective conservation strategies in Central European forests to protect threatened ground beetle species.

1. Introduction

Forests provide numerous ecosystem services, including the preservation of biodiversity. In Central Europe, especially in Germany, legal regulations have led to an ongoing, overall increase in forest coverage during the last two centuries (FAO 2012; Fuchs et al. 2013). Nevertheless, many forest species in Central Europe are threatened and red-listed (Binot-Hafke et al. 2011; Desender et al. 2008), and forest management should therefore be influenced by conservation concerns. These conservation concerns need to be accounted on the regional level as usually, only a few species are ubiquitous, while the majority of species inhabit only few sites (e.g. Gaston 2003). The majority of threatened species belong to the latter category, and are more vulnerable to extinction. To preserve species diversity across forest ecosystems, it is crucial to understand the underlying mechanisms shaping community composition. Identified drivers can then be used to determine the extinction vulnerability of species, and to develop conservation measures aimed at the rarest and most threatened species (Wang et al. 2015). This is especially important as rare species can have large effects on ecosystem functioning and on ecosystem services (Mouillot et al. 2013; Soliveres et al. 2016).

Nestedness analysis of communities is a valuable tool for identifying species which are sensitive to habitat changes and are hence more prone to extinction (Bolger et al. 1991; Martinez-Morales 2005). A nested community structure implies that species-poor sites are true subsets of species-rich sites (Patterson and Atmar 1986). Although a perfectly nested pattern is rarely found in real-world ecosystems (Fischer and Lindenmayer 2005), significant nested patterns have been shown for various habitat types and taxa (Schouten et al. 2007; Wang et al. 2013; Wright et al. 1998). Although invertebrates make up the bulk of higher eukaryotic biodiversity, their community patterns and possible nestedness are not well understood. In Central Europe, ground beetles have been frequently studied in the context of conservation science (Pearce and Venier 2006; Rainio and Niemelä 2003) as they can serve as a model taxon for understanding biodiversity patterns. Nested communities have previously been reported for the genus *Carabus* on a European scale (Calatayud et al. 2016) and for ground beetles on smaller geographic scales (within a region such as a city or a big lake and its surroundings) (Weller and Ganzhorn 2004; Zalewski and Ulrich 2006). However, to test for generality of nestedness in ground

beetle communities and the applicability to forests and forest management, studies on a larger geographic scale (across regions) are necessary but to the best of our knowledge still missing. If nestedness occurs, conservation management can focus on preserving species-rich sites, as these are expected to contain most or all of the rare species (Fleishman et al. 2002).

Among a plethora of factors (Ulrich et al. 2009), extinction and (re-)colonization dynamics within the island biogeography framework are known to explain many nested community patterns (Cutler 1991; Lomolino 1996; Patterson and Atmar 1986). Hence nestedness and other species occurrence patterns can be driven by environmental factors, such as habitat patch size, disturbance, and isolation (Wang et al. 2013), as well as by species traits, such as trophic level and dispersal ability (Soga and Koike 2012; Zalewski and Ulrich 2006). Feeley et al. (2007) used the nestedness rank of a species, which is equivalent to the number of species incidences, as an indicator of extinction vulnerability in order to demonstrate the existence of a relationship between extinction vulnerability and species traits.

For European carabid beetle species, a large amount of information about the species traits is available in the literature, much of which has recently been assembled in an online database (Homburg et al. 2014b). Species traits, such as flight capability, body size, and habitat specialization, are increasingly discussed as potential drivers of beetle community structure (Driscoll and Weir 2005; Gerisch 2011; Ribera et al. 2001). Thus, species traits can be used to identify the mechanisms underlying community compositions of forest ground beetles. Additionally species traits are of great relevance for conservation management, as they offer an understanding of why some species are rare and face higher extinction vulnerability than others (Henle et al. 2004; Soga and Koike 2012). For example, species with low dispersal power or species with high habitat specialization are expected to be more prone to extinction (e.g. Kotze and O'Hara 2003). This knowledge can inform the development of more effective management strategies for preserving species diversity.

To identify the mechanisms underlying community compositions, we analysed a large dataset on the regional abundance of forest ground beetles, based on 296 forest plots in Germany, Belgium, and the Netherlands. In order to provide recommendations for nature conservation management, we address the following three questions:

- 94 I) To which degree are the communities in the given landscapes nested?
- 95 II) Is it possible to identify species vulnerable to regional extinction?
- 96 III) Are species communities shaped by species traits?

2. Material and methods

2.1 Data compilation

We compiled seven regional datasets from several studies on epigeic active ground beetles in forests of Belgium, the Netherlands, and Germany (Table 1). All studies were carried out using pitfall traps at some points between 1981 and 2008, and covered at least the main activity period of the studied forest species. The seven datasets were each collected using slightly different methods, for example, different preservation fluids, which has been shown in laboratory experiments to not have a strong influence on catching rates (Gerlach et al. 2009). Within the given datasets, the pitfall trapping method tends to be consistent (Table 1). Each dataset comprises catches from a continuous area with comparable climatic and edaphic parameters, such as Atlantic climate and sandy soils in the lowlands of Lower Saxony, as these parameters are known to have a strong influence on species composition (e.g. Assmann 1999; Desender 2005). We refer to the datasets as ‘regions’. The number of forest plots per region ranged from 13 to 66, with a total of 296 forest plots. The forest plots differed slightly from each other, e.g. regarding the dominant tree species, forest size or habitat isolation (Assmann 1999; Desender 2005; Fischer et al. 2010). While most of the plots represent isolated forests, plots in the Hainich-Dün and in the Schorfheide-Chorin (Table 1) are mostly located within large, continuous forests (Fischer et al. 2010).

We only considered typical forest species, defined as those which reproduce exclusively in forests (Lindroth 1985, 1986; Turin 2000). We excluded species which can reproduce in forests as well as in other habitats as they are widely distributed and therefore not relevant to develop conservation strategies for specialized or rare forest species. Moreover, vagrant species were excluded from analyses as they exhibit probably different species traits, and thereby can interfere with the accuracy of the analyses. Nomenclature follows Schmidt et al. (2016).

2.2 Species traits

A set of seven species traits reflecting basic aspects of ecophysiology and habitat selection (e.g. Thiele 1977), was selected for each species (Table 2). Information about body size and hind wing morphology,

which are linked to dispersal ability, trophic level, breeding season, and hibernation stage were extracted from the carabids.org database (Homburg et al. 2014b). We used the sum of the area of the countries in which the species has been recorded as a surrogate for geographic range size (Löbl and Smetana 2011). The number of habitat types occupied by a given species was calculated from the catalogue published by the Society for Applied Carabidology (GAC 2009). This catalogue defines species habitat preferences of ground beetles using 40 habitat types. A large degree of habitat specialization represents a wide niche, while lower numbers imply a narrow niche.

2.3 Data analysis

2.3.1 Determination of nestedness

For each region we constructed species $\times$ plot presence – absence matrices with species occurrences as entries. We assessed the degree of nestedness in species composition among regions using Nestedness by **O**verlap and **D**ecreasing **F**ill (NODF) (Almeida-Neto et al. 2008) scaled between 0 and 1. NODF increases with increasing degree of nestedness. A convenient measure of how much a species or plot contributes to the total degree of nestedness is the **n**estedness **c**ontribution (NC) (Ulrich 2012) of each species or each region ($NC = NODF(i) - NODF$, with $NODF(i)$, being the degree of nestedness excluding the focal species or plot i). Species having $NC < 0$ increase the overall degree of nestedness in the matrix.

To maximize the number of presences along the matrix diagonal, seriation was used to sort rows and columns of a matrix of species occurrences (rows) among plots (columns) (Leibold and Mikkelsen 2002). Ulrich and Gotelli (2013) have shown that the rank correlation of row and column positions of all non-empty cells in the seriated matrix is a measure of directional species turnover (β -diversity) with good statistical properties. We used the respective coefficients of determination (R^2) as the test statistic for species turnover across our sample plots.

Because raw scores of R^2 and NODF depend on matrix fill and species richness, we used a null model approach (Gotelli and Ulrich 2012) and compared observed scores with those obtained from 1000 matrices in which species occurrences within the species $\times$ plot matrix were reshuffled according to two contrasting null assumptions, an equiprobable model (Wright et al. 1998) and a proportional resampling model (Ulrich and Gotelli 2010). In the first model, each cell has an equal probability of occurrences, while in the second model, occurrence probabilities are proportional to observed species abundances, though total row and column abundances remain fixed (the abundance-based IT null model of Ulrich and Gotelli 2010). Both models benchmark the end points of a continuum from maximally equitable to maximally constrained patterns of species spatial distribution, and allow for an assessment of the relative degree of species co-occurrences along this continuum (Ulrich and Gotelli 2013). Nestedness and species turnover analyses were carried out using the software application *NODF* and *Turnover* (freely available on the homepage of W. Ulrich, www.keib.umk.pl).

All other statistical analyses were computed in R 3.2.2 (R Core Team, 2015). We compiled species occurrence ranks for each region based on the order of the species in the respective seriated regional matrix. These species occurrence ranks were then used as a proxy for the frequency of species occurrences in the given region, assigning the highest rank to the most abundant species and absences a value of zero. The use of ranks instead of relative abundances reduces the bias due to non-linearity in species relative abundances inherent in such comparisons. We assessed the spatial distance decay in community composition using a Mantel test, with Euclidean distances for plots and Bray-Curtis distances for species occurrence ranks. To assess whether the species found in each region tend to have similar occurrence ranks across regions, we used Spearman's rank correlation on regional species occurrence ranks.

2.3.2 Occurrence ranks and species traits

Average occurrence ranks were calculated using the mean of the occurrence ranks of a given species in the individual regions. We used a linear model to assess the relationship between species traits and the average species occurrence ranks. The average occurrence ranks were used as the dependent variable and species traits being the explanatory variables. Explanatory variables were tested for multicollinearity

using Spearman's rank correlation (all $\rho < 0.70$, see Appendix, Table A.1). The average occurrence ranks as well as the geographic range size were square-root transformed. Furthermore, geographic range size, degree of habitat specialization and body size were z-score scaled (mean = 0, standard deviation = 1). To identify the main drivers of carabid beetle occurrence ranks, we used multi-model inference (Burnham and Anderson 2002) based on Akaike's Information Criterion values corrected for small sample size (AICc). The models were automatically simplified and selected using the 'dredge' function (R package MuMIn, Barton 2016). We then generated average parameter estimates of the top-ranked models within $\Delta AICc < 2$, using the 'model.avg' function, and additionally calculated an average adjusted R^2 .

To investigate a possible phylogenetic effect on the model results, taxonomic distances were compiled from the hierarchies of taxonomy as found in the Catalogue of Palaearctic Coleoptera (Löbl and Smetana 2011, see Appendix A.1, Table A.2 and A.3), which are highly supported by molecular phylogenetic trees (e.g. Ober and Maddison 2008). A classical phylogeny, as described by phylogenetic trees, was not applicable because for many species no DNA sequences are available. We ran a Mantel test between the distance matrix of the full model residuals and the taxonomic distances to test if the residual error of the models was affected by the taxonomic relationships among the beetle species.

3. Results

3.1 Patterns of richness and abundance

We analysed a dataset consisting of 142 109 individuals from 28 forest ground beetles species occurring in 296 forest plots. The number of species varied from 11 to 18 species per region, and from three to 15 species per forest plot. *Pterostichus oblongopunctatus*, *Abax parallelepipedus* and *Notiophilus biguttatus* were the most common species across all seven regions (Figure 1A). Species with the lowest occurrence ranks were rare in all regions in which they occurred. We found significant correlations between the pair-wise Spearman's rank order in the occurrence ranks between the regions located in Belgium, the Netherlands and North Germany (BE, NL, LS, SM and SEW, all $\rho > 0.53$, $P < 0.01$). There was also a significant correlation between the occurrence rank orders in the low mountain regions of Germany (HEW and AEW; $\rho = 0.63$, $P < 0.01$). We did not find a significant correlation between the occurrence ranks of the northern and southern groups of sites.

3.2 Species co-occurrences

We found a significant nestedness pattern of species occurrences in all regions when compared to an equiprobable distribution, but only for two regions when compared to a proportional distribution (NODF > 0.64 , Table 3). Species turnover was always less than expected from the equiprobable null model, but higher than expected from the proportional null model (Table 3). Furthermore, we found a consistent lessening in similarity with increasing spatial distance between plots, although this was only statistically significant ($P < 0.01$) in the regions LS, SM and HEW (Table 3).

Species nestedness contribution, a measure of how often a species occurs according to the overall degree of species loss among plots, decreased with increasing species occurrence ranks (Figure 1B, $\rho = -0.74$, $P < 0.001$, Spearman's rank correlation). The three most frequent species were also of major importance for the overall degree of nestedness, as the nestedness contribution ranks decreased with increasing species occurrence ranks (Figure 1B).

3.3 Occurrence ranks and species traits

Multi-model inference revealed six models with $\Delta AICc < 2$ (Table 4). Geographic range size and hind wing morphology were indicated as the most important variables explaining average occurrence ranks, as they were included in all top-ranked models (Table 4 and 5, Importance value = 1). Trophic level, breeding season and hibernation stage were not included in all top-ranked models, showing lower importance values of 0.34 - 0.63 (Table 4 and 5). Body size and habitat specialization did not appear in any of the top-ranked models. While the full model explained 67% of the overall variance, the R^2 averaged over the six top-ranked models was still 53%. Model-averaging results showed a highly significant, positive effect of dimorphic hind wing morphology on average occurrence ranks. In addition, geographic range size and the potential to hibernate both as imago and as larval instars were positively and breeding in only one season negatively related with average occurrence ranks. Predatory feeding behaviour was positively related to average occurrence ranks in a single model only and showed a marginally significant effect in the model-averaging results. We additionally conducted a second approach with a 95% confidence set of models, summing up Akaike weights from largest to smallest until the sum of their Akaike weights exceeds 0.95 (Burnham and Anderson 2002). This approach showed similar results, as the added models comprise low explanatory power (see Appendix Table A.4 and A.5).

In our analysis between model residuals and taxonomic distances, we found no evidence of an effect of taxonomic relatedness of the beetle species on the model results (see Appendix, Table A.6), which is further supported by the wide spread of average occurrence rank values for species belonging to the same genus (e.g. *Carabus*, *Abax*, *Pterostichus*; Figure 1).

4. Discussion

Contrary to the results of previous studies on nestedness of ground beetle communities, we found only a weak or no nested pattern of carabid communities across seven regions in Central Europe. Nevertheless, we found consistent species occurrence ranks across regions. A suite of species traits were positively correlated with the average occurrence ranks. Large geographic range size together with the ability to hibernate both as larval instars and as imago and to breed in two seasons, predatory feeding behaviour and dimorphic hind wing morphology was positively correlated with higher species occurrences.

4.1 Nestedness of communities

We only found significant nested community patterns when comparing to a null model with equiprobable distribution of species, and only rarely when we used proportional occurrence probabilities as a null model. Our results are typical for communities which are either not nested or only slightly nested due to colonization dynamics (Ulrich et al. 2009). Overall, the studied carabid communities do not follow a strong nested order. For this reason, preserving exclusively the most species-rich communities will not preserve the rare ones (Fischer and Lindenmayer 2005). The weak evidence for nestedness which we found in the carabid communities of all seven regions cannot be a result of too small sample size, as our dataset is clearly one of the largest datasets published for insects in this context (cf. Soga and Koike 2012; Wright et al. 1998). We therefore conclude, like Ulrich and Gotelli (2007), that overall nested community patterns are less common than previously thought, including in ground beetles (e.g. Weller and Ganzhorn 2004; Zalewski and Ulrich 2006). Previous studies may be partly biased due to weaknesses in sampling or in statistical methodology, such as artefacts of passive sampling while using the Nestedness Temperature Calculator Program (NTC) (Fischer and Lindenmayer 2002).

4.2 *Species occurrence ranks*

As far as we know, we are the first to demonstrate similar species occurrence ranks within forest carabid communities in different regions across Central Europe. As the study regions vary widely in terms of fragmentation, edaphic parameters, and numerous other parameters, such a similarity in occurrence ranks is surprising. Recorded species with high occurrence ranks were usually highly abundant in all analysed regions, and therefore community compositions seem to be relatively stable across the studied regions. This result is consistent with previous studies which have demonstrated generally high abundances of these species (cf. Luka et al. 2009; Trautner et al. 2014). Species with low occurrence ranks did not occur in all of the regions, but always occurred in low abundances within the regions in which they occurred.

4.3 *Species traits shape community composition*

We found that species average occurrence ranks can be explained by trait-driven mechanisms (Table 5). Palaearctic geographical range size was positively correlated with average occurrence ranks. This concurs with the generally assumed positive association between the range size of a species and its local population sizes (cf. Gaston 2003), which is expected to influence the occurrence probability within sites. Consequently, larger geographic range sizes lead to an overall larger population size (Blackburn et al. 2009), which in turn leads to a higher number of individuals which can exploit more potential habitats. These factors may mitigate the effects of fragmentation and habitat loss. Other studies have shown that a small geographic range size can serve as a strong predictor of extinction risk for various taxa (e.g. Gaston and Fuller 2009).

Three species trait characteristics which increase the flexibility of the given species to adapt to different environmental conditions coincide with high occurrence ranks. These trait characters were dimorphic hind wing morphology, breeding both in spring and in autumn and the ability to hibernate as larval instars and as imago. Hind wing morphology was the most important driver of carabid occurrence ranks. Differences in hind wing morphology have long been suggested as an important driver of carabid community composition as these differences can lead to differing dispersal abilities and consequentially

to different colonization and recolonization probabilities (den Boer 1977). It is generally held that macropterous species have a higher dispersal power and a higher population turnover rate than brachypterous ones (den Boer 1990). However, species colonization probability is influenced by establishment ability as well (Gaston 1994), which is expected to be higher in brachypterous carabid species (Aukema 1991). We found that the probability of a high occurrence rank increases with hind wing dimorphism. Dimorphic species are assumed to have greater colonization rates, due to their variable ecological strategy (Kotze and O'Hara 2003). These species may profit from higher colonization and reproduction rates if they are winged during the migration period. Whereas the number of flightless individuals, with higher establishment abilities, increases under stable habitat conditions (Aukema 1991; Zalewski et al. 2012). This micro-evolutionary process may explain why dimorphic species are less threatened by fragmentation and species decline (Barbaro and van Halder 2009; Kotze et al. 2003; Kotze and O'Hara 2003).

Species with the ability to hibernate both as larvae and as imago as well as to breed in spring and in autumn coincide with high occurrence ranks. However, these two species traits were less important drivers of species occurrence ranks than hind wing morphology or geographic range size. Spake et al. (2016) found that species which overwinter as imago are associated with higher canopy cover, as it is shadier in the summer which reduces mortality due to larval desiccation. Species which are able to hibernate in both stages are less vulnerable to environmental conditions during hibernation, as they may be able to adapt to environmental changes by shifting their reproductive period, a process which has been shown in *Abax parallelepipedus* (Lauterbach 1964). Moreover, species hibernating in both stages as well as species using two breeding seasons may have a lower risk of extinction as they consist of different age classes, allowing them to better tolerate fluctuating abiotic and biotic conditions (Baumgartner et al. 1997). Spreading the risk across time, here expressed by the different abilities of developmental stages to survive different environmental conditions, may lead to higher survival rates and consequently to more stable population sizes (den Boer 1968).

While general theory tells us that species at higher trophic levels are more prone to extinction risk (Davies et al. 2000), we found lower occurrence ranks for granivorous species than for predators. This

can be due to the conservation programs of Central Europe, especially of Germany, which concentrate on encouraging natural-like dynamics in ecosystems (Brang et al. 2014). In forests used for timber production, the removal of individual trees is currently the predominant forestry method in use (e.g. LOEWE 1991), while clear-cutting or intensive thinning have decreased during the last decades. As a result, many forests are developing closed canopies, resulting in fewer herbs, grasses and fewer early successional tree species, reducing the food supply for granivorous carabids as they preferably feed on the seeds of grasses and herbaceous plants (e.g. Talarico et al. 2016). In our study the species with the lowest occurrence rank, *Amara makolskii* (syn. *Amara pseudocommunis*), forages on birch seeds (Burakowski 1967), a pioneer tree species typical for early successional forests (Ellenberg and Leuschner 2010).

Although recent studies have shown that larger species and species with higher habitat specialization show a strong population decline and are more prone to extinction (Brooks et al. 2012; Kotze and O'Hara 2003), we did not find evidence that body size or habitat specialization drives ground beetle occurrence ranks in Central European forests. In comparison with recent studies which included species from a large range of habitats, we studied only species specialized in forest habitats. The higher extinction vulnerability shown for larger ground beetles (Kotze and O'Hara 2003) is explained by their generally low population densities. Especially the natural fluctuations of population densities trigger the extinction vulnerability. However, forest ground beetles show only low fluctuation in abundances (Günther and Assmann 2004).

4.4 Implications for habitat management of Central European forests

Our results suggest that occurrence ranks can be a useful tool to identify rare species. For example, *Abax parallelepipedus* showed one of the highest occurrence ranks and is known to have stable population dynamics (Chaabane et al. 1996; Günther and Assmann 2004) and consequently little genetic differentiation (Marcus et al. 2015). In contrast, *Carabus irregularis*, a species which has high levels of genetic differentiation as a result of small population sizes or low gene flow (Homburg et al. 2014a) and is listed as an endangered species in Germany (Schmidt et al. 2016), had low occurrence ranks in our study. Thus, species of conservation concern can be identified by analysing occurrence ranks and species

traits. Moreover, ecological properties derived from species traits of rare species lead to the following recommendations for habitat management.

It is likely that ground beetle species with low occurrence ranks across regions are especially sensitive to local extinction processes. Hence, macropterous forest-inhabiting carabid species, especially when they are granivorous and rely on seeds of early successional tree species, are in particular at risk of extinction. Our results also show that brachypterous, forest-inhabiting carabid species are more susceptible to extinction than dimorphic species, and therefore conservation measures should account for these species. An example of such a conservation measure is assisted migration (Homburg et al. 2014a), which has been shown to be effective in maintaining community composition, especially of ground beetles with low occurrence ranks and limited power of dispersal (Malause and Drescher 1991; Vigna Taglianti et al. 2000). Ground beetles are a suitable taxon with which to test and develop protocols for the assisted migration of large, flightless insects, as they can be studied in enclosures over several generations. Such studies investigating the establishment of carabid populations have been conducted in the past (e.g. de Vries 1996; Schwöppe et al. 1998). Moreover, enclosures allow for the complete removal of introduced species to avoid potential introductions of species which may become invasive.

In conclusion, we suggest conservation efforts which encourage diverse forest management practices in order to support a wider range of species with low occurrence ranks, as brachypterous specialists of ancient woodland sites, such as *Carabus glabratus* have different habitat requirements than granivorous species, such as *Amara makolskii*. It is important to create early successional stages of forests, such as silviculture with large gap creation or proper coppice systems, in addition to the maintenance of stable old-growth stands with high coverage (Isaia et al. 2015; Negro et al. 2009; Spake et al. 2016). The current, predominant management strategies which encourage the transformation of forests to mature stands without early successional stages (LOEWE 1991), do not account for diverse species traits and the habitat requirements of some species.

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593 Tables and figures

594 Table 1. Compiled datasets (regions), with numbers of forest plots used to test for nested patterns and
 595 species traits. Code refers to the abbreviation given to each region. The original data can be obtained in
 596 the cited source literature.

Region	Code	Number of plots	Source
Belgium: Flanders	BE	66	Desender et al. (2002) Gaublomme et al. (2008)
The Netherlands	NL	13	Heijerman and Turin (1989)
Germany: Eastern lowlands of Lower Saxony	LS	32	Assmann (unpublished) Gürlich (unpublished) Lohse (1981) Dülge (1988) Günther and Assmann (2004)
Germany: Schleswig-Holstein / Mecklenburg-Western Pomerania	SM	36	Buse (unpublished) Gürlich (unpublished) Meitzner et al. (2006)
Biodiversity-Exploratories			
Germany: Schorfheide-Chorin	SEW	50	Lange et al. (2014)
Germany: Hainich-Dün	HEW	49	Lange et al. (2014)
Germany: Schwäbische Alb	AEW	50	Lange et al. (2014)

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Table 2. Species traits used in the trait-analysis.

Trait	Trait type	Trait value
Geographic range size	continuous	Extent of occurrence in the Palaearctic realm (km ²)
Degree of habitat specialization	continuous	Number of occupied habitat types in Central Europe
Body size	continuous	Mean body size (cm)
Hind wing morphology	ordinal	Brachypterous (flightless) Dimorphic (species with long and short winged specimens) Macropterous (predominantly flight-active)
Breeding season	nominal	Spring breeder Autumn breeder Both spring and autumn breeder
Trophic level	nominal	Granivore Predator
Hibernation stage	nominal	Imago Larval instars Both imago and larval instars

Source: Carabids.org database (Homburg et al. 2014b)

Table 3. Species richness, number of plots, spatial autocorrelation of community structure (Mantel correlation), NODF, and R², and the respective effect sizes (observed score - expected scores) obtained from the equiprobable (EE) and proportional (IT) null models. Significant effect sizes (P < 0.01) are bold-typed.

Region	Species	Plots	Spatial correlation	Score		EE null model		IT null model	
				NODF	R ²	NODF	R ²	NODF	R ²
BE	16	66	0.03	0.64	0.07	0.24	-0.11	-0.15	0.06
NL	11	13	0.16	0.78	0.01	0.15	-0.11	0.15	0.01
LS	17	32	0.47	0.66	0.07	0.14	-0.06	-0.07	0.07
SM	15	36	0.30	0.74	0.06	0.20	-0.06	0.15	0.06
SEW	15	50	0.13	0.71	0.01	0.14	-0.08	0.05	0.01
HEW	18	49	0.22	0.72	0.08	0.21	-0.04	-0.07	0.07
AEW	17	50	0.03	0.74	0.00	0.11	-0.06	-0.03	0.00

Table 4. Most parsimonious mixed models between average occurrence ranks and species traits. Only the top-ranked models with $\Delta\text{AICc} < 2$ are shown, ranked by AICc weight (grs: geographic range size, hwm: hind wing morphology, trl: trophic level, brd: breeding season, hb: hibernation stage).

Model	Explanatory variables included in model	df	ΔAICc	AICc weight	Adjusted R^2
1	grs + hwm + trl + hb	8	0	0.13	0.57
2	grs + hwm + brd	7	0.5	0.10	0.52
3	grs + hwm	5	0.56	0.10	0.44
4	grs + hwm + trl	6	0.77	0.09	0.47
5	grs + hwm + trl + brd	8	1.48	0.06	0.55
6	grs + hwm + trl + brd + hb	10	1.77	0.05	0.64
Full	all selected traits	15	28.12	0	0.69

Table 5. Average parameter estimates and importance value of the six top-ranked models ($\Delta\text{AICc} < 2$, average $R^2_{\text{Adj.}} = 0.53$). Significant results are bold-typed. Intercept: granivorous, macropterous, ground beetles breeding in spring and autumn, and hibernate as imago.

Explanatory variable	Estimate	Standard error	Adjusted SE	z-value	P-value	Importance value
Intercept	0.858	0.648	0.663	1.294	0.196	
Geographic range size	0.419	0.157	0.165	2.545	0.011	1.00
Hind wing morphology, dimorph	1.776	0.440	0.463	3.838	< 0.001	1.00
Hind wing morphology, brachypterous	1.042	0.519	0.539	1.932	0.053	1.00
Trophic level, predator	0.727	0.393	0.415	1.752	0.080	0.63
Breeding season, autumn	-0.893	0.408	0.433	2.064	0.039	0.41
Breeding season, spring	-0.867	0.409	0.431	2.010	0.044	0.41
Hibernation stage, both imago and larval instars	0.887	0.358	0.379	2.340	0.019	0.34
Hibernation stage, larval instars	0.112	0.384	0.402	0.280	0.780	0.34

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619 Figure 1. Average rank of species occurrences (A) and nestedness contribution (B) ($\pm$ one standard error)
 620 across the seven regions. Species with high average occurrence ranks were most frequent. Species with
 621 low nestedness contribution ranks contribute the most to the overall degree of nestedness in the
 622 community. Both rank orders were negatively correlated ($\rho = -0.74$, $P < 0.001$, Spearman's rank
 623 correlation).