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

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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

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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:

I) To which degree are the communities in the given landscapes nested?
II) Is it possible to identify species vulnerable to regional extinction?
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).

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

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.