Contribution of semi-open areas to the long-term conservation of insects: a perspective on ground beetles (Coleoptera: Carabidae and Cicindelidae)

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Estève Boutaud

Born 13.07.1988 in Angers (France)

LEUPHANA
UNIVERSITÄT LÜNEBURG

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Summary

Insects comprise most described species and play a critical role in the functioning of ecosystems, upon which humanity's continued existence depends. Numerous studies have recently reported evidence of a general decline in insects. Land-use change, specifically the destruction of habitats, a reduction in the quality of the remnants, as well as their increased isolation, appears to be the main driver behind these declines. In order to preserve insect diversity, nature conservation should aim to maintain or re-establish high-quality nature-based heterogeneous habitats. Moreover, those habitats need to be integrated within a network of ecological corridors to ensure the provision of functional connectivity. By restoring European landscapes to a more natural or diverse state, both objectives could be achieved. These landscapes contained a significant proportion of open and semi-open habitats as a result of the activity of various large herbivores. Consequently, their reintroduction is considered a promising conservation strategy to counteract insect decline and will lead to an extension of semi-open areas in the form of wood-pastures and wilderness areas.

Semi-open areas consist of a mosaic of forest-like patches dominated by trees or shrubs, isolated or in small groups, embedded in a matrix of heathland or grassland glades dominated by dwarf shrubs or grasses, respectively. These semi-open areas could contribute to insect conservation by providing both high-quality, nature-based heterogeneous habitats and increasing functional connectivity. However, evidence to support either habitat or corridor function is scarce, in particular, in the temperate region and for semi-open areas with glades dominated by dwarf shrubs. Therefore, knowledge about the preference of insect species for and within semi-open areas is needed to evaluate their contribution to insect conservation.

Ground and tiger beetles are a species-rich and ecologically diverse group. Because of their ability to respond to abiotic conditions at multiple spatial scales and effective use of various types of corridors, carabids are suitable for studying habitat association with heterogeneous semi-open areas as well as microhabitat preference within them.

The main aim of my dissertation is to gain a better understanding of the value of semi-open areas for the long-term conservation of insects in the European temperate region. For this, I used a large dataset consisting of 43 243 ground beetles belonging to 144 species sampled with pitfall traps in semi-open areas as well as adjacent open and forest habitats. This dataset was collected in two different landscapes, the Lüneburger Heide and the Schwäbische Alb, which provided different climatic and phytosociological conditions and covered a large extent of the variation found within semi-open areas in the temperate region of Europe. To complement this dataset, environmental features describing the landscape and vegetation structure were collected to investigate their effect on the response of ground beetles.

In the first case study, I investigated whether semi-open areas harbour unique ground beetle assemblages as well as high species richness and functional diversity. Additionally, I determined ground beetle associations with open and forest habitats as well as semi-open areas for each species. Carabid beetle assemblages in semi-open areas were distinct yet intermediate between those of the adjacent forest and open habitats. Species richness and functional diversity were comparable to at least those found in open habitats. Ground beetle species could be divided into several groups according to their associations, but only a few species were exclusively associated with semi-open areas and many with either forest or open habitats. Except for the majority of threatened species, the majority of species entered semi-open areas.

After I gained insight into the species association, in the second case study, I tested the previously identified groups, differing in their habitat preference and specialisation, for their relationship with vegetation and landscape features found within semi-open areas. I found that both habitat preference and specialisation were significant in determining the ground beetles' responses to environmental variables. Furthermore, species associated with open or forest habitats displayed opposite microhabitat preferences. Open habitat species preferred structures found within the heathland or grassland glades, while forest habitat species preferred structures within the treed patches. Lastly, species with increased habitat specialisation were more sensitive to microhabitat structures. In both case studies, my results were mostly similar in both study landscapes, irrespective of the glade vegetation or climatic condition.

In conclusion, semi-open areas could fulfil several functions for ground beetles in the temperate region. As heterogeneous nature-based habitats, semi-open areas appear unsuitable for most ground beetle species, underscoring the conservation value of the existing forest, heathland, and grassland habitats. However, semi-open areas could play a significant role in increasing functional connectivity. Moreover, if managed to maintain or establish high-quality open- and forest-like vegetation structures, these semi-open corridors may also accommodate the needs of specialist species. Thus, grazing reintroduction should target enhancing connectivity rather than habitat creation for ground beetle conservation. The possibility to monitor insect diversity and intervene when necessary to ensure a desirable outcome for biodiversity conservation makes the creation of wood-pastures a more suitable approach compared to hand-off rewilding. The evaluation of the reintroduction of grazing as a long-term conservation strategy was only possible when the strength of the association between ground beetles and semi-open areas was considered. Thus, I strongly recommend using this approach, which remains rarely used, when nature conservation strategies are evaluated. As currently conceived, semi-open areas resulting from the reintroduction of grazing may not contribute to the preservation of insect diversity but instead further contribute to its decline.

Alongside my investigation of semi-open areas, I also focused on the study of ground beetle dispersal in real-world conditions, which remain poorly known. The third case study focused on the dispersal of a flightless forest ground beetle, while the fourth considered a flight-active generalist species. Unsurprisingly, a large difference between the dispersal powers of the two species was found. Those species were not a priori selected for the particularity of their dispersal power; however, the dispersal rates found could be considered one of the fastest or slowest published rates for macropterous and brachypterous ground beetles, respectively. This highlights the limitations of our knowledge on this aspect of ground beetle biology and makes predicting future distributional changes of ground beetles resulting from either climate change or landscape change due to grazing reintroduction challenging.

Zusammenfassung

Insekten stellen die meisten beschriebenen Arten dar und spielen eine entscheidende Rolle für das Funktionieren der Ökosysteme, von denen auch das Fortbestehen der Menschheit abhängt. Zahlreiche Studien haben in letzter Zeit Belege für einen allgemeinen Rückgang von Insekten festgestellt. Landnutzungsänderungen, insbesondere die Zerstörung und die qualitative Verschlechterung der verbleibenden Lebensräume sowie deren zunehmende Isolierung, scheinen die Hauptursache für diesen Rückgang zu sein. Um die Insektenvielfalt langfristig zu erhalten, sollte der Naturschutz darauf abzielen, qualitativ hochwertige, naturbasierte und heterogene Lebensräume zu erhalten oder wiederherzustellen. Darüber hinaus müssen diese Lebensräume in ein Netz ökologischer Korridore integriert werden, um eine funktionale Verbindung zu gewährleisten. Durch die Wiederherstellung der europäischen Landschaften in einem naturnäheren bzw. diverseren Zustand könnten beide Ziele erreicht werden. Diese Landschaften bestanden zu einem beträchtlichen Teil aus verschiedenen offenen und halboffenen Lebensräumen, die durch das Einwirken unterschiedlicher, großer Pflanzenfresser entstanden. Die Etablierung von ähnlichen Beweidungssystemen gilt daher als vielversprechende Erhaltungsstrategie, um dem Insektenrückgang entgegenzuwirken, und wird zu einer Ausdehnung halboffener Gebiete in Form von Waldweiden und Wildnisgebieten führen.

Halboffene Gebiete bestehen typischerweise aus einem Mosaik waldähnlicher Bereiche, mit einzeln oder in kleinen Gruppen stehenden Bäumen oder Sträuchern, eingebettet in eine Matrix aus Gras- oder Zwergstrauch-dominierten Offenlebensräumen. Halboffene Lebensräume können zum Schutz von Insekten beitragen, indem sie sowohl qualitativ hochwertige, naturbasierte und heterogene Habitate bieten als auch die funktionale Vernetzung verbessern. Allerdings gibt es bisher nur wenige Belege für eine solche Lebensraum- oder Korridorfunktion, insbesondere in den gemäßigten Zonen und für halboffene Flächen mit von Zwergsträuchern dominierten Lichtungen. Daher sind Kenntnisse über die Präferenz von Insektenarten für und innerhalb halboffener Gebiete erforderlich, um deren Beitrag zum Insektenschutz zu bewerten.

Laufkäfer, inklusive Sandlaufkäfer, sind eine artenreiche und ökologisch vielfältige Gruppe. Sie eignen sich für die Untersuchung einer möglichen Bindung an halboffenen Lebensräume sowie einer Mikrohabitatpräferenz innerhalb dieser Gebiete, da sie in der Lage sind, auf abiotische Bedingungen auf verschiedenen räumlichen Ebenen zu reagieren und verschiedene Arten von Korridoren effektiv zu nutzen.

Das Ziel meiner Dissertation ist, ein besseres Verständnis für den Wert halboffener Gebiete für die langfristige Erhaltung von Insekten zu gewinnen. Zu diesem Zweck habe ich einen großen Datensatz mit 43 243 Laufkäfer aus 144 Arten verwendet, die mit Bodenfallen in halboffenen Bereichen sowie in angrenzenden Offen- und Waldhabitaten gefangen wurden. Dieser Datensatz wurde in zwei verschiedenen Landschaften, der Lüneburger Heide und der Schwäbischen Alb, erhoben, die unterschiedliche klimatische und pflanzensoziologische Bedingungen bieten und einen Großteil der in den europäischen gemäßigten halboffen Lebensräumen anzutreffenden Diversität abdecken. Ergänzt wurde dieser Datensatz durch Umweltparameter, die die Landschaft und die Vegetationsstruktur beschreiben, um ihre Auswirkungen auf die Laufkäfer zu untersuchen.

In der ersten Fallstudie untersuchte ich, ob halboffene Gebiete einzigartige Laufkäfergemeinschaften aufweisen und wie groß der jeweilige Artenreichtum und die funktionelle Vielfalt sind. Weiterhin ermittelte ich die Zusammensetzung von Laufkäfer-Lebensgemeinschften in offenen und bewaldeten Lebensräumen sowie mit halboffenen Gebieten für jede Art. Die Laufkäfergemeinschaften in den halboffenen Gebieten waren deutlich ausgeprägt, erwiesen sich jedoch als Mischung der Arten aus den angrenzenden Wald- und offenen Lebensräumen. Der Artenreichtum und die funktionelle Vielfalt waren mit denen in offenen Lebensräumen vergleichbar. Die Laufkäferarten ließen sich je nach ihrer Präferenz in mehrere Gruppen einteilen, wobei nur wenige Arten ausschließlich mit halboffenen Gebieten assoziiert waren und viele entweder mit Wäldern oder offenen Lebensräumen. Die Mehrheit der Arten läuft in halboffene Lebensräume, mit Ausnahme jedoch der meisten bedrohten Arten.

Nachdem ich einen Einblick in den Artenverbund gewonnen hatte, untersuchte ich in der zweiten Fallstudie die zuvor identifizierten Gruppen, die sich in ihrer Habitatpräferenz und Spezialisierung unterschieden, auf ihre Beziehung zu Vegetations- und Landschaftsmerkmalen in halboffenen Gebieten. Es zeigte sich, dass sowohl die Habitatpräferenz als auch die Spezialisierung von Bedeutung waren. Darüber hinaus zeigten Arten, die mit offenen oder bewaldeten Lebensräumen assoziiert sind, gegenteilige Mikrohabitatpräferenzen. Arten, die offene Lebensräume bewohnen, bevorzugten Strukturen, die in der Heide oder auf Wiesen zu finden sind, während Arten, die Waldlebensräume bewohnen, Strukturen in baumbestandenen Flächen bevorzugen. Schließlich waren Arten mit erhöhter Habitatspezialisierung empfindlicher für Mikrohabitatstrukturen. In beiden Fallstudien waren meine Ergebnisse bezüglich der beiden untersuchten Landschaften weitgehend ähnlich, unabhängig von der Lichtungsvegetation oder den klimatischen Bedingungen.

Zusammenfassend lässt sich sagen, dass halboffene Gebiete mehrere Funktionen für Laufkäfer in der gemäßigten Zone erfüllen könnten. Als heterogene, naturnahe Lebensräume scheinen halboffene Gebiete für die meisten Laufkäferarten ungeeignet zu sein, was im Umkehrschluss den Erhaltungswert der vorhandenen Wald-, Heide- und Grünlandhabitate unterstreicht. Halboffene Gebiete könnten jedoch eine wichtige Rolle bei der Verbesserung des funktionalen Verbunds spielen. Wenn sie so bewirtschaftet werden, dass hochwertige offene und waldähnliche Vegetationsstrukturen erhalten oder geschaffen werden, können diese halboffenen Korridore auch den Bedürfnissen spezialisierter Arten gerecht werden. Die Wiedereinführung der Beweidung sollte dabei eher auf die Verbesserung der Konnektivität als auf die Schaffung neuer Lebensräumen für Laufkäfer abzielen. Die Möglichkeit, die Insektenvielfalt zu überwachen und bei Bedarf einzugreifen, um ein für die Erhaltung der biologischen Vielfalt wünschenswertes Ergebnis zu erzielen, macht die Schaffung von Hutewäldern zu einem geeigneteren Ansatz als das "rewilding"-Verfahren. Die Bewertung der Wiedereinführung der Beweidung als langfristige Erhaltungsstrategie war nur möglich, wenn die Stärke des Zusammenhangs zwischen Laufkäfern und halboffenen Flächen berücksichtigt wurde. Daher empfehle ich nachdrücklich, bei der Bewertung von Naturschutzstrategien diesen Ansatz zu verwenden, der bisher allerdings nur selten angewendet wird. Halboffene Flächen, die aus der Wiedereinführung der Beweidung resultieren, tragen in ihrer jetzigen Form möglicherweise nicht zur Erhaltung der Insektenvielfalt bei, sondern könnten deren Rückgang sogar noch verstärken.

Neben der Untersuchung halboffener Gebiete konzentrierte ich mich auch auf die Untersuchung der Ausbreitung von Laufkäfern unter realen Bedingungen, über die bisher nur wenig bekannt ist. In meiner dritten Fallstudie fokussierte ich mich auf die Ausbreitung eines flugunfähigen Waldlaufkäfers, in der vierten auf eine flugaktive Generalistenart. Es überrascht nicht, dass ein großer Unterschied zwischen den Ausbreitungsfähigkeiten der beiden Arten festgestellt wurde. Diese Arten wurden zwar nicht von vornherein wegen ihrer besonderen Ausbreitungsfähigkeit ausgewählt, aber die festgestellten Ausbreitungsraten können als die schnellsten bzw. langsamsten angesehen werden, die für makroptere bzw. brachyptere Laufkäfer veröffentlicht wurden. Damit werden die Grenzen unseres Wissens über diesen Aspekt der Laufkäferbiologie verdeutlicht. Insofern macht es die Vorhersage über künftige Änderungen der Verbreitung von Laufkäfern infolge des Klimawandels oder von Landschaftsveränderungen beispielweise durch die Wiederherstellung von Weideflächen schwierig.

Chapter I

1. Contribution of semi-open areas to the long-term conservation of insects: a perspective on ground beetles (Coleoptera: Carabidae and Cicindelidae)

Grazed semi-dry grassland with little encroachment in the Schwäbische Alb.

1.1 General introduction

1.1.1 Insect decline, drivers, and the reintroduction of grazing

Our species has managed to trigger what scientists refer to as the Earth's sixth mass extinction (Wake & Vredenburg, 2008; Dirzo *et al.*, 2014; Cardoso *et al.*, 2020). Thus, biodiversity is declining, species are losing genetic resources, populations are disappearing from locations where they used to thrive, and some species are going extinct (Wagner, 2020). With over one million species described to date, most of them insects (Stork, 2018), biodiversity loss could be referred to as insect loss. Invertebrates have received less attention from the scientific community, making the estimation of extinction rates challenging (e.g. Dunn, 2005; Cardoso *et al.*, 2011; Chowdhury *et al.*, 2022). Nevertheless, extinction rates for insects are believed to be at least comparable, if not greater, than those for plants and vertebrates, which are already 100 to 1000 times higher than background rates (Dirzo *et al.*, 2014; Sánchez-Bayo & Wyckhuys, 2019; Wagner, 2020). Consequently, insects are likely the most threatened group on earth (Dirzo *et al.*, 2014; Sánchez-Bayo & Wyckhuys, 2019; Cardoso *et al.*, 2020). They are a critical component of the biosphere due to their roles in carbon and nutrient cycling (Yang & Gratton, 2014) and for being a key part of trophic chains (Price, 1997; Lister & Garcia, 2018). Consequently, insect biodiversity is a vital element for the functioning of ecosystems, upon which humanity's continued existence depends (Wilson, 1987; Cardoso *et al.*, 2020).

Numerous studies have recently found evidence for a general decline in insects, although these studies have several limitations (Cardoso & Leather, 2019). Nevertheless, the available information indicates that insect species richness, evenness, and abundance are declining and assemblage compositions are shifting (Habel *et al.*, 2019). The drivers behind such decline appear to be varied and notably include habitat loss, degradation, and fragmentation, light, nitrogen, and pesticides, invasive species, climate change, and overexploitation (Wagner, 2020). Furthermore, the results of such studies highlight that such drivers are often space-, time-, and even taxon-specific, although certain drivers appear to play a predominant role in the current insect decline. For terrestrial insects of Western and Northern Europe, land-use changes appear to be the main driver behind the past and current declines, with climate change being a more recent contributor (Habel et al., 2019; Wagner, 2020).

Anthropogenic activities such as agriculture and forestry intensification or extensification, urbanisation, and the building of transportation networks are responsible for habitat destruction, a reduction in their quality, and increased isolation (Habel *et al.*, 2019; Cardoso *et al.*, 2020; Wagner, 2020). To slow or revert the current trends in insect populations, nature conservation should devise solutions that directly counter such drivers (Cardoso *et al.*, 2020). Such solutions will need, on the one hand, to maintain or re-establish high-quality nature-based heterogeneous habitats. Moreover, these habitats need to be well integrated within a network of ecological corridors to ensure the provision of functional connectivity, which is required not only for species' short-term persistence (Samways, 2020; Samways *et al.*, 2020) but also to facilitate the adaptation to ongoing climate change (Arribas *et al.*, 2017). European landscapes in their prehistorical state, thus without the recent adverse anthropogenic transformations, are assumed to have provided both high-quality habitats and functional connectivity (Samways, 2020).

In Europe, much debate surrounds the question of the prehistoric state of the landscapes (Svenning, 2002; Whitehouse & Smith, 2010; Sandom *et al.*, 2014b). High-forest habitats have long been assumed to have dominated the landscapes, yet this view has been challenged. The wood-pasture hypothesis (Vera, 2000) postulates that landscapes will have included a large proportion of open and semi-open habitats due to the action of various large herbivores (Bakker *et al.*, 2016; Svenning *et al.*, 2016; Feurdean *et al.*, 2018). Following the extinction or range constriction of many of these species as a result of human activities during the early Holocene, forests will have been able to thrive (Sandom *et al.*, 2014a). Open, semi-open, and open woodland habitats have been preserved temporarily to various extents due to anthropogenic activities like animal husbandry or forestry practices such as coppicing and pollarding until the 20th century. However, following agriculture and forestry intensification, such habitats have strongly regressed or even become locally extinct (Vera, 2000; Hartel *et al.*, 2015; Feurdean *et al.*, 2018), and many of them are now considered threatened (Janssen *et al.*, 2016).

The reintroduction of grazing is considered a promising conservation strategy for the maintenance of a diverse array of habitats, and it could significantly contribute to the restoration of landscapes towards their prehistorical state (Samways *et al.*, 2020; Wagner, 2020). Large herbivores can notably enhance overall biodiversity, including insects, by promoting self-regulating heterogeneous ecosystems (van Klink *et al.*, 2015; Svenning *et al.*, 2016; Samways *et al.*, 2020). These reintroductions encompass a large range of options that differ concerning the degree of human intervention. On the one hand, the establishment of grazing with large domestic livestock will create wood-pastures (e.g. Rösch *et al.*, 2019; Garrido *et al.*, 2021). On the other hand, rewilding implies introducing or reintroducing various large wild herbivores, such as deer or surrogates for aurochs or tarpans, and creating wilderness areas (Svenning *et al.*, 2016). Between those two extremes, various intermediate strategies have been suggested, and even ways to combine both approaches into one (e.g. Hall, 2018; Garrido *et al.*, 2021; Dvorský *et al.*, 2022). Many of these approaches are actively being implemented in various locations across Europe (Pettorelli *et al.*, 2019; Rösch *et al.*, 2019; Garrido *et al.*, 2021).

Studies focusing on the effect of grazing reintroduction on biodiversity have mainly focused on the large keystone species or plants and seldom considered arthropods (Merckx, 2015; van Klink & WallisDeVries, 2018; Jakobsson *et al.*, 2020). When considered, the low-intensity grazing expected to be beneficial for insect diversity is seldom provided (van Klink *et al.*, 2015; van Klink & WallisDeVries, 2018), and studies focus on the short-term effects of grazing (Schulze et al., 2018). Following the wood-pasture hypothesis, a landscape vegetation structure cycle should lead to the development of park-like landscapes and in particular semi-open areas (Vera, 2000; Schulze *et al.*, 2018). The establishment of this particular vegetation structure requires both a lower density of large herbivores and time. So far, evidence to support such a cycle is lacking, as most grazing reintroduction projects fulfil neither requirement (van Klink & WallisDeVries, 2018). However, simulation experiments indicate that semi-open landscapes could be created and maintained by low-intensity grazing. Within those virtual landscapes, semi-open areas are created by the thinning out of forests by large herbivores and the limited establishment of trees and shrubs within the open habitats (Schulze *et al.*, 2018).

1.1.2 Semi-open areas, a promising conservation strategy for insect conservation

Semi-open areas consist of a mosaic of forest-like patches dominated by trees or shrubs, isolated or in small groups, embedded in a matrix of heathland- or grassland-like glades dominated by dwarf shrubs or grasses, respectively (Bergmeier *et al.*, 2010; Garbarino & Bergmeier, 2014). Consequently, semi-open areas do not fit within any traditional plant phytosociological associations but are a habitat complex (Bergmeier *et al.*, 2010; Janssen *et al.*, 2016). Nature conservation efforts have seldom considered semi-open areas, although they are threatened in Europe (Janssen *et al.*, 2016) and are only partly benefiting from protected status under the Habitat Directive, mainly in the boreal and Mediterranean bioclimatic zones (Bergmeier *et al.*, 2010).

Because of their protected status, the insect fauna of semi-open areas has been mostly studied in either the boreal (e.g. Talvi, 1995; Söderström *et al.*, 2001; Sverdrup-Thygeson *et al.*, 2010) or the Mediterranean regions (e.g. David *et al.*, 1999; Taboada *et al.*, 2006b; Merckx, 2015; Moreno *et al.*, 2016), while the temperate region remains understudied (but see Eggers *et al.*, 2010; Rösch *et al.*, 2019). However, the temperate region is likely to see major changes in its approach to nature conservation. This will result from a combination of land abandonment and a desire to implement conservation strategies that are more economically viable, thus requiring less human intervention (Carboni *et al.*, 2015; Navarro & Pereira, 2015; Pettorelli *et al.*, 2019). Furthermore, glades dominated by dwarf shrubs within semi-open areas are a key element in the oceanic part of temperate Europe (Garbarino & Bergmeier, 2014), yet, most studies on semi-open areas have focused on grass-dominated matrices (but see Eggers *et al.*, 2010).

Contribution to high-quality nature-based heterogeneous habitats

Semi-open areas could contribute to insect conservation in two ways. Their unique structure creates gradients in canopy closure, which affect light availability, temperature, and moisture at a fine scale, making semi-open areas highly heterogeneous (Bergmeier *et al.*, 2010; Díaz *et al.*, 2013; Moreno *et al.*, 2016). The structural heterogeneity, in agreement with the “habitat heterogeneity hypothesis” (MacArthur & MacArthur, 1961), is assumed to offer a broad range of niches that allow many species to co-occur (Díaz *et al.*, 2013). As a result, high species richness and unique assemblage composition are found within semi-open areas. Evidence to support this stems from many taxa, such as flowering plants (Kull & Zobel, 1991), lichens (Paltto *et al.*, 2011), bryophytes (Ingerpuu *et al.*, 1998), birds (Hartel *et al.*, 2014; Rösch *et al.*, 2019), bats (Jakobsson *et al.*, 2020), or reptiles (Godinho et al., 2011). Accordingly, semi-open areas have long been regarded as highly valuable for nature conservation (e.g. Bergmeier et al., 2010; Rösch et al., 2019).

Although semi-open areas appear to be capable of providing high-quality nature-based heterogeneous habitats, the few existing studies on invertebrates have yielded mixed results. While some lent support to their effectiveness for conservation (Talvi, 1995; David *et al.*, 1999; Horák *et al.*, 2018), others did not reach the same conclusion (Sverdrup-Thygeson *et al.*, 2010; Merckx, 2015; Gallé *et al.*, 2017; Rösch *et al.*, 2019; Somay *et al.*, 2021). Most studies on invertebrates in semi-open areas simply consider the presence of a species as evidence that they provide the resources to support its survival and reproduction. Thus, semi-open areas are considered to function as habitat; however, this may not be the case (e.g. Riecken & Raths, 1996; Lövei & Magura, 2017). Considering the particular environmental conditions found in semi-open areas and their assumed prehistorical prevalence, many authors assume that a set of species preferring semi-open conditions should exist but seldom attempt to provide evidence to substantiate this claim (e.g. Sverdrup-Thygeson *et al.*, 2010; Rösch *et al.*, 2019).

Contribution to functional connectivity

In addition to their function as habitats, semi-open areas could increase landscape connectivity. Preliminary evidence indicates that semi-open areas are suitable as corridors for birds (Fischer & Lindenmayer, 2002), ground beetles (Eggers *et al.*, 2010), or plants (Travers *et al.*, 2020). Moreover, the resulting corridors may be more advantageous than traditional corridors due to their ability to increase connectivity without increasing fragmentation, as species associated with both forest and open habitats could use them simultaneously (Eggers *et al.*, 2010; Travers *et al.*, 2020). This property of semi-open areas is certainly linked to their unique structure. Although promising, the possibility that semi-open areas could increase functional connectivity for insects remains understudied.

Similarly to traditional corridors, the increased connectivity provided by semi-open corridors will depend on two key aspects. Firstly, their quality, namely, the ability to provide organisms with appropriate structures, resources, and suitable abiotic conditions (e.g. Charrier *et al.*, 1997; Haddad & Tewksbury, 2005; Noordijk *et al.*, 2011). Few studies have considered the effect of vegetation and landscape structures on the presence or abundance of a particular invertebrate group in semi-open areas, and none in the temperate region (e.g. David *et al.*, 1999; Söderström *et al.*, 2001; García-Tejero & Taboada, 2016). Secondly, in addition to quality, the species' ecology, and in particular their habitat preference and specialisation, are critical in influencing the suitability of corridors (e.g. Noordijk *et al.*, 2011; Bertoncelj & Dolman, 2013; Habel *et al.*, 2020). The limited evidence available indicates that the species found in semi-open areas may not be randomly distributed but instead seek patches most similar to their original habitat (David *et al.*, 1999). Therefore, to optimise semi-open corridors, an understanding of the environmental features affecting their quality while simultaneously considering the species' ecology is required.

The contribution of semi-open areas to insect conservation will depend on both the function they fulfil and the species' identity. Thus, knowledge about the preference of insect species for semi-open areas, which is of critical importance for species conservation (Cáceres & Legendre, 2009), needs to be increased. In addition, for their function as a corridor, an understanding of the species' preference within semi-open areas, the environmental features influencing species' distribution, and the influence of key life history traits is needed. At last, to provide useful information for evaluating the conservation potential of semi-open areas, they need to be studied in landscapes representative of the varied climatic, edaphic, and phytosociological conditions found within the European temperate zone, where they are likely to develop.

1.1.3 Ground and tiger beetles as model taxa

Previous studies on biodiversity in semi-open areas within temperate Europe have focused on taxa mostly restricted to open (grasshoppers: Rösch *et al.*, 2019; dung beetles: Somay *et al.*, 2021) or forest habitats (Sverdrup-Thygeson *et al.*, 2010; saproxylic beetles: Horák *et al.*, 2018). Ground and tiger beetles (Coleoptera: Carabidae and Cicindelidae; hereafter ground beetles or carabids) comprise numerous well-documented and diverse species (Kotze *et al.*, 2011; Lorenz, 2022). Carabid beetles occur in most terrestrial habitats (Lövei & Sunderland, 1996; Koivula, 2011), although ground beetle association with semi-open areas has not been explicitly considered (see e.g. Gesellschaft für Angewandte Carabidologie, 2009). So far, about 40.700 extant ground beetle species are known worldwide, allowing them to rank third by species number among the order Coleoptera, which is the most diverse insect group (Lorenz, 2022). The German fauna comprises as many as 566 carabid species (Schmidt *et al.*, 2016).

Similarly to many insect taxa, declines in ground beetle species richness, abundance, and biomass have been documented (Kotze & O'Hara, 2003; Brooks *et al.*, 2012; Homburg *et al.*, 2019; Hallmann *et al.*, 2020; Skarbek *et al.*, 2021; Turin *et al.*, 2022). These declines might have dramatic consequences for ecosystem functioning. Carabid beetles notably play a crucial role in ecosystem food chains as predators of many invertebrate taxa or as zoospermophagous herbivores, and they are also an important food source for numerous vertebrate taxa such as birds and small mammals (Lövei & Sunderland, 1996; Price, 1997; Kotze *et al.*, 2011). In addition to insect decline studies, ground beetles are useful for investigating a large range of ecological and conservation topics, including the effects of landscape heterogeneity (e.g. Woodcock *et al.*, 2010; Neumann *et al.*, 2016), land use change (da Silva *et al.*, 2008; Cajaiba *et al.*, 2018), fragmentation (Niemelä, 2001; Augenstein *et al.*, 2012), habitat alteration (Koivula, 2011), as well as corridor use and quality (Gilbert-Norton *et al.*, 2010; Bertoncelj & Dolman, 2013; Magura *et al.*, 2017).

The capacity of ground beetles to serve as model organisms results from the species' tendency to be strongly associated with particular habitat types and the environmental conditions found within them. Carabids can respond to various stimuli that help them find and remain within suitable environmental conditions. In particular, ground beetles respond to variations in vegetation structures and resource features in the environment (Lövei & Sunderland, 1996; Antvogel & Bonn, 2001; Koivula, 2011). These responses are believed to be linked to the vegetation altering microclimatic conditions or resources such as prey or seed availability (Thiele, 1977; Diehl *et al.*, 2012; Stoutjesdijk & Barkman, 2014). In particular, the most important drivers of ground beetle distribution are linked with their ability to respond to changes in moisture and temperature at a small spatial scale (Thiele, 1977; Antvogel & Bonn, 2001; Koivula, 2011). Additionally, carabids have also been shown to respond to light (Colombini *et al.*, 1994; Andersen, 2006), to orient towards or away from silhouettes (Rijnsdorp, 1980; Niehues *et al.*, 1996; Andersen, 2006), as well as to perceive volatile chemical cues specific to their habitats or preys (Evans, 1988; Kielty *et al.*, 1996; Ali *et al.*, 2022). Furthermore, the affinity of carabids for well-defined environmental conditions was instrumental in the development of statistical techniques such as the now famous indicator analysis and related methods. These methods allow for characterising the affinity of a species for a predefined set of habitats or environmental conditions (Dufrêne & Legendre, 1997; Cáceres & Legendre, 2009).

The reintroduction of grazing will need to account for all kinds of biodiversity, from habitat specialists to ubiquitous generalists and currently threatened as well as least-concern species. Ground beetles contain not only eurytopic but also numerous stenotopic species, including threatened ones, many of which are associated with various open habitats (Nolte *et al.*, 2019). Carabid beetle habitat specialisation was the most important driver of extinction risk (Kotze & O'Hara, 2003; Nolte *et al.*, 2019). This results from both the decrease in available habitats and their fragmentation, although not all ground beetle species are affected equally. Habitat specialists are reluctant to move through unfavourable habitats, while more generalist species can easily move through the landscape using various habitat types (e.g. Vermeulen, 1994b; Koivula, 2002; Noordijk *et al.*, 2011). Differences in the wing and flight muscle development often reinforce this discrepancy between generalist species, which tend to be more flight-active, and habitat specialists that are often brachypterous (Nolte, 2018). However, both specialist and generalist ground beetle species make effective use of various types of corridors (reviewed by Gilbert-Norton *et al.*, 2010).

Although carabids are considered to be well examined, dispersal remains an area where knowledge is limited or even restricted to a handful of species (Riecken & Raths, 1996; Chapman *et al.*, 2005; Jopp & Reuter, 2005). Dispersal associated with range shift requires, to be considered successful, the establishment of a population in the area where individuals move (Den Boer, 1970; Bonte *et al.*, 2012). Most studies on insect movement using methods such as mark-release-recapture or radio-tracking are characterised by relatively low recapture rates, limited observation frequencies, and short time scales (Jopp & Reuter, 2005). Additionally, the beetle movements are sensitive to extrinsic and intrinsic factors such as air temperature, individual sex, and satiation (e.g. Fournier & Loreau, 2001; Růžičková & Veselý, 2018). This limits the ability to extrapolate to the landscape level and long-term scale. Thus, expanding our understanding of ground beetle dispersal is not only desirable in general, but it may also aid in determining the value of semi-open areas in their role as corridors for ground beetle conservation.

Because of this, ground beetles are an excellent model organism for studying not only habitat association with heterogeneous semi-open areas, but also microhabitat preference within them. Besides, carabid beetles, like many other insect taxa, are declining and could benefit from improved landscapes where semi-open areas are a common feature. In summary, identifying the response of ground beetles to semi-open habitats will help develop valuable and appropriate recommendations for nature conservation regarding the reintroduction of grazing by domesticated or wild large herbivores.

1.2 Aims, research questions, and methods

This dissertation aims to identify the value of semi-open areas for long-term ground beetle conservation within temperate Europe and to use the acquired knowledge to evaluate the suitability of grazing reintroduction for insect conservation. These topics are important from both an applied and a fundamental standpoint. For nature conservation, this knowledge could shed light on the consequences of the extension of semi-open areas and, thus, on some of the proposed conservation strategies aimed at reversing insect decline. Moreover, understanding the habitat preference of ground beetles within heterogeneous landscapes and within semi-open areas is relevant for the comprehension of the basic ecology of this model taxon as well as the past and future ecology of temperate landscapes.

My dissertation addresses the following main questions:

1) Do semi-open areas constitute a heterogeneous habitat for ground beetles (Fig. 1.1)?
2) Do semi-open areas fulfil the function of a corridor for ground beetles (Fig. 1.1)?
3) Do ground beetles with different ecologies react differently to environmental features found within semi-open areas (Fig. 1.2)?
4) Are the responses of ground beetles to semi-open areas dependent on the climatic and phytosociological context in which they are found?

This dissertation is divided into two parts. The first part (**Chapters II** and **III**) considers the ground beetle assemblages found in semi-open areas in two landscapes of Central Europe.

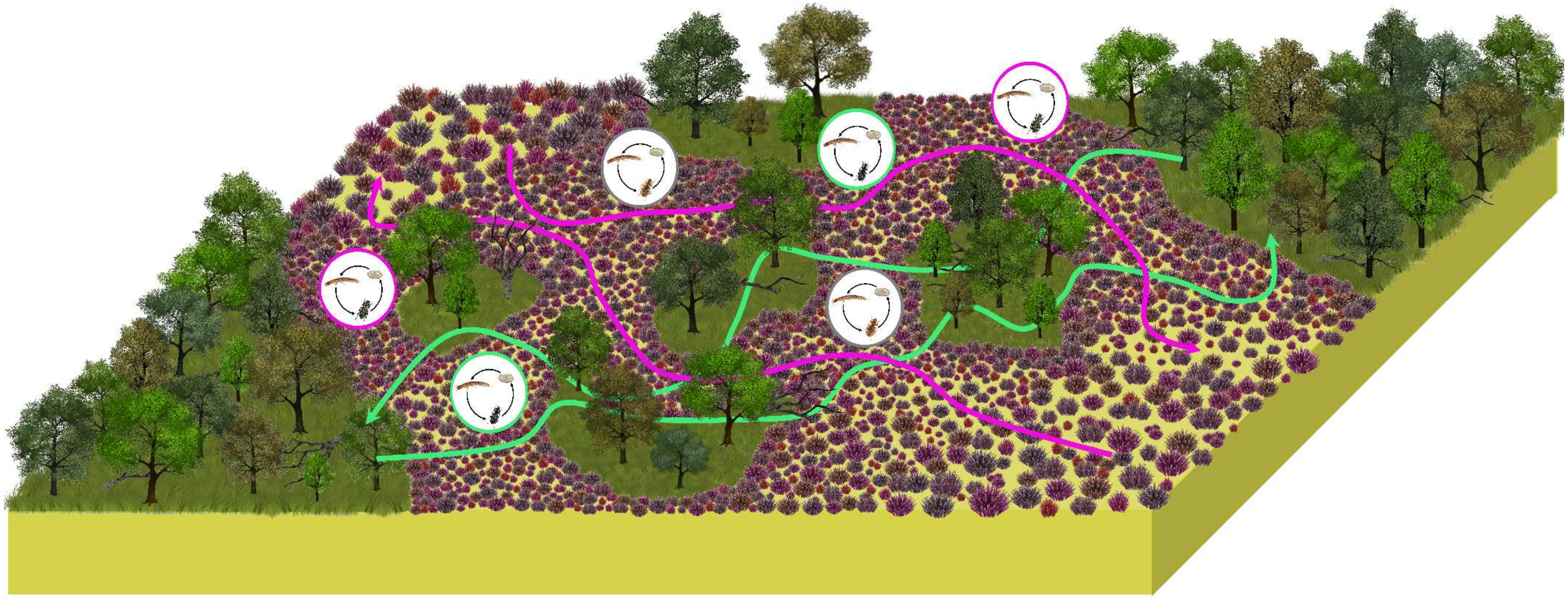

Figure 1.1: Possible functions fulfilled by semi-open areas susceptible to positively affect ground beetle conservation. The provision of habitat is indicated by the life cycle, while the improvement of functional connectivity is represented by the arrows. Semi-open, forest, and open species are indicated by grey, light green, and pink, respectively.

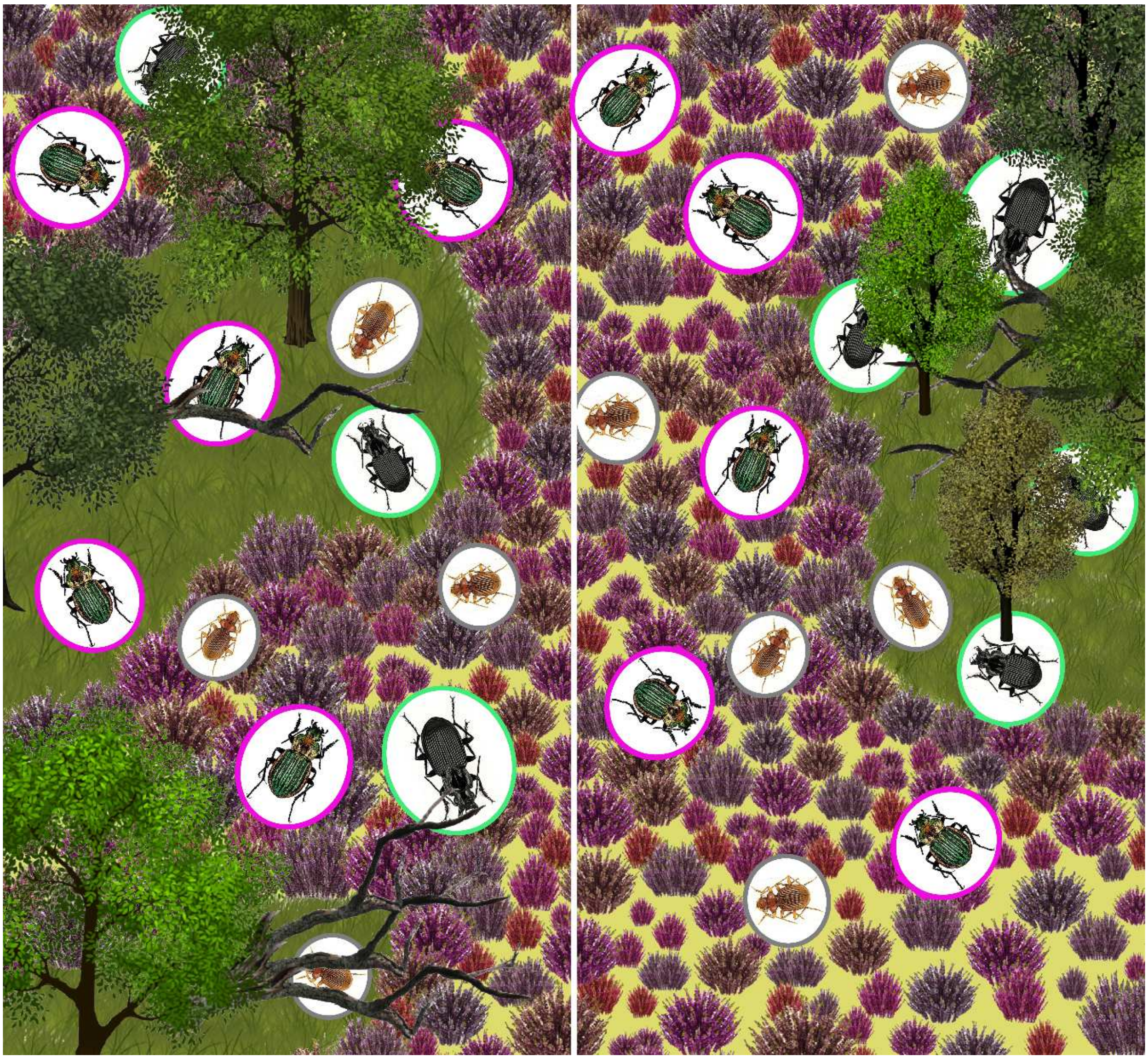

Figure 1.2: Ground beetles within semi-open areas: on the left side, no microhabitat preference is displayed by the species that use both open-like glades and forest-like patches. On the right side, open habitat species (pink) display a preference for the glades, while the species (light green) prefer the treed patches. In both cases, the semi-open species (grey) use the glades and treed patches evenly.

1.2.1 Study landscapes

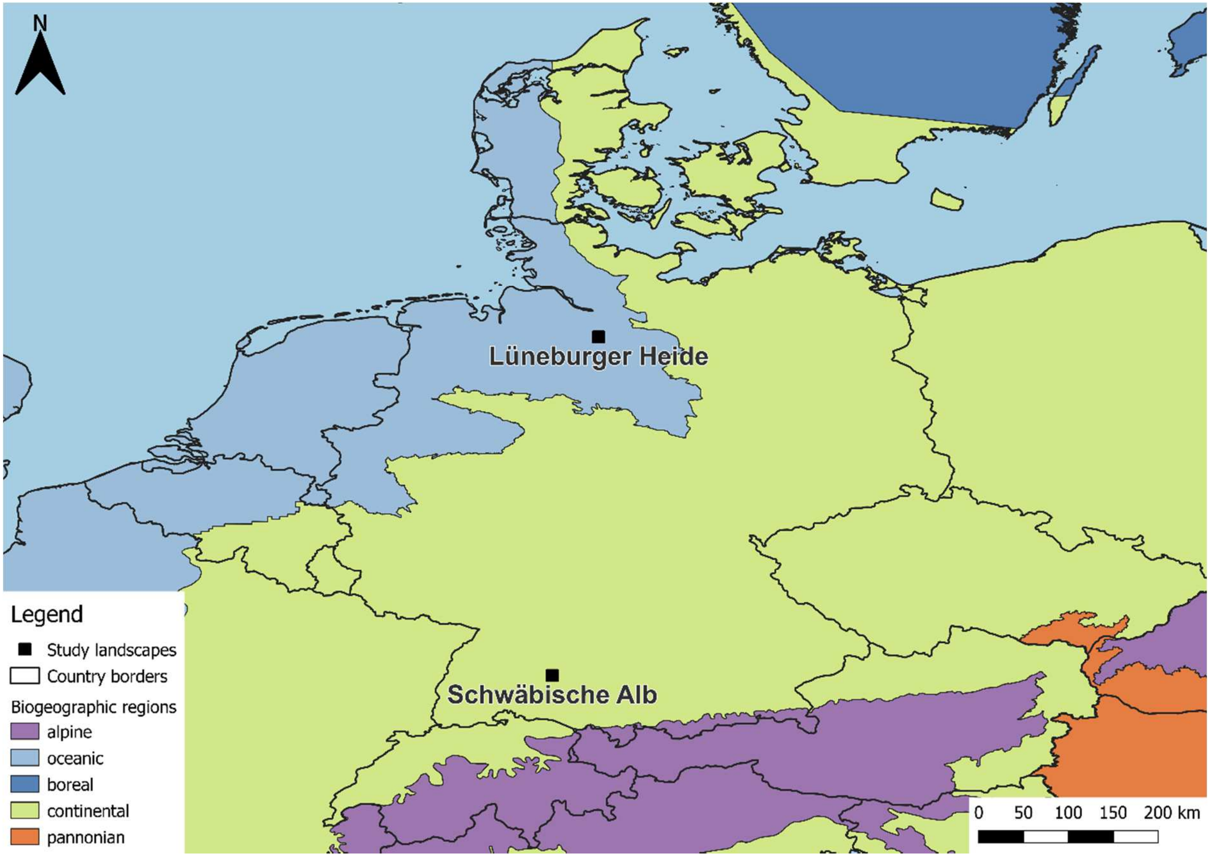

Figure 1.3: Location of the Lüneburger Heide and the Schwäbische Alb within Germany and the biogeographical regions of Europe (https://www.eea.europa.eu/data-and-maps/data/biogeo-graphical-regions-europe-3).

The first two case studies of this thesis (**Chapters II** and **III**) considered ground beetle assemblages in two landscapes whose climatic, edaphic, and phytosociological characteristics covered most of the diversity found within the European temperate region and semi-open areas. The first landscape, the Lüneburger Heide (hereafter Heide), is found within the north-western German lowland, while the second landscape, the Schwäbische Alb (hereafter Alb), is located in the south-western part of Germany (Fig. 1.3). The northern landscape is characterised by a suboceanic climate and nutrient-poor acidic podzol soils, while in the southern landscape, the climate is subcontinental with base-rich limestone soils (Beinlich & Plachter, 1995; Keienburg & Prüter, 2004). Furthermore, in the Heide, dry heathland dominated by heather (*Calluna vulgaris*) and in the Alb, semi-dry grassland dominated by the erect brome (*Bromus erectus*) are the characteristic remnants of open habitats. Accordingly, within the semi-open areas, the glades are dominated by heathland-like or dry-grassland-like vegetation in the Heide and the Alb, respectively (Fig. 1.4). In both landscapes, sheep flocks extensively graze the open habitats and semi-open areas.

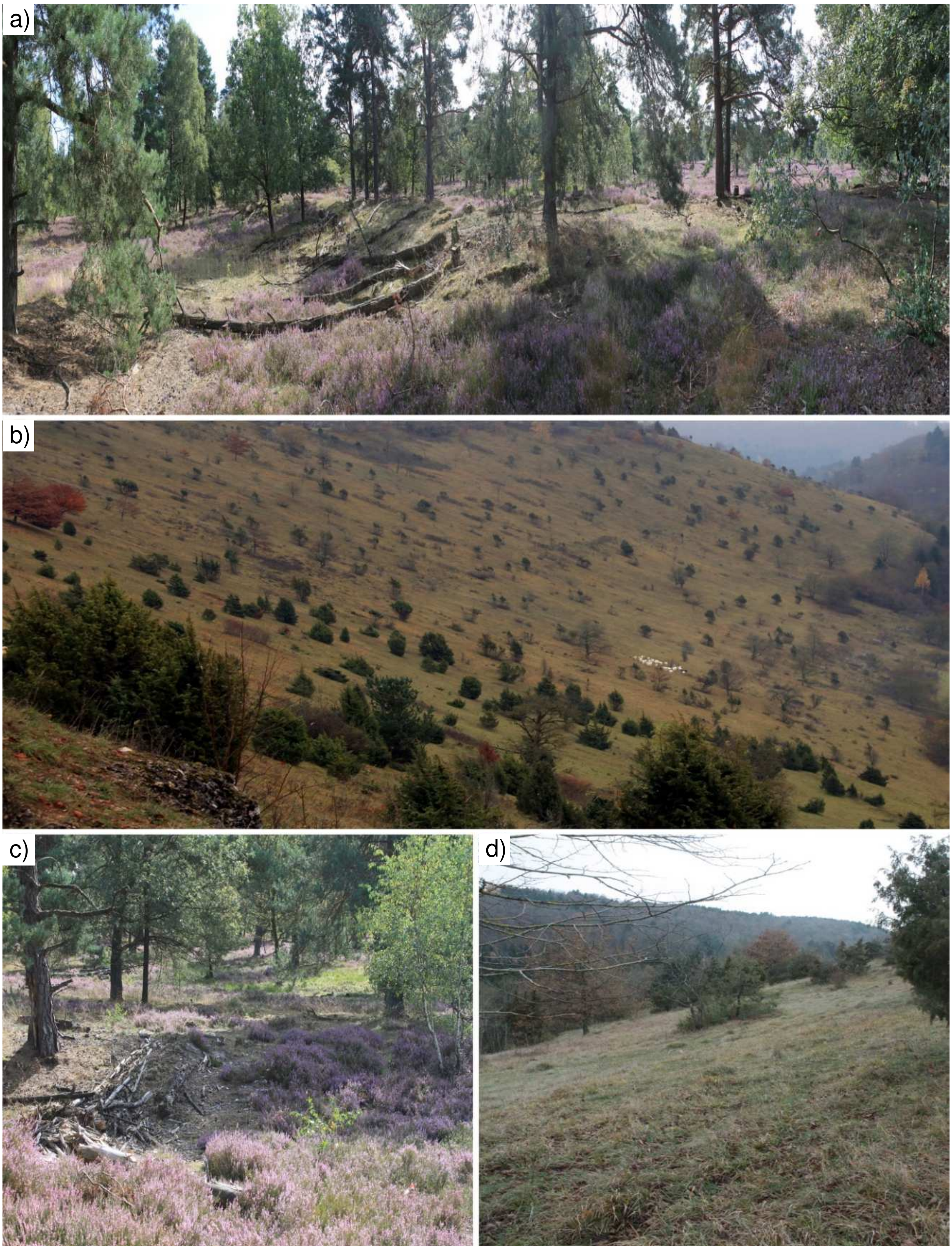

Figure 1.4: Visual aspect of semi-open areas in the Lüneburger Heide (a and c), where dwarf shrubs dominate the glades, and the Schwäbische Alb (b and d), where grassland-like vegetation dominates the glades. Note that the photos were taken in different seasons, namely summer for the Lüneburger Heide and winter for the Schwäbische Alb.

1.2.2 Sampling design

In each landscape, to obtain a large and representative dataset, ground beetles were sampled at eight sites. In each site, semi-open areas and the adjacent open and forest habitats were sampled using five pitfall traps, active year-round in the Heide and during the snow-free period in the Alb (Fig. 2.1a). The resulting dataset comprised 43 243 carabid beetles belonging to 144 species. More specimens were collected in the Heide, with 28 790 ground beetle individuals belonging to 96 species (8 671 individuals in the semi-open areas, 7 849 and 12 270 individuals in the forest and heathland habitats, respectively). In the Alb, 14 453 carabid beetles belonging to 95 species were collected (3 518 individuals in the semi-open areas, 6 926 and 4 009 individuals sampled in the forest and grassland habitats, respectively). To complement the dataset on ground beetles, many environmental features were recorded to describe the local vegetation structures surrounding the pitfall traps and the landscape context in which the study sites were located. For this, I estimated the aerial covers of ten woody, understorey, and ground vegetation features in a 1 m radius around each pitfall trap as well as two landscape ones.

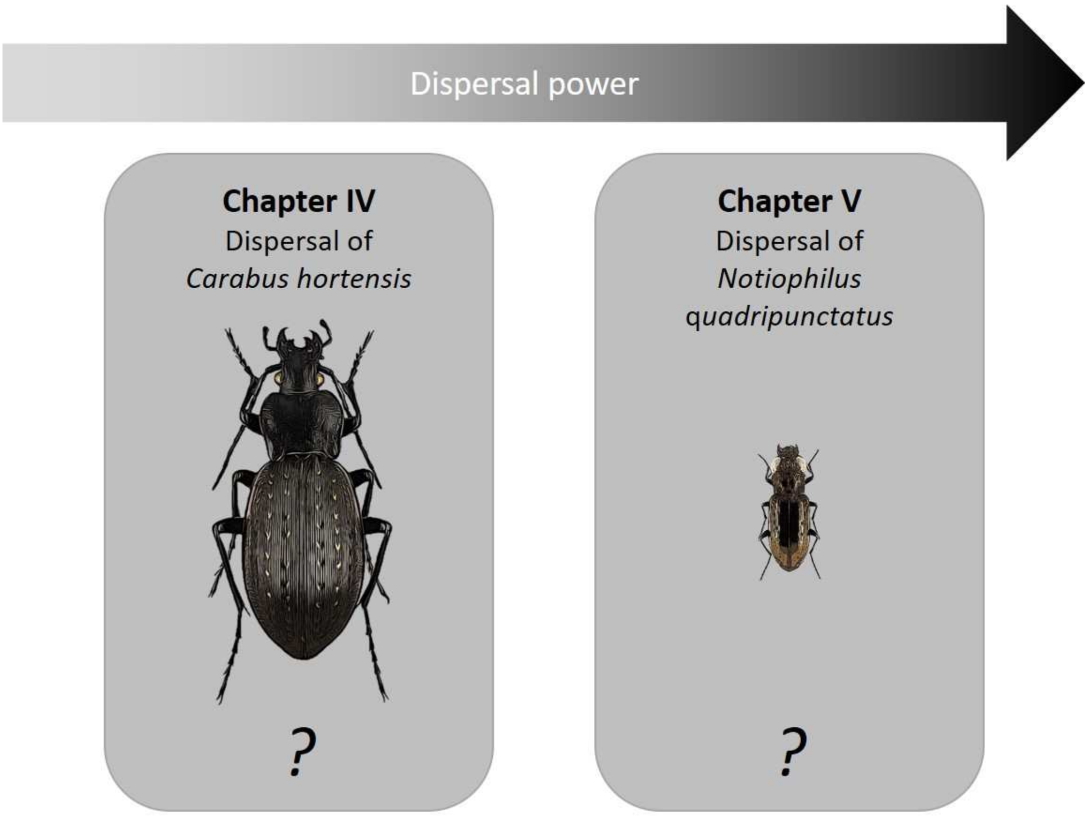

Figure 1.5: Overview of the species and assumed difference in dispersal power gradients considered in Chapters IV and V of the dissertation.

The provision of functional connectivity is critical for the long-term persistence of insect biodiversity, but information about dispersal in real-world conditions remains scarce for many insect groups, including ground beetles. Thus, in the second part of my thesis (**Chapters IV and V**), I included two case studies of the dispersal of a flightless habitat specialist and a flight-active generalist ground beetle species that correspond to the two ends of the dispersal power gradient (Fig. 1.5).

1.3 Summary of case studies

In **chapter II**, I present a study dealing with the questions of the function of semi-open areas for ground beetles (questions 1 and 2) and whether the fulfilled functions differ depending on the climatic and phytosociological context found in the study landscapes (question 3). To address these questions, I compared the carabid beetle assemblages, species richness, and functional diversity of semi-open areas to those of the adjacent forest and open habitats using permutational analysis of variance and linear regression. Moreover, I estimated ground beetle associations with semi-open areas, forest, and open habitats for each species using the point-biserial correlation coefficient. I found that carabid beetle assemblages in semi-open areas are distinct yet intermediate between those of the adjacent forest and open habitats. Furthermore, both species richness and functional diversity were similar between semi-open areas and open habitats. Ground beetle species could be divided into five groups according to their associations, which indicates that semi-open areas could fulfil several functions for ground beetles. The first group consists of a few species that are exclusively associated with semi-open areas and, contrary to popular belief, are also among the smallest. The next two groups include a larger number of species that were associated with semi-open areas and either open or forest habitats. Those three groups comprised about 40 percent of the carabid species. The last two groups include all species associated exclusively with either open or forest habitats and comprise a few species that effectively avoided semi-open areas, among them, many currently threatened species (Fig. 1.6). My results were globally similar in both landscapes, irrespective of the prevailing climatic conditions or the dominant vegetation of the glades.

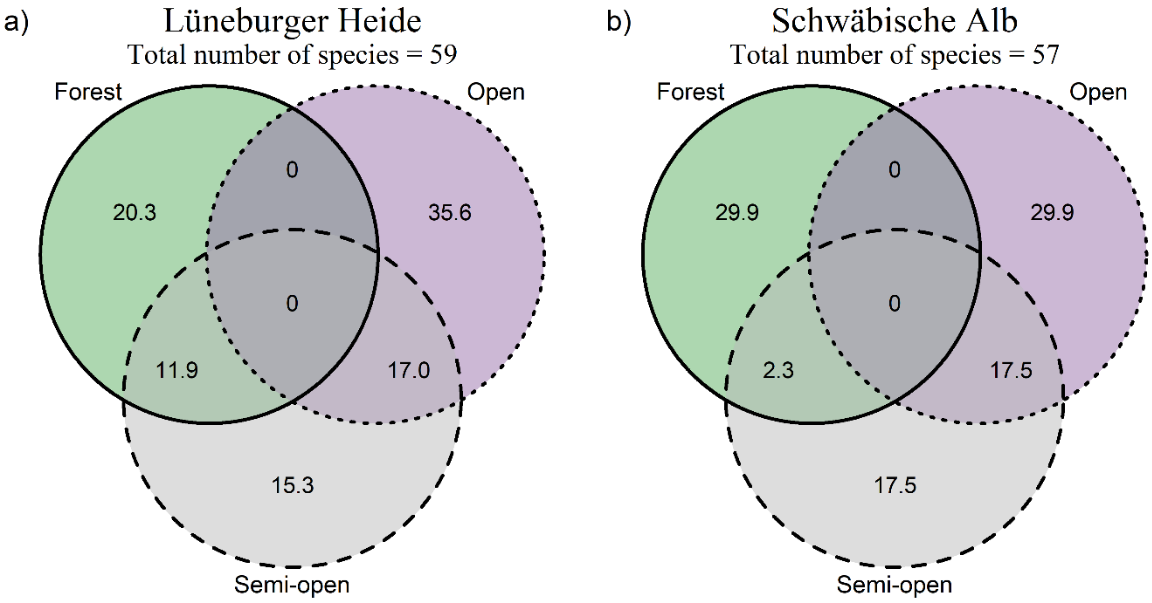

Figure 1.6: Percentage of associated species unique to or shared by the forest (green, solid line), the semi-open (grey, dashed line), and the open (purple, dotted line) habitats in the Lüneburger Heide (a) and the Schwäbische Alb (b).

Chapter III builds on the results from Chapter II and analyses part of the dataset on a finer scale. In this chapter, I address whether ground beetles with differing habitat preferences and specialisations react differently to the environmental features in semi-open areas (question 3). Similarly to the previous chapter, I also examined whether these responses to environmental features depended on the study landscapes (question 4). To answer both questions, I focused on the ground beetle data collected within the semi-open areas only. Additionally, I further divided the data into four groups based on the associations found in Chapter II, thus not considering the species exclusively associated with semi-open areas. The first two groups comprise the habitat specialists found to be exclusively associated with open or forest habitats, while the remaining two groups include less specialised species associated with semi-open areas and either open or forest habitats. Using multiple linear regression, I analysed the effects of vegetation structures and landscape features on both ground beetle taxonomic diversity and activity-density. Habitat preference and specialisation were instrumental in determining ground beetle' responses to environmental variables. Species associated with either open or forest habitats displayed opposite microhabitat preferences. Moreover, species with higher habitat specialisation responded more sensibly to microhabitat structures. With increased heather, bare soil, or reduced leaf litter cover, open habitat species richness and activity density increased in heathland or grassland glades. In contrast, the richness of forest habitat species and activity density increased in forest-like patches with high covers of bilberry, moss, and leaf litter (Table 1.1). Similarly to the previous chapter, my results were mostly similar in both study landscapes.

Table 1.1: Relationships between vegetation and landscape features and ground beetles rarefied species richness or standardised activity-density for five association groups in both the Lüneburger Heide and the Schwäbische Alb. The table also includes results for the species associated with semi-open areas exclusively, although they are not included in chapter III. Only significant relationships and trends are shown, with + and - indicating significant positive or negative relationship, respectively, while (+) and (-) indicate positive or negative trends, respectively.

Environmental features	**Open**	**Open & semi-open**	**Forest & semi-open**	**Forest**	**Semi-open**
Lüneburger Heide					
Species richness					
Heather cover	+				
Moss cover	+				
Bare soil cover	+	+		+	(+)
Bilberry cover				+	+
Distance to forest edge			-		
Activity-density					
Heather cover	(+)				
Grass cover		(-)	+		
Bare soil cover					+
Bilberry cover			(+)	+	
Deadwood cover				+	+
Distance to nearest tree	+				
Distance to open edge	-				
Schwäbische Alb					
Species richness					
Litter cover	-	(-)		+	+
Moss cover			+	+	
Distance to nearest tree			-		-
Distance to open edge				-	
Distance to forest edge					(+)
Activity-density					
Litter cover	-			+	+
Moss cover	-			+	-
Bare soil cover					+
Distance to nearest tree	+	(+)			(-)
Distance to open edge			-	-	(-)
Distance to forest edge					+

In **chapter IV**, I investigated the dispersal rate of the brachypterous ground beetle, *Carabus hortensis*. This study was also conducted in the Heide landscape, where forest stenotopic species started to re-establish new populations in recent woodlands in a westward direction. The presence of the species was monitored for 22 years, from 1995 to 2017, using baited live pitfall traps during its main activity season. From the first record in 1995 to the last record in 2017, *C. hortensis* covered a distance of nearly 2.7 km (Fig. 1.7). On average, *C. hortensis* disperses 127 m per year at a relatively constant rate over the study period. Although the locomotory activity of *C. hortensis* is comparable to or slightly lower than that found in similar-sized *Carabus* species, its dispersal rate appears comparatively low.

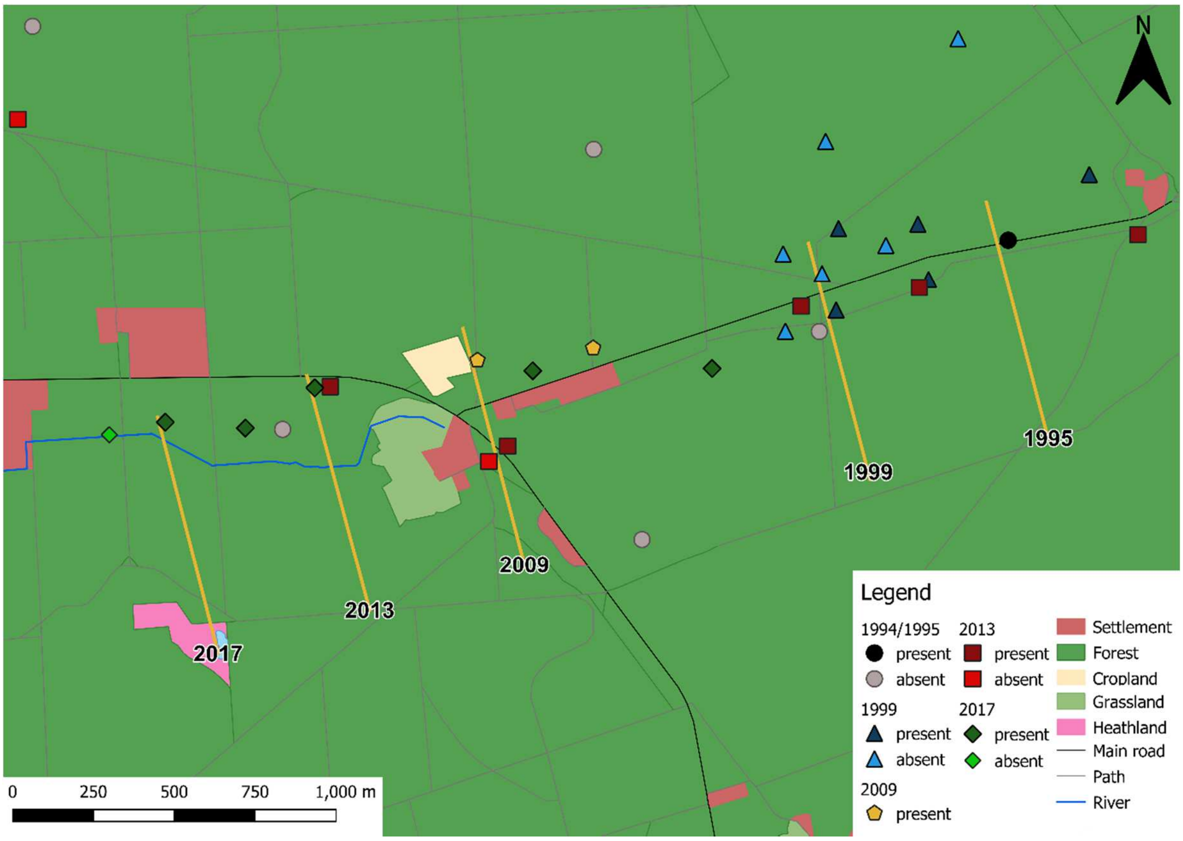

Figure 1.7: Detailed map of the *Carabus hortensis* dispersal investigation in the Lüneburger Heide, indicating sampling locations from the first detection in 1995 to 2017.

In **chapter V**, I studied the dispersal rate of the dimorphic ground beetle *Notiophilus quadripunctatus*. This study was triggered after the habitat generalist species, which was recently added to the German carabid fauna, was recorded for the first time in the Heide in 2018. To gain a better idea of *N. quadripunctatus*'s current distribution and estimate its dispersal rate in Central Europe, I compiled the information published in the literature or available on various online databases pertaining to the species. The species was recorded in the surrounding of Aachen in 2011 from a location that is about 350 km away from the Lüneburger Heide as the crow flies (Fig. 1.8). Thus, *Notiophilus quadripunctatus* is spreading in northern Europe at a rate of about 50 km per year. In addition, in the Heide, the newly established populations included exclusively winged individuals, confirming that dispersal occurs via flight. The estimated dispersal rate of *N. quadripunctatus* appears much greater than rates reported in the literature for other macropterous ground beetle species.

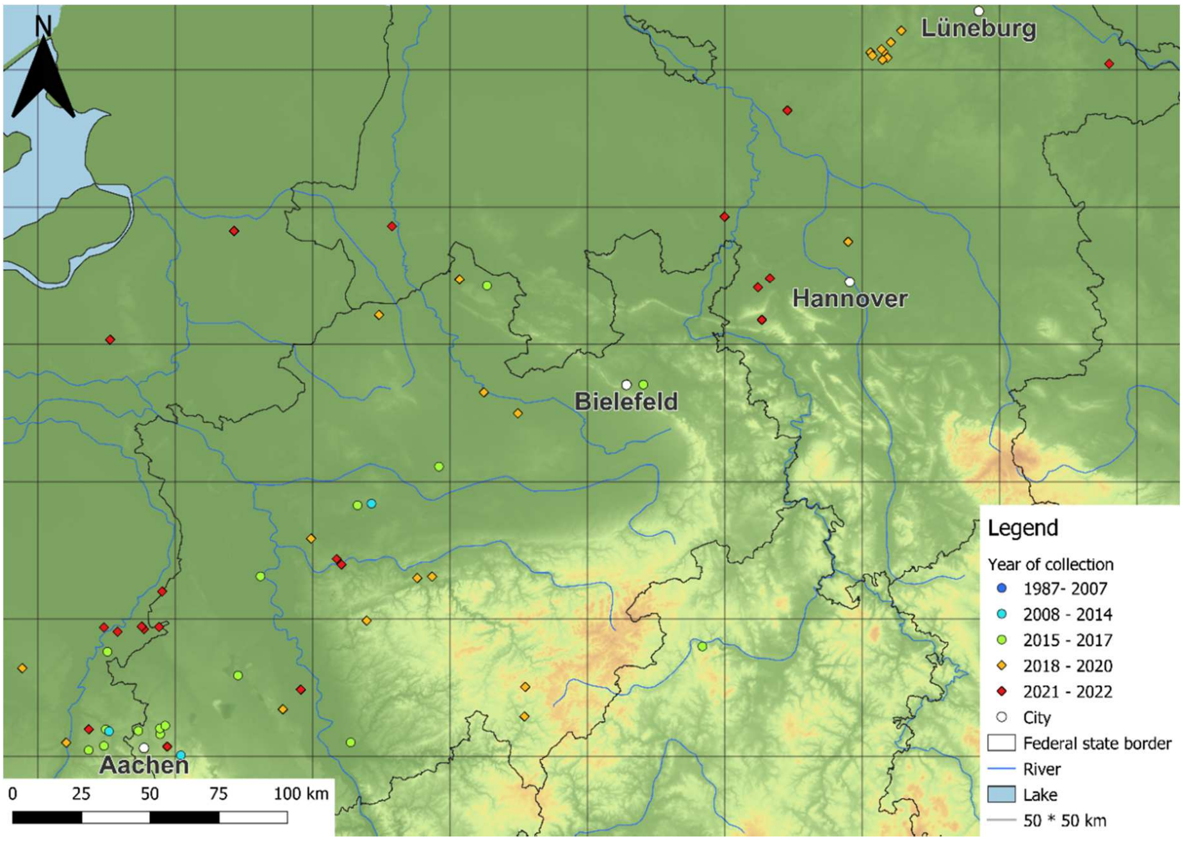

Figure 1.8: Detailed map of the investigation of *Notiophilus quadripunctatus* dispersal in northern Central Europe, indicating For the German lowland, the earliest record of the species was close to Aachen in 2011 (lower left corner), while the north-eastern most are around Lüneburg (upper right corner).

1.4 General discussion

My dissertation was one of the few that looked into ground beetle assemblages in heterogeneous semi-open areas within the temperate region. This allowed me to gain new insight into the role semi-open areas fulfil and the likely consequences of an extension of semi-open areas. I discovered that although semi-open areas have high species and functional diversity, only a limited number of species are exclusively associated with such environments. The remaining species could be further divided into four groups along gradients of habitat preference and specialisation. Furthermore, both life history traits were consequential in determining the ground beetles' responses to vegetation structures. At one end of the habitat specialisation gradient, species with high habitat specialisation could be found that were associated with either forest or open habitats exclusively. Moreover, within the semi-open areas, these species preferred microhabitats that were most similar in structure to those found in either forest or open habitats. At the other end of the gradient, species with lower habitat specialisation were associated with forest or open habitats and semi-open areas. While vegetation structures were less influential in determining microhabitat preference for these species, they still preferred vegetation structures that were typical for either forest or open habitats.

By investigating ground beetle dispersal in real-world conditions, I found extensive differences in the dispersal abilities of the two haphazardly selected species. As expected, the dispersal rate of the dimorphic generalist species, *Notiophilus quadripunctatus,* was higher than that of the brachypterous forest specialist, *Carabus hortensis*. Moreover, I found that the former species had what appears to be the fastest reported dispersal rate for a ground beetle, while the latter species appeared to have one of the slowest. Those results will be first discussed in a broader ecological context, and then the implications for ground beetle conservation as well as insect conservation will be considered.

1.4.1 Functions fulfilled by semi-open areas for ground beetles

The high heterogeneity found within semi-open habitats is assumed to offer a range of different abiotic conditions, allowing many species to coexist (Díaz *et al.*, 2013). This belief has been one of the main arguments for supporting semi-open areas like wood-pastures due to their obvious contribution to nature conservation. When I considered whether the presence of the species effectively indicates a preference for semi-open areas, I discovered that only 15 to 18% of the species studied were exclu-

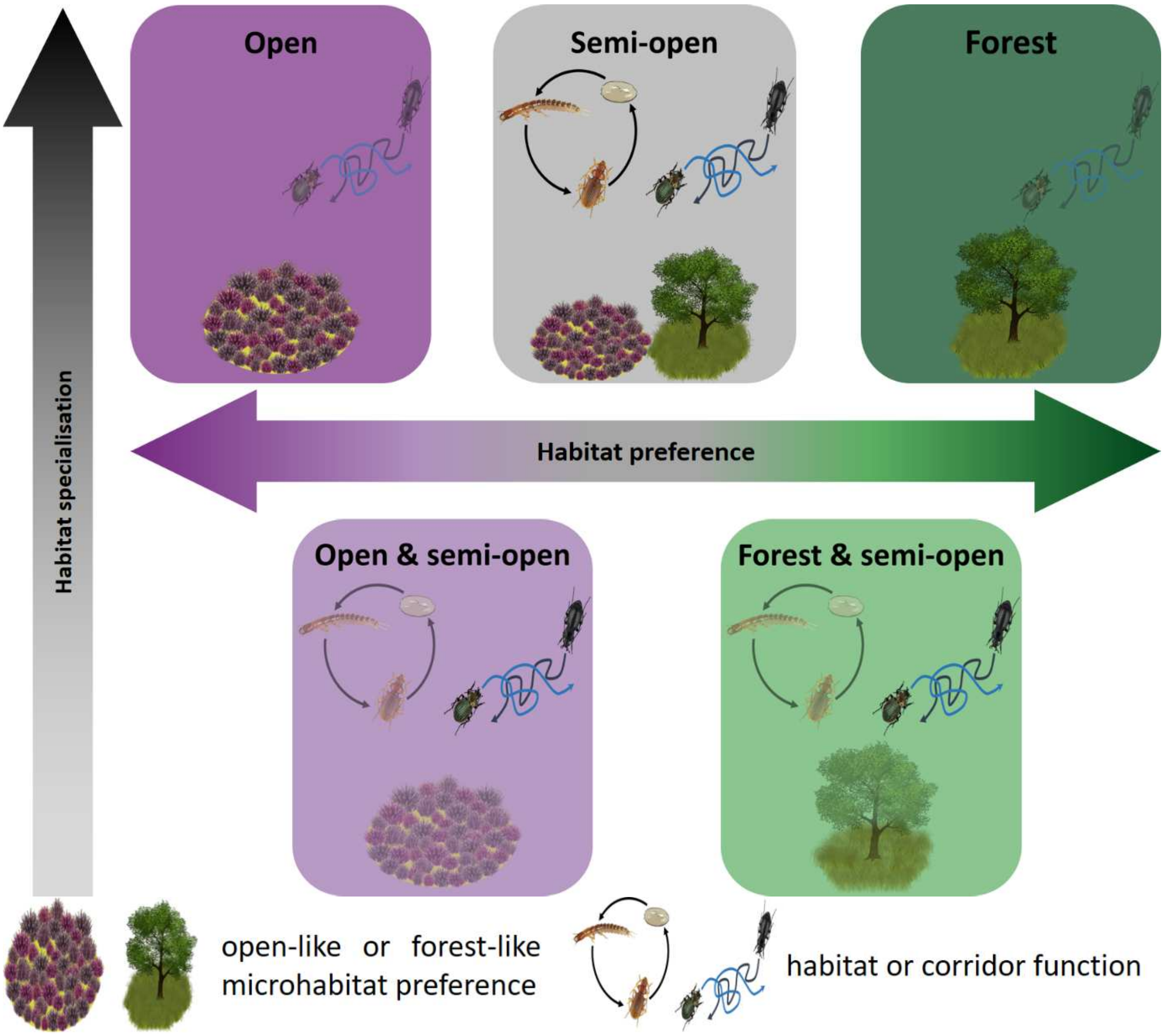

Figure 1.9: Semi-open areas' functions and microhabitat preferences within them for each habitat association group. The greyed out symbols indicate either that the function is only partly fulfilled or that the microhabitat preferences are weak for the given association group.

sively positively associated with semi-open habitats (Fig. 1.6). Thus, semi-open areas do appear to effectively fulfil the role of a habitat, at least for some species that may prefer the particular environmental conditions prevailing in those patches over those found within forest, heathland, or grassland habitats.

This percentage of species associated with semi-open areas is almost certainly an overestimate, with the true value almost certainly lower. Only a few of those species associated with forest edges and thus regarded as ecotone species (Heide: *Leistus ferrugineus* and *Pterostichus quadrifoveolatus*; Alb: *Panagaeus bipustulatus*) are likely to be truly dependent on semi-open areas (Molnár *et al.*, 2001; Tóthmérész *et al.*, 2014). The remaining species are well-known generalist species, many of them associated with various frequently disturbed open habitats such as arable fields or ruderal areas (Gesellschaft für Angewandte Carabidologie, 2009). Considering the microhabitat preference for these species, they effectively appear to be attracted to unique combinations that are likely to be rare outside of semi-open areas. In the Heide, typical microhabitats were characterised by the presence of both deadwood and bare soil, a combination that is mostly found in disturbed sites resulting from the forest thinning that created semi-open areas. In the Alb, the richness and activity-density of semi-open associated species increase with the proximity of trees and litter but decrease if the forest habitats are close by. At last, the trend of a decrease in activity with increasing distance to open habitats is in line with many of those species being open habitat generalists (Fig. A1.1 and A1.2). Similarly to our findings, ground beetles considered eurytopic and open habitat generalist species were typical in semi-open Dehesa assemblages (Taboada *et al.*, 2006a, 2011). Similarly to our result, ground beetles considered as eurytopic and open habitat generalist species were found to be characteristic of the assemblages within semi-open Dehesa (Taboada *et al.*, 2006a, 2011). Within the temperate region, the grasshopper *Oedipoda caerulescens*, which is dependent on such frequently disturbed microsites, has also been found to be strongly associated with semi-open areas created through forest thinning over less disturbed pastures (Rösch *et al.*, 2019).

Given their intermediate nature and their high proportions of forest-open habitat edges, semi-open areas are regarded by some authors as extended ecotones (Bergmeier *et al.*, 2010; Somay *et al.*, 2021). However, studies focusing on ground beetles at forest-open habitat ecotones found assemblages highly similar to the forest assemblages (e.g. Heliölä *et al.*, 2001; Lacasella *et al.*, 2015), while we retrieved semi-open habitat assemblages that were distinct from the forest ones. Moreover, studies on ecotones found an absence or a very low number of species that were associated with this particular environment (Roume *et al.*, 2011). We discovered a greater number of species associated with semi-open habitats, even though this number may be overestimated. Similar dissimilarities between forest ecotones and semi-open habitats have been reported for dung beetles (Somay *et al.*, 2021). The physionomic difference between forest edges and semi-open areas is likely the main factor explaining such a difference. Forest edges entail a narrow, abrupt transition between open and forest habitats and environmental characteristics that are most similar to the forest interior (Heliölä *et al.*, 2001; Roume *et al.*, 2011). On the contrary, semi-open areas are much wider and appear to exhibit distinct environmental conditions (see Travers *et al.*, 2020), which in turn result in specific ground beetle assemblages. Consequently, semi-open habitats appear to be different from ecotones and should likely not be regarded as such.

Unexpectedly, the majority of species I recorded within semi-open areas were found to be exclusively associated with long-recognised habitats such as forests, heathlands, or grasslands (Díaz *et al.*, 2013; Moreno *et al.*, 2016). The presence and activity-density of these habitat-specialist species within semi-open areas depended strongly on the particular vegetation structures found within them. Furthermore, forest and open habitat species had opposing preferences within semi-open areas. A similar distribution pattern within semi-open areas has been reported for open- and forest-associated Mediterranean saprophagous macroarthropods (David *et al.*, 1999). In my case study, species associated with open habitats preferred open-like microhabitats as found within the glades. Characteristics of these microhabitats were higher heather and bare soil cover in the Heide and, in the Alb, a low cover of leaf litter as well as wider glades in both landscapes. On the contrary, species associated with forest habitats preferred forest-like microhabitats as found within the treed patches. These microhabitats were characterised by the increased cover of bilberry and dead wood in the Heide and, in the Alb, by higher leaf litter and moss cover. In both cases, these preferences are in agreement with the ecology of heathland and grassland species (e.g. Eversham & Telfer, 1994; Vermeulen, 1994b; Noordijk *et al.*, 2011; Bertoncelj & Dolman, 2013), as well as forest ground beetle ones (e.g. Heliölä et al., 2001; García-Tejero & Taboada, 2016; Lövei & Magura, 2017).

Considering the limited number of individuals entering semi-open areas and their preference for one-half of the available microhabitats, it appears that the range of different abiotic conditions provided do not suit species associated with open and forest habitats. Thus, these species are unlikely to use semi-open areas as habitat. However, only a few of these species avoided semi-open areas effectively, indicating that they can be used for dispersal (Eggers *et al.*, 2010). Two main factors could be responsible for the avoidance displayed by some species. Firstly, the inability of the species to reach the sampled locations within the semi-open areas, or secondly, the unsuitability of these areas due to inadequate microhabitat conditions. Specific information about most of those species' dispersal rates is not available; nevertheless, our sampling locations within the semi-open habitats are well within the range of what even brachypterous species could reach within one activity period (Baars, 1979; Rijnsdorp, 1980; Vermeulen, 1994a). In addition, a decent number of individuals of those species were recorded in a decent number in some of the studied semi-open areas while being mostly missing from others, which tends to indicate that microhabitat suitability is the likely driver (see table A1.1 for the Lüneburger Heide). Consequently, improving the quality of microhabitats in semi-open areas is likely to lead to an improvement in their ability to function as a corridor for stenotopic species associated with open and forest habitats, including those currently threatened.

The remaining species were found to be associated with both semi-open areas and either forest or open habitats and displayed a weaker preference for either glade or treed patch vegetation structures. Thus, semi-open areas appear to function as habitat corridors (sensu Noordijk *et al.*, 2011) for species with lower habitat specialization. However, this interpretation is only valid if the mechanism considered to drive the presence of those species in semi-open areas is niche differentiation. Habitat patches are not isolated from one another, and, as mentioned previously, our sampling locations were not so far away as to prevent ground beetles, even with weak dispersal abilities, from reaching our pitfall traps. In fact, carabids are known to regularly cross habitat edges, so mass effects (also referred to as spillover) could also be an important but overlooked mechanism (Mouquet & Loreau, 2002; Ewers & Didham, 2008; Boetzl *et al.*, 2016). Resulting from the recurrent dispersal of individuals from adjacent habitats with higher reproduction success, mass effects may be responsible for the presence and abundance of these species in semi-open areas (Shmida & Wilson, 1985; Mouquet & Loreau, 2002). Mass effects appear neglectible compared to niche differentiation across similar environments (Brooks *et al.*, 2008). However, mass effects are expected to be maximal when differences between environments are moderate, such as between semi-open areas and adjacent open and forest habitats ("intermediate difference hypothesis", Kunin, 1998).

The ability of ground beetles to avoid entering unsuitable habitats through the perception of various environmental cues is likely to be reduced due to the intermediate nature of vegetation structures found in semi-open areas. Limited evidence effectively confirms that ground beetle species have an increased tendency to move from open and forest habitats into semi-open areas (Assmann & Günther, 2000; Assmann *et al.*, 2016). In addition, within the semi-open areas, neither the narrow glades nor the treed patches are likely to support sufficient reproduction of most of these species (e.g. Petit, 1994; Vermeulen, 1994a; Noordijk *et al.*, 2011). The available evidence based on teneral found in the Heide (data about teneral were not available in the Alb) effectively confirms that reproduction is likely limited (Table A1.1). Consequently, the continuous presence of many of these species in semi-open habitats at comparable abundance with either forest or open habitats likely depends on mass effects and thus on constant immigration from the adjacent source habitats. In some instances, however, semi-open habitats will allow species that reproduce in distinct habitats to exploit a greater proportion of the landscape, for example for foraging or finding mates (Rijnsdorp, 1980; Riecken & Raths, 1996; Růžičková & Veselý, 2018). In either case, increased functional connectivity will result from the presence of semi-open areas, as they will fulfil the role of a corridor for these species. In addition, this function of semi-open areas will be fulfilled even if the vegetation structures, and thus the corridor quality, are less than optimal.

1.4.2 Influence of landscape climatic and phytosociological features

Although my results were generally consistent for both landscapes, they differed in some respects. The carabid assemblages of semi-open habitats in the Heide were more similar to those in the forest, and the species associated with heathland habitats or heathlands and semi-open areas responded more sensitively to vegetation structures. In the Alb, assemblages were more similar to those found in the grasslands, while the species associated with forest habitats or forests and semi-open areas responded more sensitively to vegetation structures. Few studies compared insect assemblages in semi-open areas from different locations, but the limited evidence points to an absence of difference (Somay *et al.*, 2021). However, similar patterns were found when comparing plant assemblages in the same studied landscapes (Travers *et al.*, 2020). Furthermore, the Ellenberg indicator values for the plant assemblages found in the semi-open areas of the Heide indicated higher moisture than in the Alb (Travers *et al.*, 2020). These alterations of microclimatic conditions could be explained either by the prevailing climate or by the dominant vegetation in the glades, or a combination of both.

In the Heide, the cooler and moister oceanic climate is likely to result in a lesser contrast in the microclimatic conditions found within semi-open areas when compared with the forest. In addition, heather and mosses, which are dominant vegetation elements in the Heide semi-open glades, have been shown to alter microclimatic conditions toward higher moisture and cooler temperatures too (Gimingham, 1972; Schirmel *et al.*, 2011). In the Alb, comparable microclimatic conditions between the semi-open areas and the semi-dry grasslands likely result from both the warmer and drier subcontinental climate and the absence of vegetation capable of altering microclimatic conditions, such as heather. Those alterations of the microclimate are likely to favour a specific pool of species in accordance with their habitat preferences in each landscape. In fact, species associated with forest habitats are known to prefer cooler and moister conditions, while species of open habitats prefer warmer and drier conditions (Thiele, 1977). Consequently, a larger number of the forest-associated species enter semi-open areas in the Heide compared to the Alb. In addition, these species are more sensitive to the vegetation structure that creates suitable microclimatic conditions in the Alb than in the Heide. For species associated with open habitats, the opposite was found, with a higher number entering the semi-open areas in the Alb and a stronger dependence on vegetation structure in the Heide.

1.4.3 Ground beetle dispersal in real-world conditions

Dispersal ability varies among ground beetle species, even between closely related species. Due to the challenges involved, the dispersal ability of a species is often not directly measured but estimated based on morphological traits. The most commonly used trait is wing morphology, with macropterous and dimorphic species having a greater dispersal power compared to brachypterous species (Den Boer, 1970). Unsurprisingly, I found that the dimorphic species *Notiophilus quadripunctatus*' dispersal rate is nearly 400 times greater than that of the brachypterous *Carabus hortensis* (Fig. 1.9). These results confirm the difference between species able to disperse by flight and those limited to walking. However, for each species, the recorded dispersal rates stand out compared with the information available in the literature, even within their respective groups.

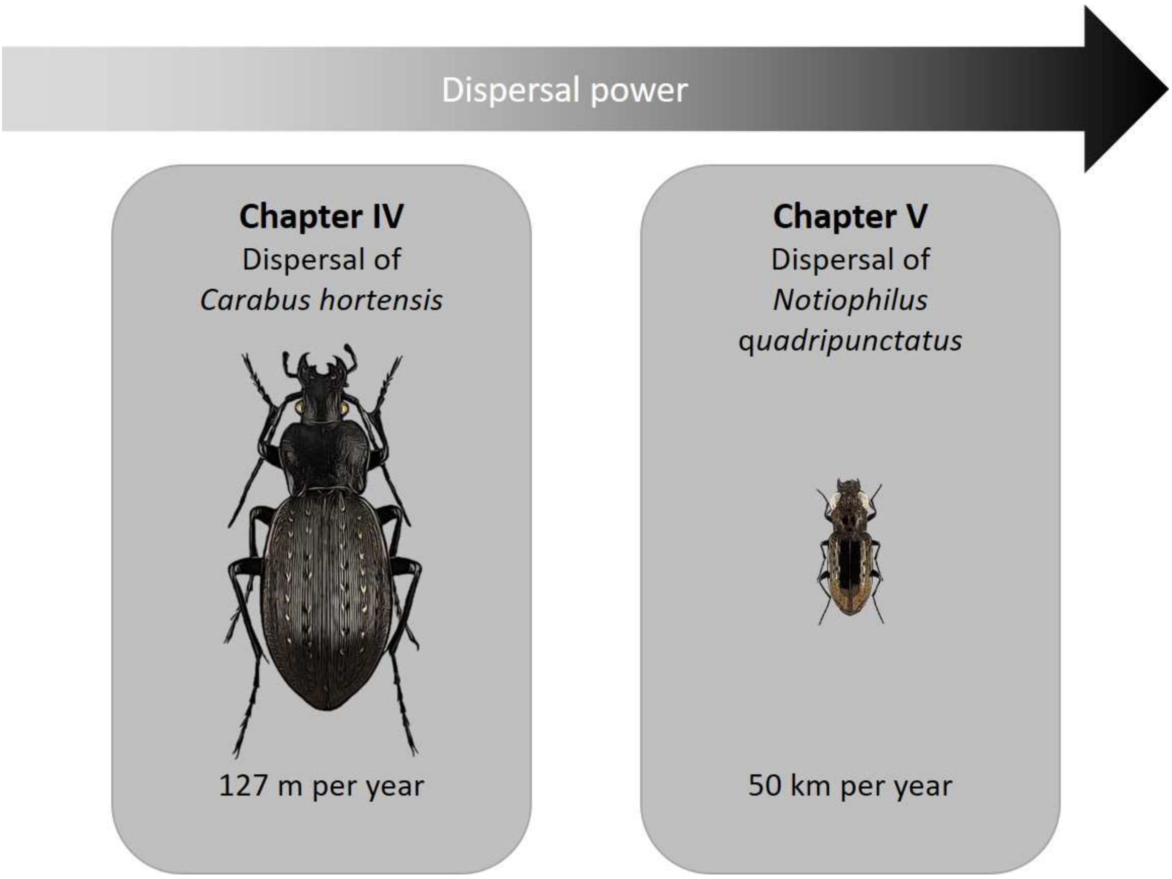

Figure 1.10: Estimated dispersal rates for the brachypterous species *Carabus hortensis* and the dimorphic *Notiophilus quadripunctatus*.

In the case of *Carabus hortensis*, the similarly sized, forest-dwelling species *C. auronitens* dispersed at a rate of 500 – 650 m per year (Niehues *et al.*, 1996; Drees *et al.*, 2008). The difference between the two species could be due to differences in the movement rate, which is slightly higher for *C. auronitens* with 6 m.day^{-1} on average (Niehues *et al.*, 1996) compared to 3.88 m.day^{-1} for *C. hortensis* (Skłodowski, 1999). Furthermore, the latter species spreads through a continuously forested area, finding suitable habitats, whereas the former spreads through a network of more or less well-connected forests and hedgerows. In these less suitable conditions for dispersal, ground beetles have displayed shifts in locomotory behaviour that significantly increase their movement rate (Baars, 1979; Niehues *et al.*, 1996; Drees *et al.*, 2008). While *C. hortensis* is reluctant to move into open habitats such as heathlands (only four individuals recorded), it is found in a comparatively high number in semi-open areas (84 individuals, Table A1.1). Thus, semi-open areas are also likely to be suitable for the dispersal of the species.

Nevertheless, the dispersal rate of *C. hortensis* appears to be rather low and may have been insufficient to allow the species to successfully recolonise northern Europe after the end of the last ice age. Limited evidence from northern Norway indicates that the species may have expanded its distribution range northward over more than 150 km within a few decades, although the exact timing is unknown, making an accurate estimation of dispersal rate challenging (Hatteland & Hauge, 2007). This discrepancy could be explained by a reduction in the species' dispersal power resulting from selection pressure against dispersal in populations from the Heide in recent times. Anthropogenic fragmentation is expected to lead to a reduction in dispersal power due to increased risk when dispersing through the hostile matrix (Den Boer *et al.*, 1980; Balmford, 1996; Cheptou *et al.*, 2017). This reduction in dispersal power could have happened during the peak of deforestation in the region, when *C. hortensis* survived in small, isolated populations in forest fragments. Comparing the dispersal rate of different populations with different histories could help to shed light on this particular effect of fragmentation, which remains understudied.

Many shifts in the distribution ranges of various ground beetle species have been reported in recent decades. Most of them concern poleward expansion and are thought to be the result of climate change. Hickling *et al.* (2006) showed that over a 25-year period, the ground beetle distribution range shifted on average by about 50 km. As such, even for a flight-active species, *Notiophilus quadripunctatus* appears to be spreading much faster. The range shift documented for *Stenolophus mixtus* in Scandinavia is, to my knowledge, the closest, with a covered distance of about 600 km in 25 years (Lindroth, 1972).

A possible explanation for this discrepancy may lie in the northeastward direction of the spread. The presence of only macropterous individuals in the Heide population suggested that *N. quadripunctatus* spread by flight. Additionally, during the main activity period of the species, the winds in Northern Europe mostly blow towards the east. As such, the species is achieving record dispersal rates by being mostly carried by the wind. Evidence for a such possibility exists for the closely related species *Notiophilus biguttatus*, which was unexpectedly recorded in high numbers at elevations of up to 200 m (Chapman *et al.*, 2005). This ability to exploit high altitude and fast-flowing wind could provide both species with the ability to disperse over a dozen kilometres in a very short period of time (see also Den Boer, 1970). Finally, the fact that N. quadripunctatus is an open habitat generalist increases the likelihood that beetle individuals will quickly establish new populations after dispersing. Although the species has only recently arrived in the Heide, given its affinity for disturbed environments such as arable fields, it is not unreasonable to expect it to be found in semi-open areas in the future.

While dispersal has always been considered a key process, its importance has risen in recent years, most notably as a consequence of ongoing climate change or fragmentation due to land use change (Arribas *et al.*, 2017). The fast and large-scale change expected to result from the reintroduction of grazing will certainly not diminish the importance of dispersal. Methods such as species distribution modelling could be instrumental in the identification of conservation priorities; however, uncertainty about the dispersal ability of the study species could result in overconfident predictions for the future (e.g. Mendes *et al.*, 2020). As a result, information on dispersal is in high demand but remains scarce, as demonstrated by my modest contribution to this field. For species such as *C. hortensis* and many similar species with low dispersal power, if left to themselves, the challenges that lay ahead appear unsurmountable.

1.4.4 Implications for the conservation of insect diversity in temperate Europe

Any proposed solution for biodiversity conservation needs to be objectively evaluated (Godet & Devictor, 2018). The planned extension of semi-open areas as the result of various schemes to reintroduce large grazing herbivores into modern landscapes remains unevaluated. Semi-open areas are considered valuable assets for nature conservation based on their high species richness as well as the presence of threatened species (e.g. Gallé et al., 2017; Rösch et al., 2019; Somay et al., 2021). Species richness is often used to set conservation priorities due to its convenience, although it has many drawbacks (Fleishman *et al.*, 2006; Cadotte & Tucker, 2018). A trending alternative to species richness is the use of functional diversity indices, which are thought to provide better insight into the functioning of ecosystems (Cadotte *et al.*, 2011; Cadotte & Tucker, 2018) and have been shown to sometimes provide useful information in a conservation context (e.g. Birkhofer *et al.*, 2015). However, for either measure, no or only limited consideration is given to the process leading to high species richness or functional diversity. Furthermore, the strength of the association between a given species, threatened or not, and the particular environment being investigated is seldom considered. Studying ground beetles in semi-open areas, I found that the high species richness and functional diversity resulted from the presence of a few semi-open-preferring species potentially using them as a habitat combined with a much greater number of species regularly dispersing from adjacent forest and open habitats due to mass effects. Thus, neither species richness nor functional diversity should be used as the principal criterion for assessing semi-open areas' effectiveness for biodiversity conservation.

Additionally, most threatened species for which we evaluated habitat associations were found to avoid semi-open habitats, although a few were recorded in some semi-open areas. Consequently, my findings question the conservation value of semi-open areas for ground beetles in the temperate region and underline the tremendous value of preserving existing forest, heathland, and grassland habitats. Thus, semi-open areas appear unlikely to make a major contribution toward the provision of heterogeneous nature-based habitats needed for the conservation of insect diversity (Habel *et al.*, 2019; Samways *et al.*, 2020). Nevertheless, semi-open areas appear to host a few specialised ground beetle species, and considering that modern landscapes are mostly devoid of such habitats, they do appear vital for the conservation of those few species. Within the European temperate region, the expected large-scale increase in semi-open areas through rewilding or restoration and the establishment of wood-pastures will be detrimental to most ground beetle species. This is of particular concern for species with a high habitat specialisation, which include many currently threatened species (Nolte *et al.*, 2019) if these newly created semi-open areas come to replace valuable existing habitats (Merckx, 2015). Thus, the reintroduction of grazing should be implemented with caution.

The property of semi-open habitats to attract a large number of species from adjacent habitats could be beneficial for the conservation of ground beetles. To achieve this goal, semi-open areas must be designed and established to function as dispersal corridors, which could significantly contribute to increasing functional connectivity (Eggers *et al.*, 2010; Travers *et al.*, 2020). In addition, ensuring the presence of both high-quality glades and high-quality treed patches will not only improve semi-open areas' potential as corridors, in particular for habitat specialists, but also make them suitable for a larger number of species (Haddad & Tewksbury, 2005; Habel *et al.*, 2020). If semi-open areas are expected to make a significant contribution to the provision of functional connectivity, they will need to fulfil two requirements. Firstly, their location and dimensions within landscapes will have to be adapted accordingly. To be suitable for organisms with low dispersal power, such as many ground beetles or the studied *Carabus hortensis,* semi-open corridors should be local corridors with a suggested length of less than a kilometre (Vos *et al.*, 2002). These recommendations appear to fit well with early data on ground beetle dispersal power, in particular for macropterous or dimorphic species (Den Boer, 1970; Baars, 1979). However, a better recommendation based on my data for the brachypterous *Carabus hortensis* will be to consider a length of less than 150 m, which was also found to be the maximal distance individuals from heathland species could reach along roadside verge corridors (Vermeulen, 1994b). This recommendation is certainly even more critical in the case of semi-open corridors, which do not provide optimal environmental conditions for those species, making it challenging for them to disperse over multiple generations (Vermeulen, 1994a; Vos *et al.*, 2002).

Secondly, semi-open areas will have to be appropriately managed. The main aim of such management should be to produce high-quality habitat structures so that one corridor can effectively serve a broad variety of species. This will require establishing management strategies that will ensure the presence of high-quality glades of heathland or grassland with a suitable amount of typical structures like bare soil as well as high-quality forest-like patches embedded within them with associated tree shading and leaf litter. Furthermore, in oceanic climates, priority should be given to the quality of open-like glades, whereas in continental climates, priority should be given to forest-like patches. Differential management will need to be implemented between the different elements found in the semi-open corridors. Specific management practices similar to existing management recommendations for classical corridors and having demonstrated their effects on other invertebrate taxa could be directly applied (e.g. Berg *et al.*, 2013; Pedley *et al.*, 2013). An alternative will be to reintroduce large domestic grazers in the context of wood-pasture (Rösch *et al.*, 2019), which, given the level of anthropogenic control, could be fine-tuned to achieve the desired level of quality and dimensions. At last, rewilding with large herbivores not only aims to minimise human interventions but also considers a much larger scale (van Klink & WallisDeVries, 2018), making it an unlikely management method to provide suitable semi-open corridors. Independently from the management method selected, the fulfilment of those two recommendations will ensure that semi-open areas do function as a corridor. Failure to successfully implement the management will turn semi-open areas into sinks, detrimental to nature conservation.

1.5 Conclusion

My dissertation provided a realistic and scientifically sound evaluation of the potential of semi-open areas for nature conservation. I was able to identify several functions that semi-open areas could fulfil for ground beetles in the temperate region. Semi-open areas appear mostly unsuitable as heterogeneous nature-based habitats for most ground beetle species. However, semi-open areas could play a significant role as a corridor to increase the functional connectivity of modern landscapes. If appropriately managed to maintain or establish high-quality open- and forest-like vegetation structures, these semi-open corridors may accommodate the needs of endangered specialist species. If management is inappropriate or even non-existent, the resulting low quality will undermine their effectiveness. Thus, both trophic rewilding or restoration and the establishment of wood pastures, which have been suggested as solutions for insect conservation (Samways et al., 2020), might be especially effective for ground beetle conservation when they target enhancing connectivity rather than habitat creation. An identical recommendation for the long-term conservation of insects could be made given the similarity between our results and findings from the Mediterranean region for invertebrates (Díaz *et al.*, 2013; Merckx, 2015). At last, a careful re-examination of already published evidence on the conservation value of semi-open areas for insects is required.

In the near future, the question of whether controlled management or rewilding should be the preferred approach to nature conservation will arise. Rewilding is gaining popularity at the expense of more hands-on approaches such as the establishment of high-nature value farmlands such as wood pastures (Merckx, 2015; Navarro & Pereira, 2015). Both approaches have been suggested as solutions for insect conservation (Samways et al., 2020) and will lead to the expansion of semi-open areas. However, their value for long-term insect conservation is unequal due to fundamental differences between the two approaches concerning the degree of human intervention. The wood pasture approaches will allow for adaptive management, which, combined with biodiversity monitoring, could take full advantage of the potential of semi-open areas. In the case of rewilding, the subsequent broad-scale extension of semi-open areas will likely result in a decrease in the local biodiversity resulting from a large part of the landscape being unsuitable for many species and increased isolation (Merckx, 2015).

My findings can take into account long-term habitat change within temperate landscapes (Schulze *et al.*, 2018), but do not allow for the consideration of the spatial scale typical of rewilding. Large herbivores typically have different preferences for different grazing areas based on topography, season, vegetation productivity, and predation risk (Bailey & Provenza, 2008). As a result, grazing intensity varies, and the early Holocene landscape has been noted to include varying degrees of canopy openness ranging from open floodplains to heavily forested uplands (Svenning, 2002). The reintroduction of grazing is likely to lead to a large-scale land use change in modern landscapes and the migration of entire habitats towards new areas. As a result, nature conservation, which typically focuses on the preservation of species in a given geographic area, often through the establishment of reserves, will need to take this dynamic into account. This will necessitate allowing and facilitating the migration of entire communities across landscapes, not as a result of climate change but as a result of land use change in rewilded landscapes. Those changes will take place in a short time frame, and assisted migration may be required for the least mobile species.

My results could also help in understanding the past. Subfossil beetle remains have been suggested as particularly useful indicators for the presence of grazing animals and the degree of openness of the landscape (Whitehouse, 2006; Whitehouse & Smith, 2010). Beetle species are classified as indicators for open or forested environments; however, considering certain species as indicators for semi-open environments may lead to a reinterpretation of the results. The species I identified as semi-open specialists are rarely found in prehistorical deposits, but *Leistus ferrugineus* was notably found in a deposit from the early Holocene in southern Sweden, where this species is regarded as a dry grassland indicator. In this study, based on the various sources of information, the landscape is assumed to have been characterised by open, pine-dominated woodlands (Olsson & Lemdahl, 2009). The presence of *L. ferrugineus* may indicate that the landscape surrounding the studied peatbog was semi-open, with grassy glades encompassing isolated single or grouped pine trees instead.

The evaluation of semi-open areas for the long-term conservation of the ground beetle fauna painted a bleak picture. As currently conceived, semi-open areas resulting from the reintroduction of grazing may not contribute to the preservation of insect diversity but instead further contribute to its decline. More research into modern semi-open areas is needed to better identify semi-open specialist species and understand the responses of species that are not associated with such environments. Despite evidence that many taxonomic groups respond similarly to semi-open areas, expanding taxonomic coverage will aid in gaining a better understanding of the future of insect faunas as well as their past.

Appendix 1

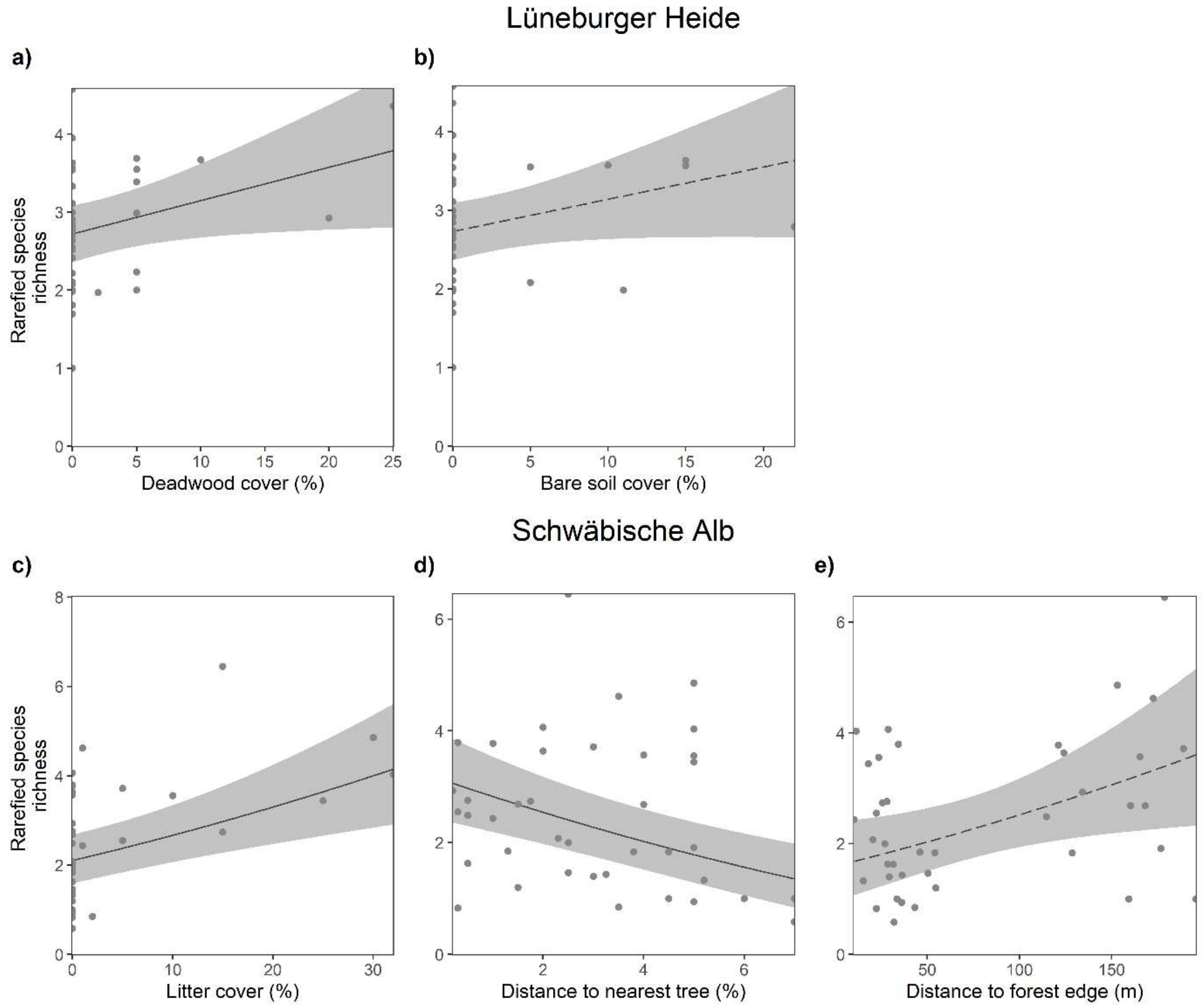

Figure A1.1: Relationships between the rarefied species richness of ground beetles associated with semi-open areas and their environmental features in the Lüneburger Heide and the Schwäbiche Alb. Marginal R^2 had a value of 20 and the conditional R^2 value was about 40. Black regression lines indicate significant ($p \leq 0.05$) relationships, while long dashed lines indicate a trend ($p < 0.1$), and shaded areas correspond to 95 percent confidence intervals. Means and confidence intervals are based on the back-transformed values estimated by the model when the original response variables were transformed. Points represent observed values per trap.

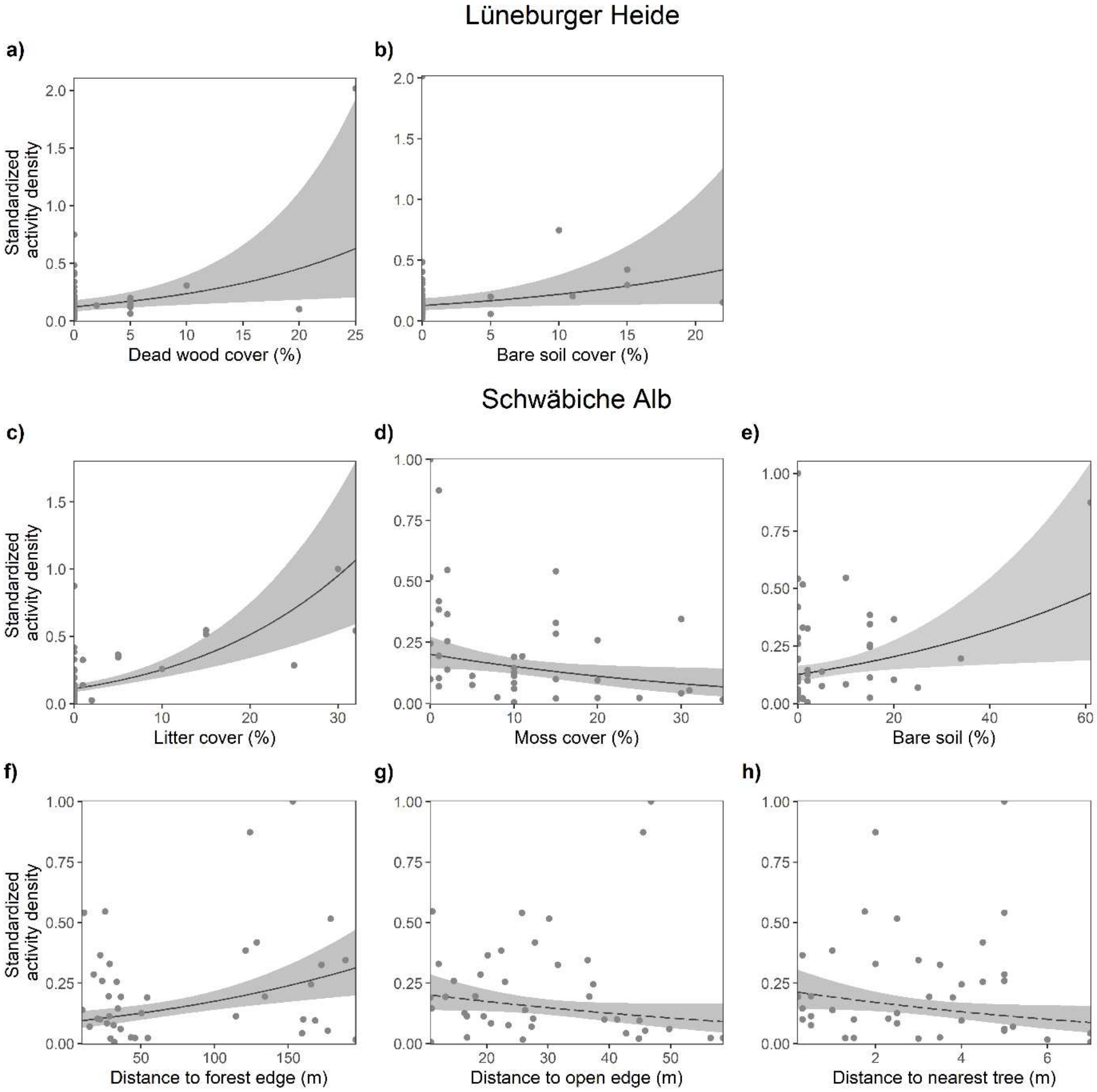

Figure A1.2: Relationships between the standardised activity-density of ground beetles associated with semi-open areas and their environmental features in the Lüneburger Heide and the Schwäbiche Alb. The R^2 value of the linear model explained was 62. Black regression lines indicate significant ($p \leq 0.05$) relationships, while long dashed lines indicate a trend ($p < 0.1$), and shaded areas correspond to 95 percent confidence intervals. Means and confidence intervals are based on the back-transformed values estimated by the model when the original response variables were transformed. Points represent observed values per trap.

Table A1.1: Number of teneral and imagines individuals recorded in the Lüneburger Heide in forest and open habitats as well as semi-open areas. Species are grouped by habitat association with either forest (dark green), both forest and semi-open (light green), both open and semi-open (light purple), open (dark purple) habitats, and semi-open areas (grey, diamond) and are further sorted alphabetically. Threatened species are indicated by an asterisk.

Species	Teneral			Imago		
	Forest	Open	Semi-open	Forest	Open	Semi-open
Abax parallelepipedus	9 (5)	-	1 (1)	872 (8)	19 (7)	253 (8)
Amara brunnea	1 (1)	-	-	57 (2)	-	14 (2)
Amara makolskii	4 (2)	-	-	78 (3)	-	16 (3)
Carabus auronitens	3 (3)	-	-	45 (4)	-	3 (2)
Carabus violaceus	5 (3)	1 (1)	7 (4)	811 (8)	158 (8)	389 (8)
Cychrus caraboides	-	-	-	30 (8)	1 (1)	10 (4)
Leistus rufomarginatus	-	-	-	407 (4)	-	1 (1)
Loricera pilicornis	-	-	-	8 (4)	1 (1)	1 (1)
Nebria brevicollis	-	2 (2)	16 (1)	414 (6)	15 (5)	91 (7)
Notiophilus biguttatus	1 (1)	-	-	224 (6)	-	73 (7)
Pterostichus niger	25 (4)	1 (1)	9 (2)	927 (8)	277 (8)	847 (8)
Pterostichus oblongopunctatus	41 (6)	1 (1)	34 (5)	975 (8)	2 (2)	536 (8)
Amara convexior	2 (1)	-	2 (2)	40 (2)	1 (1)	46 (6)
Carabus convexus*	1 (1)	-	10 (4)	113 (7)	22 (4)	148 (8)
Carabus hortensis	2 (1)	-	4 (1)	63 (4)	4 (1)	84 (1)
Harpalus latus	5 (2)	-	6 (2)	78 (6)	21 (5)	120 (8)
Notiophilus palustris	2 (1)	-	-	36 (6)	3 (3)	63 (8)
Pterostichus strenuus	-	-	-	3 (3)	-	2 (2)
Syntomus truncatellus	-	-	2 (2)	17 (3)	1 (1)	17 (4)
Amara lunicollis	-	8 (2)	6 (3)	68 (7)	57 (7)	192 (8)
Amara similata	-	-	-	1 (1)	-	10 (5)
Bembidion lampros	-	-	3 (2)	21 (6)	3 (2)	139 (6)
Bradycellus harpalinus	-	-	-	4 (2)	11 (7)	21 (6)

Species	Teneral			Imago		
	Forest	Open	Semi-open	Forest	Open	Semi-open
Calathus micropterus		1 (1)	4 (3)	65 (3)	56 (4)	223 (5)
Carabus problematicus	66 (4)	22 (5)	95 (5)	1300 (8)	958 (8)	1981 (8)
Leistus ferrugineus	-	-	-	10 (2)	22 (6)	59 (5)
Pterostichus quadrifoveolatus	-	-	-	4 (2)	-	117 (3)
Trechus obtusus	-	-	3 (2)	4 (2)	11 (3)	25 (5)
Amara equestris	-	1 (1)	1 (1)	-	16 (5)	22 (6)
Calathus erratus	-	20 (3)	1 (1)	2 (1)	1381 (7)	1090 (4)
Harpalus rufipes	-	1 (1)	-	1 (1)	12 (6)	19 (6)
Microlestes minutulus	-	-	-	1 (1)	5 (5)	6 (3)
Nebria salina	1 (1)	23 (4)	10 (1)	13 (5)	227 (8)	180 (8)
Notiophilus aquaticus	-	2 (1)	-	22 (2)	109 (6)	183 (8)
Oxypselaphus obscurus	-	-	1 (1)	4 (3)	26 (2)	25 (5)
Pterostichus nigrita	-	-	-	-	3 (2)	3 (3)
Pterostichus rhaeticus	-	-	-	1 (1)	2 (2)	2 (2)
Synuchus vivalis	-	5 (3)	-	10 (2)	73 (4)	47 (6)
Amara tibialis	-	-	-	-	7 (3)	1 (1)
Bembidion nigricorne*	-	3 (1)	-	-	100 (6)	6 (1)
Bradycellus caucasicus*	-	-	-	-	14 (1)	5 (3)
Bradycellus ruficollis*	-	1 (1)	1	1 (1)	123 (7)	15 (3)
Calathus fuscipes	2 (1)	98 (4)	27 (4)	451 (6)	2276 (7)	1176 (8)
Calathus melanocephalus	-	7 (1)	-	3 (2)	134 (6)	38 (5)
Carabus arcensis	-	11 (3)	1 (1)	7 (4)	286 (6)	37 (5)
Carabus nemoralis	14 (2)	56 (4)	6 (2)	164 (8)	445 (5)	192 (7)
Carabus nitens*	-	1 (1)	-	-	55 (4)	15 (2)
Cicindela campestris	-	3 (1)	-	1 (1)	835 (8)	155 (6)
Cymindis humeralis*	-	6 (1)	-	-	21 (3)	-
Cymindis vaporariorum*	-	-	-	-	12 (5)	2 (2)
Dyschirius globosus	-	24 (1)	1 (1)	4 (2)	48 (4)	21 (4)
Harpalus rubripes	-	-	-	-	14 (3)	-

Species	Teneral			Imago		
	Forest	Open	Semi-open	Forest	Open	Semi-open
Olisthopus rotundatus*	-	3 (2)	-	-	56 (6)	4 (1)
Poecilus cupreus	-	1 (1)	-	3 (1)	140 (6)	18 (5)
Poecilus lepidus	-	70 (5)	5 (2)	1 (1)	2684 (8)	139 (8)
Poecilus versicolor	-	120 (6)	30 (4)	11 (4)	1841 (8)	675 (8)
Pterostichus diligens	-	2 (2)	1 (1)	24 (4)	43 (6)	25 (4)
Pterostichus vernalis	-	1 (1)	-	-	53 (7)	7 (2)
Syntomus foveatus	-	2 (1)	1 (1)	5 (3)	29 (5)	17 (6)

Chapter II

2. Conservation value of semi-open habitats for ground beetles (Coleoptera: Carabidae, Cicindelidae) in Central Europe

Estève Boutaud, Dorothea Nolte, Ingmar Harry, Thorsten Assmann, and Claudia Drees

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Aspect of one of the studied semi-open area.

Abstract

Reintroduction of grazing to counteract insect decline will lead to an increase of semi-open habitats. Semi-open habitats are highly heterogeneous, consisting of a mosaic of patches of trees or shrubs embedded in a matrix dominated by dwarf shrubs or grasses. Despite a lack of evidence, structural heterogeneity is expected to allow many species to co-occur, making semi-open habitats appear highly valuable for invertebrate conservation. We studied ground beetles in eight sites in two landscapes of Central Europe each encompassing semi-open, open, and forest habitats. Rapid response to environmental change and limited dispersal abilities make ground beetles an excellent model taxon to evaluate the effectiveness of such conservations measures. In both studied landscapes, ground beetle assemblages in semi-open habitats tended to be distinct and intermediate between those from the forest and open habitats. Species richness and functional diversity in semi-open habitats were similar to open habitats at site level. The majority of species entered the semi-open habitats, except for most threatened species, yet, few species were exclusively associated with semi-open habitats. We conclude that the continuous presence of many species in semi-open habitats likely results from mass effects rather than habitat heterogeneity per se. Our findings underline the conservation value of the existing forest, heathland, and grassland habitats over semi-open habitats which can, however, function as dispersal habitats and increase landscape connectivity. Strategies aiming at promoting semi-open habitats to counteract insect decline should target enhancing connectivity rather than the creation of habitats only.

2.1 Introduction

Conservationists call for increasing structural diversity in forest and open habitats to support insect conservation (Samways et al., 2020). In various locations in Europe, this is achieved by the reintroduction of grazing, through trophic rewilding (sensu Svenning et al., 2016) or restoration and establishment of wood pastures (e.g. Vera, 2009; Rösch et al., 2019; Garrido et al., 2021) leading to an increase of semi-open habitats (e.g. Hall, 2018; Schulze et al., 2018). Semi-open habitats were once a common feature of temperate Europe (Vera, 2000; Sandom *et al.*, 2014b) and consist of a mosaic of patches of trees or shrubs embedded in a matrix dominated by grasses or dwarf shrubs (Garbarino & Bergmeier, 2014). Gradients in canopy closure affect light availability, temperature, and moisture at fine-scale, making semi-open habitats highly heterogeneous (Bergmeier et al., 2010; Díaz et al., 2013). The structural heterogeneity (cf. "habitat heterogeneity hypothesis" MacArthur & MacArthur, 1961) is assumed to offer a range of niches allowing many species to co-occur (Díaz et al., 2013) and is seen to influence assembly rules (Magura & Lövei, 2019). Consequently, semi-open habitats are regarded as highly valuable for conservation due to both their high species richness and unique assemblage composition (e.g. Bergmeier et al., 2010; Rösch et al., 2019). For invertebrates in semi-open habitats, however, the few existing studies showed non-equivocal results with few supporting their effectiveness for conservation (Talvi, 1995; David et al., 1999; Horák et al., 2018), while others did not come to the same conclusion (Sverdrup-Thygeson et al., 2010; Gallé et al., 2017; Rösch et al., 2019; Somay et al., 2021).

To assess the effectiveness of semi-open habitats for invertebrate conservation in the temperate region, four aspects must be considered. Firstly, considering the particular environmental conditions found in semi-open habitats, many authors assume that a set of specific species preferring semi-open conditions exist (Sverdrup-Thygeson et al., 2010; e.g. Rösch et al., 2019). Despite its importance for species conservation (Cáceres & Legendre, 2009), this knowledge remains limited for invertebrates and available evidence indicates that a rather small number of species likely rely on semi-open habitats (Díaz et al., 2013). Secondly, whether semi-open habitats do effectively harbour a large number of species seems affected by the scale at which species richness is considered (e.g. Moreno et al., 2016). Most studies that reported higher species richness in semi-open habitats focussed on γ-diversity (across habitat patches; e.g. Talvi, 1995; Horák et al., 2018) while α-diversities (at patch level) appeared at least similar to one of the adjacent habitats (e.g. Rösch et al., 2019; Somay et al., 2021). Thirdly, most studies were conducted in either the boreal (e.g. Talvi, 1995; Sverdrup-Thygeson et al., 2010) or the Mediterranean regions (e.g. David et al., 1999; Taboada et al., 2006a; Moreno et al., 2016) where some semi-open habitats are under protection (Bergmeier et al., 2010) while studies in the temperate region remain limited. Fourth, dwarf shrubs dominated semi-open habitats are a key element in the oceanic part of temperate Europe (Garbarino & Bergmeier, 2014), yet most studies on semi-open habitats focused on grass-dominated matrices (but see Eggers et al., 2010).

It is assumed that habitats with a higher functional diversity are more stable, better functioning, and, thus, of high conservation value (Cadotte et al., 2011). This can also be expected for semi-open habitats, however, in these habitats mainly taxonomic diversity has been studied and little attention has been paid to functional diversity (but see Jakobsson et al., 2020). The high niche availability in semi-open habitats is expected to increase the functional diversity as functionally divergent species occupy those diverse niches (MacArthur & MacArthur, 1961). For birds and bats, Jakobsson et al. (2020) found that increasing structural complexity in semi-open habitats increased the taxonomic diversity but no similar tendency in functional diversity was found. It is, though, likely that a relationship between habitat heterogeneity and functional diversity occurs as increased habitat heterogeneity drives a higher species richness which, in turn, increases functional diversity (but see Gerisch et al., 2012). In addition, as assemblages in semi-open habitats are expected to be a combination of species from open and forest habitats (Díaz et al., 2013), with usually distinct functional traits, semi-open habitats are likely to exhibit a high functional diversity.

Previous studies on diversity in semi-open habitats focussed on taxa mostly restricted to open (grasshoppers: Rösch et al., 2019; dung beetles: Somay et al., 2021) or forest habitats (saproxylic beetles: Sverdrup-Thygeson et al., 2010; Horák et al., 2018). Ground and tiger beetles (hereafter ground beetles), however, occur more evenly in all terrestrial habitats (Lövei & Sunderland, 1996; Koivula, 2011) and are known to respond to changes in moisture and temperature parameters at a very small spatial scale (Antvogel & Bonn, 2001; Koivula, 2011) making them suitable for studying habitat association in heterogeneous semi-open habitats. However, up to now, studies on ground beetle assemblages in semi-open habitats exist mostly for the Mediterranean (Taboada et al., 2006b, 2006a) or the boreal regions (e.g. Talvi, 1995; Söderström et al., 2001) and are rare for the temperate one (but see Eggers et al., 2010).

In this study, we aim to evaluate the conservation potential of semi-open habitats for ground beetles in the temperate region where we sampled ground beetles in two climatically different landscapes containing remnants of semi-open habitats. We hypothesize that species richness and functional diversity will be higher in semi-open habitats than in adjacent forests, heathlands, or grasslands. Furthermore, we expect ground beetle assemblages to be distinct and intermediate between those of the forest and open habitats. Finally, we identify potential ground beetle species with a specific preference for semi-open habitats with a particular focus on threatened species.

2.2 Materials and methods

2.2.1 Study landscapes, history, and habitat characteristics

The study was conducted in two landscapes in Germany with different climatic and edaphic conditions. In both landscapes, the open habitats developed as the result of deforestation culminating in the Middle Ages and have been traditionally maintained by sheep grazing. When in the 19th century the traditional management became economically non-viable, many of the formerly grazed heathlands and dry calcareous grasslands have been afforested or transformed into arable lands (Beinlich & Plachter, 1995; Keienburg & Prüter, 2004).

The Lüneburger Heide (hereafter Heide) is located in the north-western German lowland (70 – 170 m.a.s.l.; 53.1675 N, 9.91345 E), has a suboceanic climate (mean annual precipitation: 854 mm, mean annual temperature 9 °C) on podzol as the predominant soil type (Keienburg & Prüter, 2004). The open habitats consist of dry heathland dominated by heather (Calluna vulgaris) and represent the remnants of formerly widespread heathland. The semi-open habitats developed more recently and comprise a mosaic dominated by heather with shrubs, single trees, or groups of trees (Betula pendula, Quercus robur, Pinus sylvestris), which resulted either from a combination of trees and shrubs encroachment and extensive sheep and goats grazing on former heathland or they were established by forest thinning followed by extensive grazing. Sheep and goats herds (about 0.8 animal/hectare) are grazing year-round in both open and semi-open habitats which are part of the same grazing area (personal communication Dirk Mertens, Verein Naturschutzpark). The forest habitats, which are not grazed, developed in the 19th century and are dominated by the same tree species as found in the semi-open habitats with the addition of Picea abies. Tree canopy cover (visually estimated for each pitfall trap) was on average 0 % in the heathland, 20 % in the semi-open, and 51 % in the forest habitats (Table 2.1 and Table A2.1).

The Schwäbische Alb (hereafter Alb) is located in a low mountain range in south-west Germany (450 – 1 000 m.a.s.l. ; 48.2983 N, 9.24926 E), has a subcontinental climate (mean annual precipitation: 750 mm, mean annual temperature 7 °C) and limestone derived rendzic leptosol soil (Beinlich & Plachter, 1995). The open habitats, which are remnants of the former widespread grasslands, consist of semi-dry calcareous grassland dominated by Bromus erectus. In this landscape, the semi-open habitats resulted from a combination of tree encroachment and extensive sheep grazing. They comprise a mosaic dominated by the grass Bromus erectus with shrubs (Juniperus communis) and trees (Quercus robur and Sorbus aucuparia) isolated or in small groups. Sheep herds (about 3.5 to 4.6 animals/hectare) are grazing in a way that imitates the former transhumance (one grazing event in late spring followed by a second one in late summer to remove two-thirds of the biomass on each grazing event (Ministerium für Ernährung Ländlichen Raum und Verbraucherschutz, 2021). Open and semi-open habitats are part of the same grazing area. The forest habitats are ungrazed and are mainly dominated by Fagus sylvatica. Tree canopy cover was on average of 0 %, 26 %, and 77% in the open, semi-open, and forest habitats, respectively habitats (Table 2.1 and Table A2.1). More details about the studied landscapes and plant composition can be found in Travers et al. (2020).

Table 2.1: Characteristics of the studied landscapes and semi-open habitats in the Lüneburger Heide and the Schwäbische Alb. For both landscapes mean values and standard deviation (in parenthesis) are provided. We tested for differences for each parameter using Wilcoxon two-sided tests, test statistic W and p-value are provided.

	Lüneburger Heide	Schwäbische Alb	W	p-value
Patch size (ha)	4.41(3.38)	2.38 (1.84)	45	0.2
Canopy cover (%)	20.38 (15.70)	26.25 (18.65)	27	0.63
Distance to forest edge (m)	66.25 (29.25)	77.59 (62.84)	34	0.88
Distance to open edge (m)	50.87 (22.28)	28.72 (11.86)	50	0.07
% forest in 500 m radius	43.57 (14.21)	48.15 (13.31)	25	0.51
% semi-open in 500 m radius	12.81 (9.24)	6.49 (2.80)	43	0.28
% open in 500 m radius	37.32 (12.27)	27.80 (12.37)	46	0.16
% other open in 500 m radius	6.30 (7.77)	17.56 (19.53)	22	0.32

We measured the proportion of the main habitat types (forest, semi-open, open (heathland or dry grassland depending on the region), other open habitats (include arable lands and other types of grassland) in a 500 m radius centered on each sampling site (radius sufficiently large to include all three habitats) with the measuring tool using Google Earth Pro (version 7.3.4.8248). Urbanized and other artificial “habitats” (constructed, road networks, small gardens) were excluded as they are unlikely to offer suitable environments for the studied ground beetle species. In both landscapes, the semi-open habitats were not significantly different with regard to patch size, canopy cover, and proportion of forest, semi-open, open, and other open habitats

(Table 2.1). Detailed information on the studied habitats and sites can be found in Table A2.1.

2.2.2 Ground beetle sampling

In each landscape, we selected eight sites (> 2 km apart) of which we surveyed half of them in 2013-2014 and the other half in 2014-2015 (Online Resource Table A1). Each site comprised patches of the three habitat types - open, semi-open, and forest habitats - in direct vicinity (Fig. 2.1). In each of the three habitats within a site, a row of five pitfall traps with 10 m between traps was used. The average distance between habitat rows was 218 m in the Heide (ranged from 81 to 809 m) and 207 m (ranged from 37 to 586 m) in the Alb.

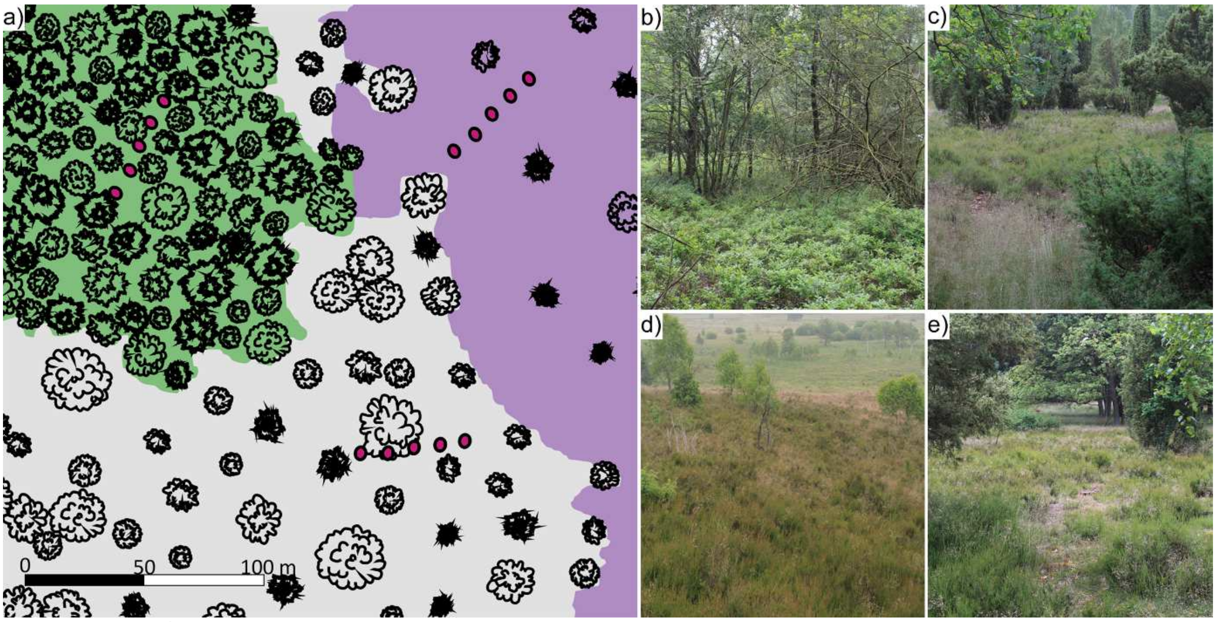

Figure 2.1: Schematic representation of the sampling design based on one studied site from the Lüneburger Heide (a) in which the red-violet dots indicate the position of the trapping rows in the forest (green), semi-open (grey), and heathland (purple) and perspective at ground level in the forest (b), semi-open (c and e), and open heathland (d).

A total of 120 traps were used in each landscape (8 sites x 3 habitats x 5 traps). In the Heide, traps were serviced year-round from January 2013 to February 2014 and from March 2014 to January 2015 every three weeks (except for extended trapping periods caused by snow cover in winter). In the Alb, traps were serviced every three weeks from April to September in 2013 and 2014. This resulted in 18 collection events per site in the Heide in 2013-2014 (1 080 traps collected in total), 15 in 2014-2015 (900 traps), and, in the Alb, eight collection events in both years (960 traps). As pitfall traps, we used transparent plastic cups (500 ml, 10 cm diameter) filled with 150 ml of Renner solution (Renner, 1982) set flush with the ground. To reduce disturbance by sheep an acrylic glass roof was added in the Alb, 3-4 cm above the trap.

Distances to the habitat edges were measured as the distance between a given trap and the limit of the tree crowns at the forest or semi-open habitat edges. In the Heide, the distance from the heathland and forest edges to the sampled locations within the semi-open habitats ranged from 10 to 115 m. In the Alb, the distance to the grasslands and the forest edges ranged from 13 to 68 m and 33 to 187 m, respectively (Table 2.1 and Table A2.1). The distance from the forest or open habitat edges did not significantly differ between both landscapes (Table 2.1).

Ground beetles were counted and identified to species level in the laboratory using standard literature (Müller-Motzfeld, 2006) and nomenclature followed Schmidt et al. (2016). Species were classified as threatened if they were listed as vulnerable, endangered, or critically endangered on either the German Red List (Schmidt et al., 2016) or the Red List of the respective federal states (Assmann et al., 2003; Trautner et al., 2006). We selected six traits commonly used for ground beetles characterizing their spatial and temporal resources use (one continuous: mean body size (mm); five nominal variables: wing development (brachypterous, dimorphic, and macropterous), food preference (predator, herbivore, and omnivore), hibernation type (imagines, larvae, or both stages), reproduction time (spring, autumn, spring and autumn, and winter), and region-specific habitat preference (forest, open, wetland, and eurytopic)). Trait information was compiled from www.carabids.org (Homburg *et al.*, 2014b) amended with information from Nolte et al. (2019), and region-specific habitat preferences were based on the catalogue of the Gesellschaft für Angewandte Carabidologie (2009).

2.2.3 Statistical analyses

Due to the activity of large mammals, 37 traps (1.9%) in the Heide and 55 traps (5.7%) in the Alb were lost. The missing information was replaced by the average catch value corresponding to the remaining undisturbed traps of the given site, habitat, and trapping interval. Prior to statistical analyses, we pooled the catches of all five pitfall traps over the entire trapping period within each habitat and site to receive one sample per habitat and site which resulted in eight per habitat and landscape. Statistical analyses were performed using the software R, version 3.5.3 (R Core Team, 2019) with packages ggplot2 for graphics (Wickam, 2016).

Sample-based rarefaction curves were used to estimate rarefied species richness for each habitat type (γ-diversity). Rarefaction curves for each habitat type in each landscape were calculated using the “specaccum” function (2 500 permutations) with 84 % confidence intervals (Payton et al., 2003). To correct for differences in numbers of individuals sampled, the rarefaction curves were re-plotted with an individual-based x-axis (Gotelli & Colwell, 2001). We calculated site-rarefied species richness (α-diversity) using the function “rarefy” considering the minimum number of individuals trapped in a site in each landscape (423 individuals in the Heide; 231 in the Alb). Both functions are part of the package vegan (Oksanen et al., 2019).

As functional diversity index, we used Rao's quadratic entropy, which represents the mean trait distance between pairs of individuals in one assemblage (Botta-Dukát, 2005), calculated using the function “dbFD” of the FD package (Laliberté & Legendre, 2010). Rao's quadratic entropy is expected to increase with increasing divergence of species traits independently from species richness which could be expected in semi-open habitats if species from both open and forest habitats co-occur.

As ground beetle assemblages and, thus, species richness and functional diversity can be influenced by landscape and site characteristics we checked for linear relationships with α- or functional diversity found in the semi-open habitats. We analysed site characteristics (patch size, canopy cover, and distance to the forest or open edges) and landscape characteristics (proportion of forest, semi-open, open, and other open habitats) by building two sets of linear models. No significant effect of any of the variables on α- or functional diversity was found (Table A2.2). However, such questions should be addressed with targeted study designs.

The effect of habitat types and year of sampling on α- and functional diversity were first tested with a linear mixed model using the study site as a random factor. As the variance explained by the random factor was close to 0, it was excluded and linear models were used instead. Significant differences between habitat types were assessed, using the “glht” function from the multcomp package (Hothorn et al., 2008), with post hoc tests of pairwise differences (Tukey test). Model validation was carried out graphically.

To compare the carabid beetle assemblages in the different habitat types, non-metric multidimensional scaling (NMDS, vegan package) was conducted for each landscape separately. We omitted carabid species with fewer than five individuals recorded individuals per landscape. NMDS ordinations with Horn dissimilarity measures, which give more weight to rarer species (Jost et al., 2011), were restricted to two dimensions. Two ordinations were built for each landscape. The first one focussed exclusively on the semi-open habitats and using the function “envfit” (5 000 permutations) we checked whether the patch size, canopy cover, distance to the forest or open edges, proportion of forest, semi-open, open, and other open habitats significantly influenced the structure of the assemblages. The second ordination included all habitat types and was used to test for significant differences between all habitats, pairs of habitats, and sampling years using PERMANOVAs (5 000 permutations) based on the dissimilarity matrices used for the ordination. The obtained p-values from “envfit” and those of the pairwise comparisons of habitats were corrected using the false discovery rate (function “p.ajust”; Benjamini & Hochberg, 1995).

Furthermore, we calculated the point-biserial correlation coefficient (rpb) for each species and habitat type combination to test for associations of carabid species with habitat types correcting for unequal group size. Rpb is the correlation coefficient between two vectors, one containing the species abundances in the habitat types and the other one the habitat type values, and ranges from -1 (complete avoidance) to 1 (absolute preference). As rpb considers both species presence in the target habitat and absence in the other habitats, we further excluded species that occurred on fewer than three sites per landscape. Rpb was calculated using the function “signassoc” and the significance of association was tested using two-sided permutation tests (1 000 permutations) with p-values corrected for multiple testing (Šidák’s correction). We calculated 95 % confidence intervals for the association with semi-open habitats by bootstrapping the observed data 1 000 times with replacement using the function “strassoc”. Both functions are part of the package indicspecies (Cáceres & Legendre, 2009).

2.3 Results

In total, we sampled 28 790 carabid beetles belonging to 96 species in the Heide (7 849, 8 671, and 12 270 individuals in the forest, semi-open, and heathland habitats, respectively). We found 26 species with fewer than five individuals. In the Alb, we recorded 14 453 carabid beetles belonging to 95 species (6 926, 3 518, and 4 009 individuals sampled in the forest, semi-open, and grassland habitats, respectively) with 19 species for which fewer than five individuals were recorded. We recorded 15 and 11 threatened species in the Heide and the Alb, respectively (Table A2.3).

Corrected sample-based rarefaction curve slopes were similar for the three habitats in both landscapes, except for the forest in the Alb with a shallower slope, indicating similar sampling completeness was achieved in most habitats (Fig. 2.2a and b). Ground beetles exhibited a significantly higher γ-diversity in the semi-open habitats (not overlapping confidence interval) followed by the open and forest habitats in both studied landscapes (Heide: rarefied species richness for 7 927 individuals of 71, 61.3, and 61 for semi-open, open, and forest habitats, respectively; Alb: rarefied species richness for 3 708 individuals of 74, 67, and 37.4 for semi-open, open, and forest habitats, respectively).

No significant differences in α-diversity and functional diversity were found between the sampling years in both landscapes (Table 2.2 and Table A2.4). Contrary to γ-diversity, in both landscapes, α-diversity was comparable between the semi-open and the open habitats while being higher than in the forests (Fig. 2.2c and d, Table 2.2 and Table A2.4). In the Heide, functional diversity was similar between the three habitats while in the Alb both semi-open and open habitats had higher functional diversity compared to the forest (Fig. 2.2e and f, Table 2.2 and Table A2.4).

The results of the NMDS analysis showed that the different habitats in each study landscape clustered together (Fig. 2.3). Assemblages in semi-open habitats were intermediate between the open and forest habitats thus influenced by both adjacent habitats. PERMANOVAs revealed significant differences between the habitats for both landscapes along the first axis of the ordination with the forest and open habitat assemblages clearly separated and significantly different from each other. In the Heide, the assemblages from semi-open habitats showed higher similarity to those from the forests than from the open habitats, although all assemblages were significantly different. In the Alb, a trend existed for a difference between the assemblages from semi-open and open habitats while semi-open assemblages were significantly different from those from the forests. In addition, in the Heide, no effect sampling year could be found, however, in the Alb a significant difference between the assemblages was found along the second axis (Table 2.3, Fig. A2.1).

Table 2.2: Results of the linear models and post hoc tests for the effect of habitat types and sampling year on α- and functional diversity (FD) in the Lüneburger Heide and the Schwäbische Alb. Results for post hoc tests are only shown in case an explanatory variable is significant. Significant values are in bold and t values are in italic.

Landscapes	Diversity metrics	Variables	df	F or t-values	p-values
Lüneburger Heide	α- diversity	Habitat type	2	4.08	**0.03**
		Forest - Semi-open		*2.85*	**0.02**
		Forest - Open		*1.71*	0.22
		Semi-open - Open		*-1.05*	0.55
		Sampling year	1	0.47	0.5
	FD	Habitat type	2	1.33	0.28
		Sampling year	1	0.02	0.89
Schwäbische Alb	α- diversity	Habitat type	2	15.3	**<0.001**
		Forest - Semi-open		*5.45*	**<0.001**
		Forest - Open		*3.55*	**0.005**
		Semi-open - Open		*-1.89*	0.16
		Sampling year	1	1.16	0.29
	FD	Habitat type	2	9.36	**0.001**
		Forest - Semi-open		*3.957*	**0.002**
		Forest - Open		*3.494*	**0.005**
		Semi-open - Open		*-0.463*	0.88
		Sampling year	1	0.89	0.35

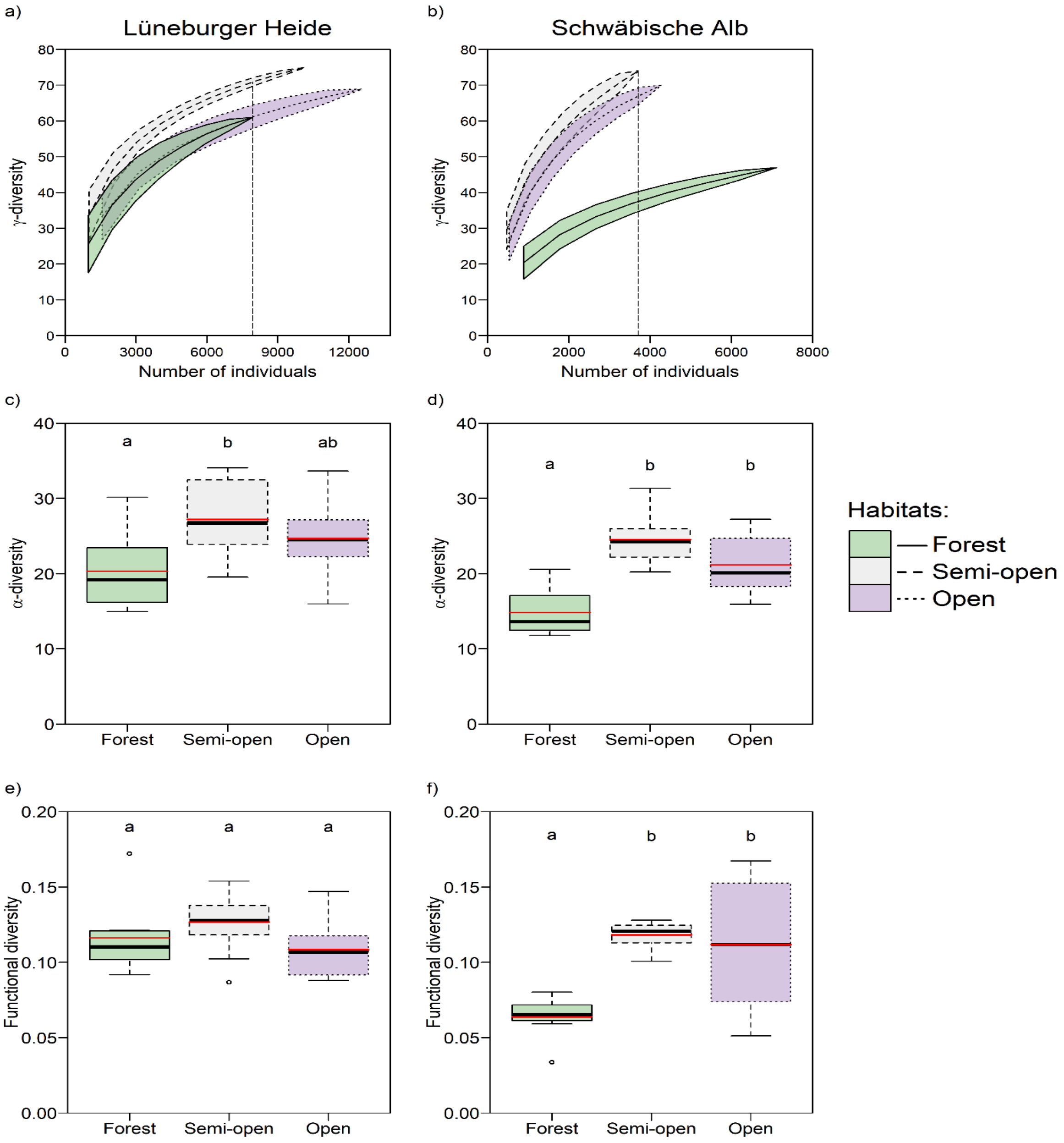

Figure 2.2: Corrected sample-based rarefaction curves (γ- diversity, a and b), rarefied species richness (α diversity, c and d), and functional diversity (Rao's Q, e and f) of ground beetles for forest (green, solid line), semi-open (grey, dashed line), and open (purple, dotted line) habitats in the Lüneburger Heide (left column) and the Schwäbische Alb (right column). The a) and b) panels display 84 % confidence intervals. Different letters in c) to f) above the boxplots indicate significant differences between the habitats (Online Resource 2) and the red-violet dot-dashed line the mean value.

No correlation between single landscape or site variables and the ordination locations of semi-open habitats was found for the Heide. In the Alb, only the proportion of other open habitats significantly correlated with the second axis of the ordination (Table A2.5).

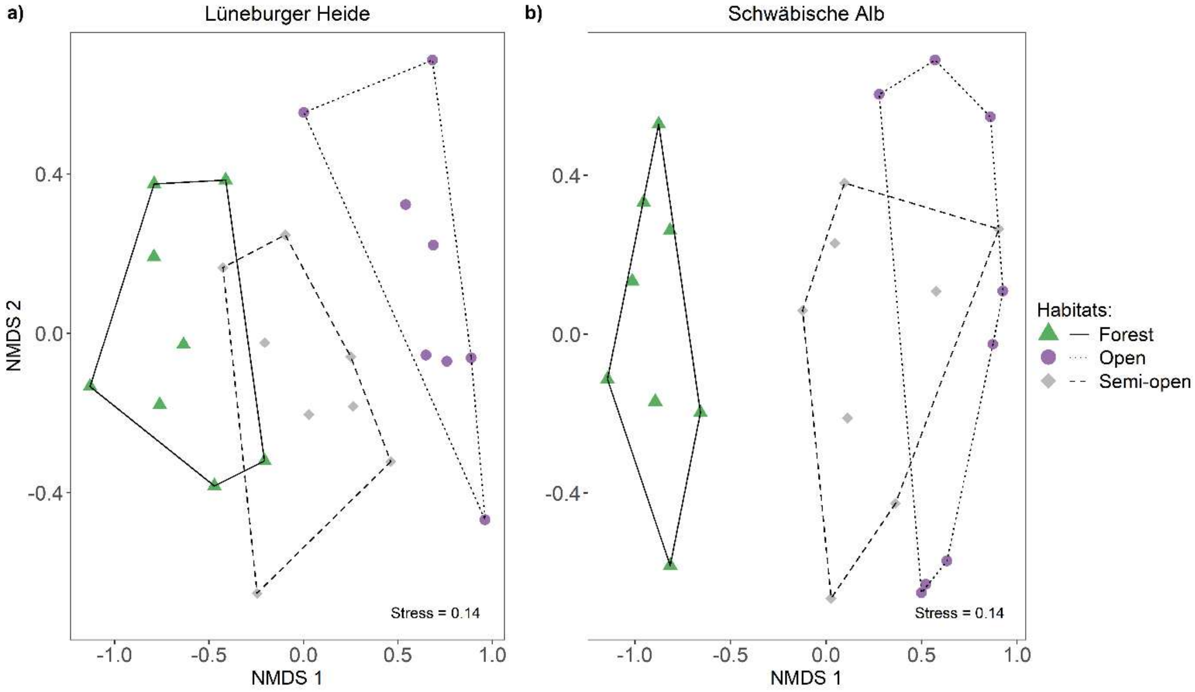

Figure 2.3: Non-metric multidimensional scaling ordinations of carabid beetle assemblages of forest (triangle, green), semi-open (diamond, grey), and open (circle, purple) habitats in the Lüneburger Heide (a) and the Schwäbische Alb (b) based on Horn distance (two dimensions). Minimum convex polygons are shown for forest (solid line), semi-open (dashed line), and open habitat (dotted line).

Table 2.3: Results of PERMANOVAs for the effect of habitat types on the ground beetle assemblages. df are degrees of freedom and Resid. df are the residual degrees of freedom. P-values for pairwise comparisons have been corrected for multiple testing and significant p-values are in bold.

Landscapes	Habitat types	df	Resid. df	F values	R^2	p-value
Lüneburger Heide	All habitats	2	20	7.33	0.42	**0.0002**
	Sampling year	1	20	0.67	0.01	0.59
Schwäbische Alb	All habitats	2	20	7.86	0.43	**0.0002**
	Sampling year	1	20	5.75	0.12	**0.002**
Pairwise comparison for habitat types						
Lüneburger Heide	Forest *vs.* open	1	14	14.18	0.5	**0.002**
	Forest *vs.* semi-open	1	14	4.23	0.23	**0.007**
	Semi-open *vs.* open	1	14	4.56	0.24	**0.012**
Schwäbische Alb	Forest *vs.* open	1	14	17.8	0.56	**0.001**
	Forest *vs.* semi-open	1	14	6.79	0.33	**0.002**
	Semi-open *vs.* open	1	14	2.76	0.15	0.068

In both landscapes, similar proportions of species were positively associated with the semi-open habitat only (Heide: 15.2 % and Alb: 17.5 %) and both the semi-open and open habitats (Heide: 17 % and Alb: 17.5 %). While a lower proportion of species was positively associated with both the semi-open and the forest habitats in the Heide (11.9 %), this proportion was much lower in the Alb (5.3 %). Those associations with the semi-open habitats only were significant for one species in the Heide (Amara similata) and three species in the Alb (Panagaeus bipustulatus, Carabus nemoralis, and C. granulatus). In addition, two species were significantly associated with either the semi-open and the open habitats (Nebria salina) or the semi-open and the forest habitats (Pterostichus niger) in the Heide (Online Resource Table A6). Two species (Badister bullatus and Pterostichus ovoideus) were also significantly positively associated with both the semi-open and the open habitats in the Alb (Fig. 2.4 and Table A2.7).

Most of the threatened species were associated with the open habitats in both landscapes including five of them significantly associated with the heathlands in the Heide. In addition, in the Heide, only one species was positively associated with both semi-open and forest habitats (Carabus convexus) while, in the Alb, one species was positively associated with both the semi-open and the open habitats (Harpalus dimidiatus). The number of threatened species in the forest was overall very low and only one species was found to be significantly associated with forest in the Alb (Carabus irregularis) (Fig. 2.5, and Tables A2.6 and A2.7).

A large number of species in both landscapes were neither positively nor negatively associated with semi-open habitats (Heide: 88.1 % of the species; Alb: 84.2 %). Only one species associated with forest habitats (1.7 %) and four species associated with open habitats (6.8 % including the threatened species Bembidion nigricorne and Bradycellus ruficollis) were significantly negatively associated with semi-open habitats in the Heide. In the Alb, nine of the forest-associated species (14 % including the threatened species Carabus irregularis) and one of the open-associated species (1.8 %) were significantly negatively associated with semi-open habitat (Fig. 2.5, Tables A2.6 and A2.7).

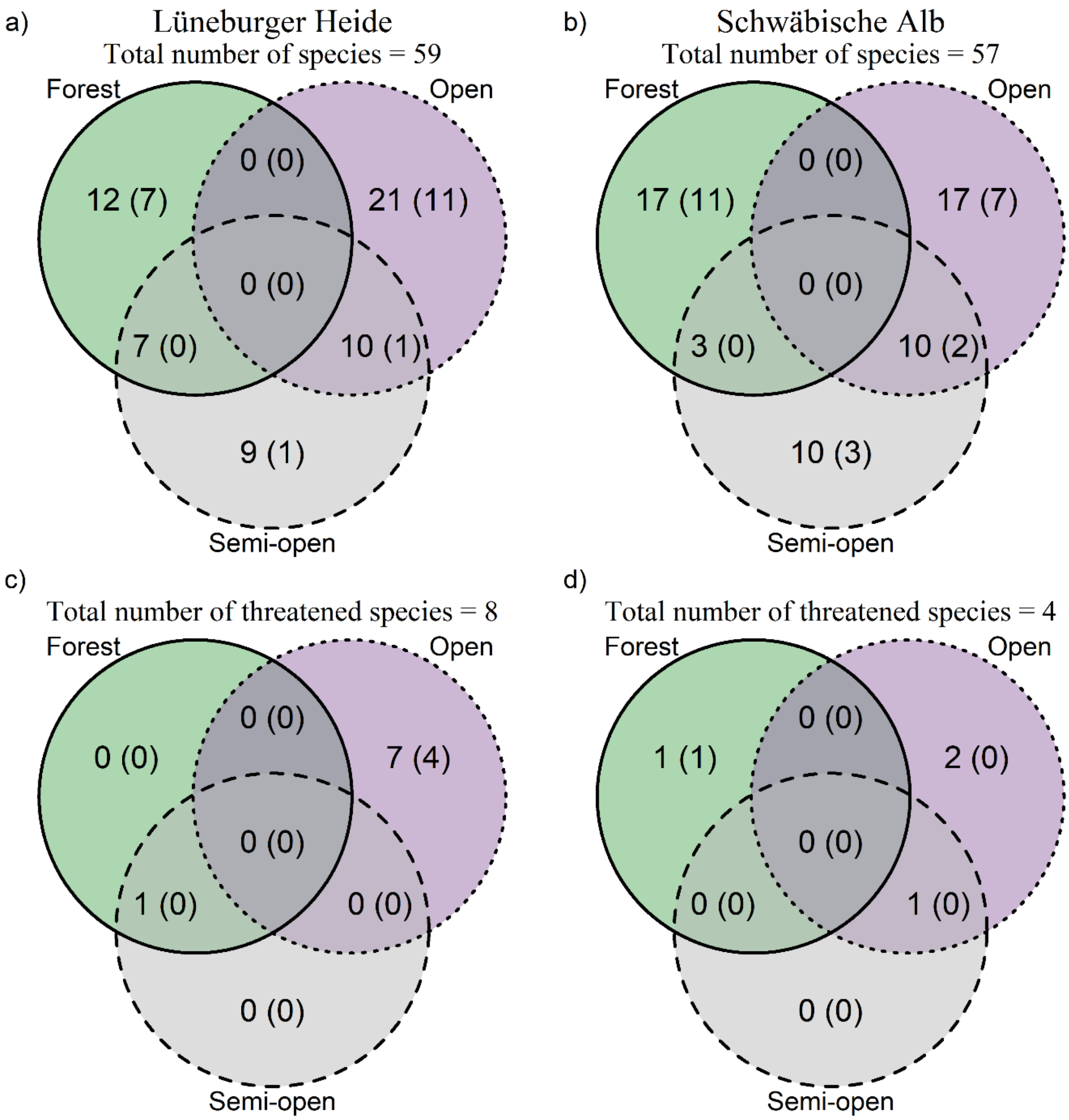

Figure 2.4: Number of associated species (a and b) and threatened species (c and d) unique to or shared by the forest (green, solid line), the semi-open (grey, dashed line), and the open (purple, dotted line) habitats in the Lüneburger Heide (left column) and the Schwäbische Alb (right column). Values in parentheses correspond to the number of species significantly associated with the given habitat.

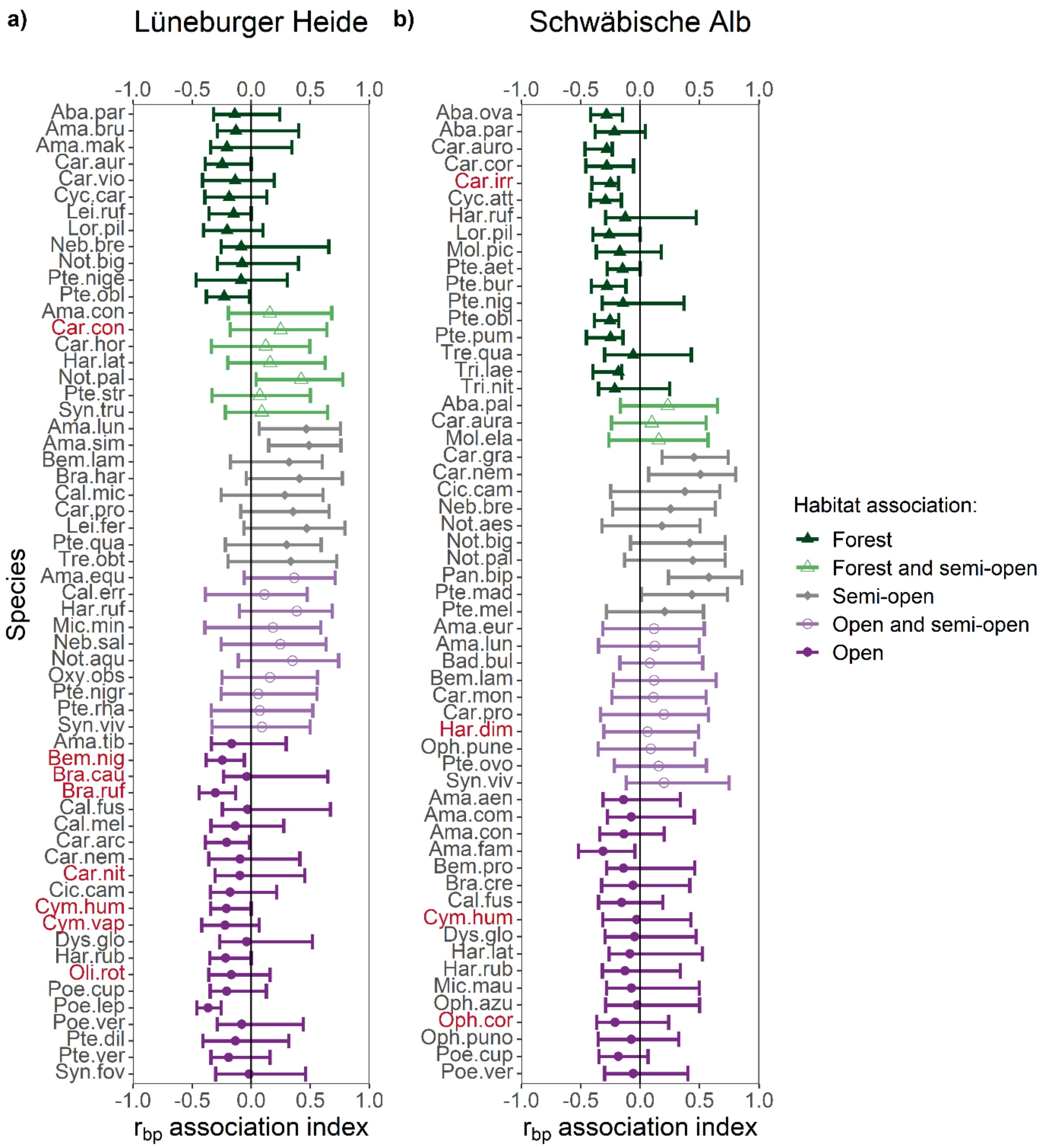

Figure 2.5: Ground beetle species association with semi-open habitats in both studied landscapes. Species are grouped by habitat association with either forest (dark green, filled triangle), both forest and semi-open (light green, empty triangle), semi-open (grey, diamond), both the open and the semi-open (light purple, empty circle), and open (dark purple, filled circle) habitats and further sorted alphabetically. The symbols correspond to the point-biserial correlation coefficient and the error bars show the 95% confidence interval. Threatened species are written in red. Explanation about abbreviated species names can be found in Table A2.3

2.4 Discussion

We found a higher γ-diversity of ground beetle species in semi-open habitats than in adjacent heathlands or grasslands, and forests in two landscapes in Germany. In contrast, both α- and functional diversity of ground beetles in semi-open habitats were similar to those of open habitats. The assemblages found in semi-open habitats were distinct yet intermediate between those of their adjacent open and forest habitats. About 40 to 45 % of the species recorded in semi-open habitats show a preference for semi-open habitats exclusively or in combination with either open or forest habitats. While most of the species recorded did not significantly avoid semi-open habitats, the small proportion (8-15 %) of species avoiding it comprised numerous threatened ones. We found similar results in both studied landscapes irrespective of the dominant type of vegetation in the matrix and neither habitat nor landscape characteristics nor sampling year were influential in determining the difference between habitats or within the semi-open ones.

2.4.1 Ground beetle species richness and assemblages

A comparison of our results with other studies needs to consider the scale. At patch level, α-diversity was comparable to that of open habitats while at landscape level, γ diversity was highest in semi-open habitats. The former is in agreement with ground beetle studies from the Mediterranean regions (Taboada et al., 2006a, 2006b) while the latter is comparable to a study in the boreal region (Talvi, 1995). This pattern appears to contradict most studies on semi-open habitats which are considered of high conservation value because of their higher species richness (e.g. Bergmeier et al., 2010). However, usually studies only report either α- or γ-diversity. Moreno et al. (2016) found similar discrepancies between landscape and site level diversities for other invertebrate groups in the Spanish Dehesa as a consequence of a higher species turnover between sites. In our case, no such difference in β-diversity existed (data not shown but see ordination in Fig. 2.3). Thus, similar richness values at site and landscape levels were expected. However although not significantly different on average, species richness at site level was higher in the semi-open than in the open habitats which likely resulted in the higher species richness found at landscape level.

Following the “habitat heterogeneity hypothesis”, we expected both higher species richness and functional diversity in semi-open habitats at site level due to the simultaneous presence of forest and open habitats ground beetle species (Díaz et al., 2013). Indeed, we found that semi-open habitat ground beetle assemblages consisted of species associated with both open or forest habitats. Contrary to expectation, species richness and functional diversity of the semi-open were not higher than those of open habitats in both landscapes. We also found several forest species in the open habitats. Forest ground beetles have a higher tendency to disperse into adjacent open habitats while open habitat species are less likely to enter forests (Lacasella et al., 2015; Magura & Lövei, 2017). Despite being recorded in low numbers in the open habitats, those forest species contribute to the increase of both species richness and functional diversity. Thus, the similar species richness and functional diversity values found between semi-open and open habitats likely result from the latter having both increased species richness and functional diversity due to the presence of few forest species. In contrast, forest habitats displayed lower species richness and functional diversity attributable to the absence of open habitats species.

2.4.2 Function of semi-open habitats for ground beetles

The presumed mechanism driving the high species richness or functional diversity in semi-open habitats is niche differentiation resulting from the higher habitat heterogeneity, which allows more species adapted to a range of different abiotic conditions to coexist. However, habitat patches are not isolated from one another and mass effects could also be an important contributor to species richness. Mass effects could increase assemblages' species richness as a result of recurrent dispersal of individuals from adjacent habitats with a higher reproduction success (Shmida & Wilson, 1985; Mouquet & Loreau, 2002). Mass effects have been found to be neglectable compared to niche differentiation across similar habitats (Brooks et al., 2008). However, mass effects are expected to be maximal when differences between habitats are moderate such as between semi-open habitats and adjacent open and forest habitats ((“intermediate difference hypothesis” Kunin, 1998). While ground beetle species have limited and varying dispersal abilities, our sampling locations within the semi-open habitats are well within the range of what could be covered by such taxa within one activity period (Baars, 1979; Rijnsdorp, 1980; Vermeulen, 1994a). In semi-open habitats, neither the narrow glades of heathland or grassland-like patches nor the small wooded patches dominated by trees or shrubs are likely to support sufficient reproduction of most open or forest ground beetle species found in this study (Petit, 1994; Vermeulen, 1994a; Noordijk *et al.*, 2011). Thus, the continuous presence of many species in semi-open habitats at comparable abundance with either forest or open habitats is likely to depend on immigration from the adjacent source habitats. Consequently, mass effects rather than habitat heterogeneity are likely to be the main driver of the high species richness and functional diversity of semi-open habitats. In some instances, semi-open habitats will allow species preferring distinct habitats to exploit a greater proportion of the landscape, for example for foraging (Rijnsdorp, 1980; Taboada et al., 2011).

While the potential of semi-open habitats as corridors has rarely been investigated (but see Eggers et al., 2010; Travers et al., 2020), semi-open habitats can have positive effects on landscape connectivity. In our study, only a limited number of species (8 to 15 %) tended to effectively avoid semi-open habitats, though, the high tendency of a large number of forest and open habitat species to enter semi-open habitats indicates that semi-open habitats can be also used for dispersal (Eggers et al., 2010). Of course, if intended to be used for dispersal in addition to habitat quality, semi-open habitats location and dimension will have to be adapted to the target species to avoid that they instead act as a sink.

We found that 15 to 18 % of the analysed species were exclusively positively associated with semi-open habitats. Thus, semi-open habitat patches do appear to function as a habitat for some species preferring the particular environmental conditions prevailing in those patches. The addition of those species, to the above-mentioned forest and open habitat species, explains the higher species richness of our semi-open habitats. However, only a few species typically associated with forest edges (Heide: Leistus ferrugineus and Pterostichus quadrifoveolatus; Alb: Panagaeus bipustulatus) are likely to be truly dependent on semi-open habitats, while the remaining species being either eurytopic, open, or (more rarely) forest habitat specialist species (Gesellschaft für Angewandte Carabidologie, 2009). In concordance with our results, the semi-open Dehesa habitats have similarly been shown to predominantly host eurytopic and open habitat specialist species (Taboada et al., 2006a, 2011). In our case, many of the open habitat specialists are associated with regular disturbance as occurring in arable fields or ruderal habitats and their preference for semi-open habitat is likely caused by disturbances from both the effect of trees and shrub management and trampling from grazing animals. Similarly, Oedipoda caerulescens, a grasshopper also dependent on such frequently disturbed microsites was found in semi-open habitats (Rösch et al., 2019).

Some authors have considered semi-open habitats as ecotones, given their intermediate nature combined with their high proportions of forest-open habitat edges (Bergmeier et al., 2010; Somay et al., 2021). However, studies focussing on ground beetles at forest-open habitat ecotones found assemblages highly similar to the forest assemblages (e.g. Heliölä et al., 2001; Lacasella et al., 2015) while we retrieved semi-open habitat assemblages which were distinct from the forest ones. In addition, studies on ecotones found an absence or a very low number of species that were associated with this particular environment. We comparatively found a higher number of species associated with semi-open habitats. Similar dissimilarities between forest ecotones and semi-open habitats have been reported for dung beetles (Somay et al., 2021). While forest edges entail a narrow, abrupt transition between open and forest habitats with environmental characteristics most similar to the forest interior (Heliölä et al., 2001), semi-open habitats, like those studied here, are much wider and appear to exhibit distinct environmental conditions (Travers et al., 2020). Consequently, semi-open habitats appear to be different from an ecotone and should likely not be regarded as such.

2.4.3 Difference between studied landscapes

Although generally consistent for both landscapes, our results differed in some respects. The ground beetle assemblages of semi-open habitats in the Heide were more similar to the ones in the forest while they were more similar to the open habitat assemblages in the Alb. A comparatively higher proportion of species associated with forest habitats in the Alb avoided the semi-open habitats while this proportion was lower in the Heide. The opposite was found for species associated with open habitats in both landscapes. Few studies have compared assemblages from semi-open habitats in different locations. Studying dung beetles across Hungary, Somay et al. (2021) did not find a comparable alteration of the composition of semi-open habitat assemblages under similar climatic conditions and in the presence of an identical matrix. In contrast, a similar pattern was found for plants in our studied landscapes (some sites in common, Travers et al., 2020). Furthermore, the Ellenberg indicator values for the plant assemblages found in the semi-open habitats in the Heide indicated higher moisture than for the Alb (see Travers et al., 2020). The different climatic conditions between the two studied landscapes may be the driver for this pattern. The microclimatic conditions in the semi-open habitats under oceanic climate are likely to be more similar to those in forests thus in the Heide, hence a larger number of forest-associated species, preferring on average cooler and moister conditions (Thiele, 1977), enter the semi-open habitats. Under sub-continental climate, in contrast, habitat conditions in the semi-open are likely to be more similar to those in open habitats (see Travers et al., 2020), thus in the Alb, a larger proportion of open-associated species, preferring dryer and sunnier conditions (Thiele, 1977), enter the semi-open habitats. In addition, dwarf shrubs such as Calluna vulgaris, which dominate the semi-open matrix in the Heide, have been shown to alter microclimatic conditions by stabilising humidity and temperature levels within the vegetation layer (Gimingham, 1972). Thus the matrix could contribute to reinforcing the difference between the two landscapes. In dry calcareous grasslands, such as those found in the Alb, no dwarf shrub species occur so humidity levels depend strictly on weather conditions. However, it remains to be investigated further by considering semi-open habitats with oceanic climate and grassland vegetation. Nevertheless, Somay's expectation (Somay et al., 2021) that assemblages from semi-open habitats are intermediate between those of forest and open habitats independently from locations can now be extended to further taxa (ground beetles or plants) and presumably to the entire temperate region.

2.4.4 Implications for conservation

Any proposed solution for biodiversity conservation needs to be objectively evaluated (Godet & Devictor, 2018) and species richness has often been used to set conservation priorities (e.g. Gutiérrez et al., 2004). The high species richness found in semi-open habitats in combination with the occurrence of threatened species are repeatedly used to justify their conservation value (e.g. Gallé et al., 2017; Rösch et al., 2019; Somay et al., 2021). However, no or only limited consideration has been given to the process leading to the high species richness or the strength of the association between a given species and semi-open habitats. For ground beetles, we found that high species richness and functional diversity were presumably a result of only a few semi-open preferring species living in these habitats combined with those species regularly dispersing from both forest and open habitats into semi-open habitats due to mass effects. Thus, it appears, that neither species richness nor functional diversity are suitable tools for assessing the effectiveness of semi-open habitats as habitats with unique properties for biodiversity conservation. In addition, most threatened species, for which we evaluated habitat preference, were found to avoid semi-open habitats. Our findings question the conservation value of semi-open habitats for ground beetles in the temperate region.

Instead, our results underline the value of preserving the existing forest, heathland, and grassland habitats as such. The expected increase in semi-open habitats in the European temperate region through trophic rewilding or restoration and establishment of wood pastures may thus possibly be detrimental to many ground beetle species, including many threatened ones if they come to replace existing valuable habitats. Such measures should consequently be implemented with caution. However, as semi-open habitats appear to host a few specialized ground beetle species and considering that modern landscapes are mostly void of such habitat types, they do appear vital for the conservation of (at least) those few species. Also, the property of semi-open habitats to attract a large number of species from adjacent habitats could be beneficial for the conservation of ground beetles if such habitats are designed and established in a way so that they function as dispersal corridors.

Thus, both trophic rewilding or restoration and establishment of wood pastures, which have been suggested as solutions for insect conservation (Samways et al., 2020), might be especially effective for ground beetle conservation when they target enhancing connectivity rather than habitat creation. Given the similarity between our results and findings from the Mediterranean region for invertebrates (Díaz et al., 2013), a careful re-examination of already published evidence on the conservation value of semi-open habitats is required.

Acknowledgements

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Appendix 2

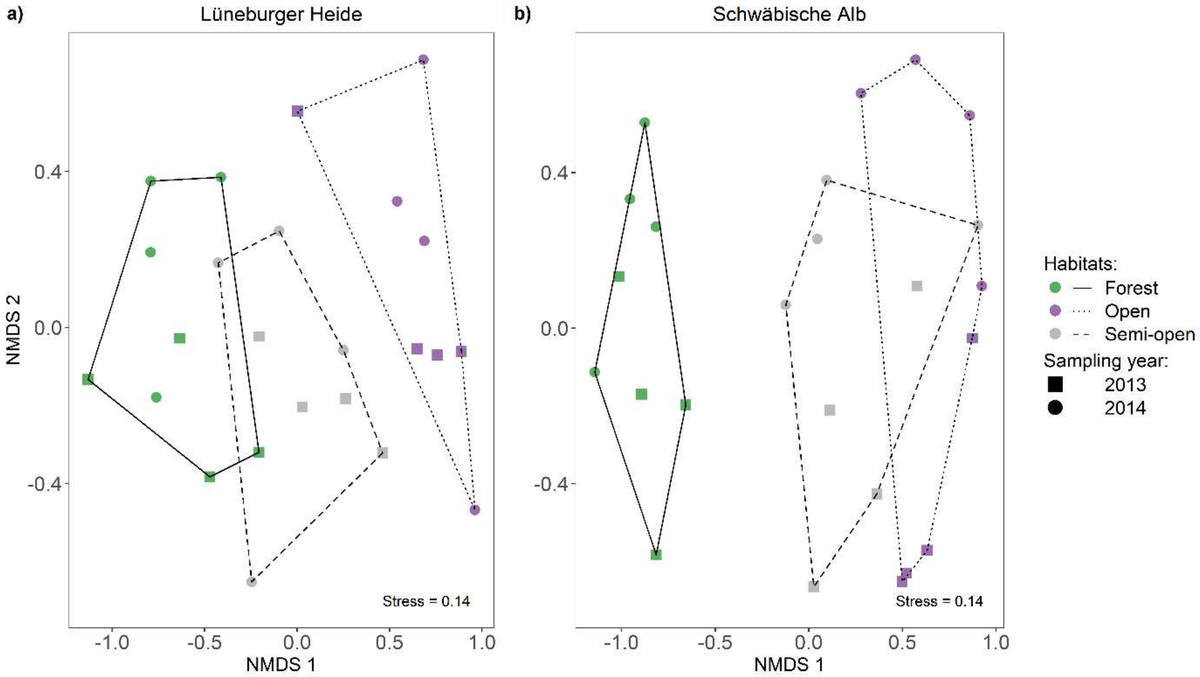

Figure A2.1: Non-metric multidimensional scaling ordinations of carabid beetle assemblages of forest (green), semi-open (grey), and open (purple) habitats sampled in the years 2013 (square) or 2014 (circle) in the Lüneburger Heide (a) and the Schwäbische Alb (b) based on Horn distance (two dimensions). Minimum convex polygons are shown for forest (solid line), semi-open (dashed line), and open habitat (dotted line).

Table A2.1: Characteristics of the studied landscapes and semi-open habitats in the Lüneburger Heide and the Schwäbische Alb. Large habitat patches with a size over 50 ha were not measured. The proportions of forest, semi-open, open, and other open habitats were measured in a 500 m radius using Google Earth pro aerial photographs. Age values were estimated from available topographic maps for forest and open habitats or aerial photographs for the semi-open habitats. For the variables canopy cover, distance to the forest, and open edges mean value and standard deviation (in parenthesis) are provided. Site numbers 01 to 04 were studied in 2013 while site numbers 05 to 08 were studied in 2014.

Landscapes	Sites	Habitat types	Patch size (ha)	Age (y)	Canopy cover (%)	Distance to forest edge (m)	Distance to open edge (m)	% forest	% semi-open	% open	% other open
Lüneburger Heide	01	forest	>50	>100	74 (21)	0	123.2 (9.8)	43.34	11.57	45.08	0.00
	02	forest	>50	>100	70 (39)	0	81.4 (6.5)	34.41	19.04	41.09	5.46
	03	forest	15.8	>100	20 (19)	0	53.4 (7.9)	37.34	4.50	58.15	0.00
	04	forest	20.23	>29	92 (6)	0	56.2 (1.3)	38.31	18.40	27.25	16.05
	05	forest	47.33	>29	33 (40)	0	68 (7.0)	56.22	2.30	19.59	21.89
	06	forest	>50	>100	63 (39)	0	54.6 (6.3)	53.55	11.44	29.30	5.71
	07	forest	>50	>70	18 (16)	0	75.2 (15.2)	67.25	3.74	28.81	0.20
	08	forest	>50	>100	44 (42)	0	60.4 (8.2)	18.15	31.49	49.26	1.09
	01	semi-open	3.63	>13	56 (37)	79.8 (13.9)	61.8 (10.7)	43.34	11.57	45.08	0.00
	02	semi-open	7.73	>13	20 (39)	84.8 (12.5)	57.6 (14.2)	34.41	19.04	41.09	5.46
	03	semi-open	0.45	>13	20 (28)	84.4 (5.6)	22 (6.7)	37.34	4.50	58.15	0.00
	04	semi-open	11.46	>13	20 (45)	115.4 (13.9)	46.8 (6.5)	38.31	18.40	27.25	16.05
	05	semi-open	1.45	>13	18 (35)	44.2 (6.8)	70.6 (10)	56.22	2.30	19.59	21.89
	06	semi-open	2.61	2	25 (40)	33.2 (6.5)	80.2 (16.5)	53.55	11.44	29.30	5.71
	07	semi-open	3.05	>13	2 (5)	21.6 (5.9)	10.13 (5.8)	67.25	3.74	28.81	0.20
	08	semi-open	4.93	4	2 (5)	66.6 (13.8)	57.8 (16.2)	18.15	31.49	49.26	1.09
	01	open	>50	>100	0	132.6 (20.6)	0	43.34	11.57	45.08	0.00
	02	open	>50	>100	0	58 (12.8)	0	34.41	19.04	41.09	5.46
	03	open	>50	>100	0	71.4 (15.8)	0	37.34	4.50	58.15	0.00
	04	open	16.27	>100	0	133.6 (2.4)	0	38.31	18.40	27.25	16.05
	05	open	5.51	>100	0	56.2 (2.7)	0	56.22	2.30	19.59	21.89
	06	open	32	>100	0	72.8 (1.1)	0	53.55	11.44	29.30	5.71
	07	open	>50	>70	0	49.8 (0.5)	0	67.25	3.74	28.81	0.20

Landscapes	Sites	Habitat types	Patch size (ha)	Age (y)	Canopy cover (%)	Distance to forest edge (m)	Distance to open edge (m)	% forest	% semi-open	% open	% other open
	08	open	>50	>100	0	122.4 (9.1)	0	18.15	31.49	49.26	1.09
Schwäbische Alb	01	forest	8.65	>73	82 (11)	0	29.4 (8.0)	40.80	4.48	23.87	30.85
	02	forest	>50	>77	74 (9)	0	52.1 (2.2)	51.33	11.50	33.88	3.29
	03	forest	>50	>79	62 (17)	0	114.3 (16.4)	53.88	3.76	24.69	17.67
	04	forest	>50	>73	69 (8)	0	47.4 (3.2)	21.75	3.19	13.84	61.23
	05	forest	>50	>69	79 (19)	0	92.4 (8.5)	41.69	6.45	45.93	5.93
	06	forest	>50	>77	81 (12)	0	103.3 (16.7)	65.63	8.22	26.14	0.00
	07	forest	>50	>69	88 (7)	0	34.7 (5.0)	64.55	4.73	9.22	21.49
	08	forest	>50	>74	84 (16)	0	64.9 (2.7)	45.60	9.56	44.84	0.00
	01	semi-open	1.19	<10, >3	24 (33)	29.6 (2.7)	20.9 (2.3)	40.80	4.48	23.87	30.85
	02	semi-open	6.01	<45, >3	40 (50)	124.5 (7.4)	29.8 (11.5)	51.33	11.50	33.88	3.29
	03	semi-open	0.73	>10	62 (40)	18.7 (6.1)	22.5 (7.0)	53.88	3.76	24.69	17.67
	04	semi-open	1.53	>45	7 (8)	43.2 (9.3)	13.6 (2.3)	21.75	3.19	13.84	61.23
	05	semi-open	2.19	>45	41 (54)	166.1 (10)	37.4 (6.9)	41.69	6.45	45.93	5.93
	06	semi-open	2.34	<45, >3	13 (26)	37.6 (12.9)	49.8 (8.1)	65.63	8.22	26.14	0.00
	07	semi-open	0.4	>45	19 (29)	23.2 (9.0)	16.5 (6.0)	64.55	4.73	9.22	21.49
	08	semi-open	4.61	>45	4 (9)	177.9 (14.8)	39.2 (8.3)	45.60	9.56	44.84	0.00
	01	open	4.67	>73	1 (2)	40.6 (13.2)	0	40.80	4.48	23.87	30.85
	02	open	15.67	>77	0	76.7 (16.0)	0	51.33	11.50	33.88	3.29
	03	open	>50	>79	0	61.5 (1.1)	0	53.88	3.76	24.69	17.67
	04	open	6.48	>73	0	32.4 (9.7)	0	21.75	3.19	13.84	61.23
	05	open	>50	>69	0	122.6 (9.6)	0	41.69	6.45	45.93	5.93
	06	open	32.69	>77	0	52.8 (2.1)	0	65.63	8.22	26.14	0.00
	07	open	3.07	>69	0	30.8 (9.7)	0	64.55	4.73	9.22	21.49
	08	open	>50	>74	0	152.5 (4.4)	0	45.60	9.56	44.84	0.00

Table A2.2: Results of the linear model for the effects of patch size, canopy cover, distance from the forest or open habitat edges, the proportions of forest, semi-open, open, and other open habitats in a 500 m radius on α- and functional diversity (FD) in the Lüneburger Heide and the Schwäbische Alb.

Explanatory variables	Lüneburger Heide				Schwäbische Alb			
	α- diversity		FD		α- diversity		FD	
	F values	p-values	F values	p-values	F values	p-values	F values	p-values
Patch size (ha)	0.36	0.57	0.04	0.84	2.7	0.15	3.6	0.13
Canopy cover (%)	2.38	0.17	0.16	0.71	0.03	0.85	2.51	0.16
Distance to forest edge (m)	0.77	0.41	2.42	0.17	1.34	0.29	0.52	0.5
Distance to open edge (m)	0.04	0.85	0.12	0.74	0.02	0.88	1.84	0.27
% forest	1.7	0.26	1.99	0.2	1.28	0.3	0.09	0.78
% semi-open	1.68	0.24	3.3	0.13	2.37	0.18	0.07	0.79
% open	0.81	0.4	0.39	0.57	0.18	0.68	0.14	0.72
% other open	3.7	0.103	0.39	0.57	0.19	0.69	0.21	0.67

Table A2.3: List of ground beetle (Carabidae) and tiger beetle (Cicindelidae) species, species names abbreviation, red list status, and numbers of individuals in forest, semi-open, and open habitats in the Lüneburger Heide and Schwäbische Alb. Species are listed by decreasing total number of individuals. The classification of threatened species and the nomenclature followed Schmidt et al. (2016). LC: least concern, NT: near threatened, NT*: near threatened but either vulnerable or endangered in Lower Saxony or Baden Württemberg, VU: vulnerable, EN: endangered, CR: critically endangered.

Species	Abbreviation	Red list status	Lüneburger Heide			Schwäbische Alb			Total
			Forest (8)	Semi-open (8)	Open (8)	Forest (8)	Semi-open (8)	Open (8)	
Calathus fuscipes	Cal.fus	LC	451	1 162	2 174		372	1 415	5 574
Carabus problematicus	Car.pro	LC	1 318	1 692	896	165	427	311	4 809
Abax parallelepipedus	Aba.par	LC	872	235	17	2 028	469	26	3 647
Poecilus versicolor	Poe.ver	LC	11	647	1 840		238	608	3 344
Poecilus lepidus	Poe.lep	LC	1	139	2 627		3	82	2 852
Calathus erratus	Cal.err	LC	2	1 088	1 311				2 401
Pterostichus burmeisteri	Pte.bur	LC				1 782	155	8	1 945
Pterostichus oblongopunctatus	Pte.obl	LC	974	202	2	701	2	1	1 882
Pterostichus niger	Pte.nige	LC	959	523	265	100	5	2	1 854

Species	Abbreviation	Red list status	Lüneburger Heide			Schwäbische Alb			Total
			Forest (8)	Semi-open (8)	Open (8)	Forest (8)	Semi-open (8)	Open (8)	
Carabus violaceus	Car.vio	LC	815	358	158	1	8	7	1 347
Cicindela campestris	Cic.cam	LC	1	155	791		88	19	1 054
Carabus nemoralis	Car.nem	LC	164	187	437	41	170	25	1 024
Carabus convexus	Car.con	NT	321	363	28	2	5	14	733
Abax ovalis	Aba.ova	LC	4			603	40	1	648
Nebria brevicollis	Neb.bre	LC	409	91	13	14	51	26	604
Pterostichus madidus	Pte.mad	LC				121	325	55	501
Leistus rufomarginatus	Lei.ruf	LC	380	1		1	1		383
Nebria salina	Neb.sal	LC	13	179	183				375
Notiophilus biguttatus	Not.big	LC	224	73		11	29	1	338
Amara lunicollis	Ama.lun	LC	68	179	56		13	16	332
Notiophilus aquaticus	Not.aqu	LC	22	182	105				309
Calathus micropterus	Cal.mic	LC	65	192	49				306
Carabus auronitens	Car.auro	LC	45	2		246	4		297
Carabus coriaceus	Car.cor	LC				225	39	33	297
Molops piceus	Mol.pic	LC				226	61	7	294
Harpalus latus	Har.lat	LC	78	74	21	3	28	86	290
Brachinus crepitans	Bra.cre	NT					80	197	277
Carabus arcensis	Car.arc	LC	7	27	239				273
Poecilus cupreus	Poe.cup	LC	3	18	139		18	65	243
Pterostichus melanarius	Pte.mel	LC	16			15	127	71	229
Molops elatus	Mol.ela	LC				102	101	24	227
Bembidion lampros	Bem.lam	LC	21	137	3	1	17	22	201
Carabus auratus	Car.aura	LC				96	87	6	189
Abax parallelus	Aba.par	LC				87	95	3	185
Calathus melanocephalus	Cal.mel	LC	3	37	132			11	183
Bembidion properans	Bem.pro	LC					12	171	183
Synuchus vivalis	Syn.viv	LC	10	47	55	1	18	19	150

Species	Abbreviation	Red list status	Lüneburger Heide			Schwäbische Alb			Total
			Forest (8)	Semi-open (8)	Open (8)	Forest (8)	Semi-open (8)	Open (8)	
Carabus glabratus	Car.gla	LC	112	23	3				138
Carabus hortensis	Car.hor	LC	63	71	4				138
Amara convexior	Ama.con	LC	40	46	1		11	35	133
Notiophilus palustris	Not.pal	LC	36	63	3		23	2	127
Bradycellus ruficollis	Bra.ruf	VU	1	11	111				123
Carabus irregularis	Car.irr	VU				122	1		123
Pterostichus quadrifoveolatus	Pte.qua	NT	4	117					121
Harpalus dimidiatus	Har.dim	VU					47	72	119
Ophonus azureus	Oph.azu	LC					38	77	115
Carabus monilis	Car.mon	NT					52	58	110
Bembidion nigricorne	Bem.nig	EN		6	96				102
Dyschirius globosus	Dys.glo	LC	4	21	48		8	21	102
Harpalus rubripes	Har.rub	LC			13		20	68	101
Leistus ferrugineus	Lei.fer	LC	10	59	21	3	6		99
Ophonus puncticollis	Oph.puno	NT					26	65	91
Amara equestris	Ama.equ	LC		22	14		10	43	89
Amara makolskii	Ama.mak	LC	81	3					84
Pterostichus diligens	Pte.dil	LC	24	20	40				84
Harpalus rufipes	Har.ruf	LC	1	19	12	32	6	7	77
Pterostichus ovoideus	Pte.ovo	LC				3	32	38	73
Carabus nitens	Car.nit	CR		15	54				69
Calathus rotundicolis	Cal.rot	LC	67	1					68
Pterostichus vernalis	Pte.ver	LC		6	51			8	65
Amara brunnea	Ama.bru	LC	57	7					64
Olisthopus rotundatus	Oli.rot	NT		4	55				59
Cychrus caraboides	Cyc.car	LC	30	8	1	18			57
Syntomus foveatus	Syn.fov	LC	5	16	29				50
Trechus obtusus	Tre.obt	LC	4	24	11	5			44

Species	Abbreviation	Red list status	Lüneburger Heide			Schwäbische Alb			Total
			Forest (8)	Semi-open (8)	Open (8)	Forest (8)	Semi-open (8)	Open (8)	
Oxypselaphus obscurus	Oxy.obs	LC	4	21	18				43
Pterostichus pumilio	Pte.pum	LC				34	1	4	39
Badister bullatus	Bad.bul	LC	1				15	23	39
Trichotichnus laevicollis	Tri.lae	LC				38			38
Carabus granulatus	Car.gra	LC				6	29	3	38
Bradycellus harpalinus	Bra.har	LC	4	19	11				34
Syntomus truncatellus	Syn.tru	LC	17	13	1				31
Trichotichnus nitens	Tri.nit	LC				30	1		31
Cymindis humeralis	Cym.hum	VU			21		2	3	26
Amara communis	Ama.com	LC		5	1		5	14	25
Microlestes minutulus	Mic.min	LC	1	5	5		4	8	23
Ophonus puncticeps	Oph.pune	LC					9	11	20
Amara infima	Ama.inf	VU			20				20
Amara aenea	Ama.aen	LC			3		2	14	19
Bradycellus caucasicus	Bra.cau	NT		5	14				19
Anchomenus dorsalis	Anc.dor	LC			2		16		18
Loricera pilicornis	Lor.pil	LC	8	1	1	8			18
Limodromus assimilis	Lim.ass	LC				17			17
Bembidion obtusum	Bem.obt	LC					9	8	17
Ophonus parallelus	Oph.par	EN					1	15	16
Panagaeus bipustulatus	Pan.bip	LC					12	3	15
Pterostichus strenuus	Pte.str	LC	3	2		9		1	15
Amara curta	Ama.cur	LC						14	14
Cymindis vaporariorum	Cym.vap	EN		2	11				13
Ophonus cordatus	Oph.cor	VU					1	12	13
Amara familiaris	Ama.fam	LC		1		2	1	8	12
Amara similata	Ama.sim	LC	1	8		2		1	12
Carabus cancellatus	Car.can	NT			12				12

Species	Abbreviation	Red list status	Lüneburger Heide			Schwäbische Alb			Total
			Forest (8)	Semi-open (8)	Open (8)	Forest (8)	Semi-open (8)	Open (8)	
Clivina fossor	Cli.fos	LC			2		7	3	12
Pterostichus macer	Pte.mac	NT						12	12
Microlestes maurus	Mic.mau	LC					3	9	12
Amara nitida	Ama.nit	NT					4	7	11
Cychrus attenuatus	Cyc.att	LC				11			11
Amara tibialis	Ama.tib	LC		1	7				8
Calosoma inquisitor	Cal.inq	VU		8					8
Notiophilus germinyi	Not.ger	LC			6			1	7
Amara eurynota	Ama.eur	LC				1	3	3	7
Ophonus melletii	Oph.mel	NT					6		6
Harpalus rufipalpis	Har.ruf	LC		5	1				6
Cymindis macularis	Cym.mac	EN			6				6
Pterostichus rhaeticus	Pte.rha	LC	1	2	2				5
Notiophilus aestuans	Not.aes	NT				1	3	1	5
Amara praetermissa	Ama.pra	EN		4	1				5
Harpalus laevipes	Har.lae	LC		4		1			5
Pterostichus nigrita	Pte.nigr	LC		2	3				5
Trechus quadristriatus	Tre.qua	LC				3	1	1	5
Bembidion quadrimaculatum	Bem.qua	LC		1	3				4
Pterostichus aethiops	Pte.aet	LC				4			4
Abax carinatus	Aba.car	NT					4		4
Harpalus tardus	Har.tar	LC		2	2				4
Stomis pumicatus	Sto.pum	LC	2				2		4
Cicindela sylvatica	Cic.syl	EN			4				4
Licinus depressus	Lic.dep	NT					3		3
Leistus terminatus	Lei.ter	LC	3						3
Patrobus atrorufus	Pat.atr	LC				2			2
Amara ovata	Ama.ova	LC		2					2

Species	Abbreviation	Red list status	Lüneburger Heide			Schwäbische Alb			Total
			Forest (8)	Semi-open (8)	Open (8)	Forest (8)	Semi-open (8)	Open (8)	
Harpalus affinis	Har.aff	LC	1		1				2
Bembidion mannerheimii	Bem.man	LC					2		2
Agonum fuliginosum	Ago.ful	LC	2						2
Amara spreta	Ama.spr	LC		1	1				2
Harpalus smaragdinus	Har.sma	LC			2				2
Calodromius spilotus	Cal.spi	LC	2						2
Agonum sexpunctatum	Ago.sex	LC		2					2
Amara consularis	Ama.con	LC					1	1	2
Amara aulica	Ama.aul	LC					1		1
Trechus secalis	Tre.sec	LC					1		1
Amara anthobia	Ama.ant	LC		1					1
Elaphrus cupreus	Ela.cup	LC	1						1
Agonum muelleri	Ago.mue	LC					1		1
Harpalus xanthopus	Har.xan	LC	1						1
Badister sodalis	Bad.sod	LC						1	1
Lebia cruxminor	Leb.cru	VU						1	1
Calosoma maderae auropunctatum	Cal.aur	NT			1				1
Harpalus distinguendus	Har.dis	LC						1	1
Trichocellus placidus	Tri.pla	LC	1						1
Badister lacertosus	Bad.lac	LC				1			1
Dromius angustus	Dro.ang	LC		1					1
Harpalus griseus	Har.gri	LC		1					1
Bembidion stephensii	Bem.ste	LC				1			1
Total			**7 849**	**8 671**	**12 270**	**6 926**	**3 518**	**4 009**	**43 243**

Table A2.4: Results of the linear model for the effects of habitat types and sampling year on α- and functional diversity (FD) in the Lüneburger Heide and the Schwäbische Alb. df provide the degree of freedom and the residual degrees of freedom. Significant values are in bold.

Landscapes	Diversity metrics	Variables	Estimate	Std. error	df	F values	p-values
Lüneburger Heide	α- diversity	Habitat types	-	-	2, 20	4.08	**0.03**
		Forest	20.33	1.8			
		Semi-open	28.59	2.47			
		Open	24.69	2.55			
		Sampling year	-	-	1, 20	0.47	0.5
		2013	25.24	1.71			
		2014	23.84	2.42			
	FD	Habitat types	-	-	2, 20	1.33	0.28
		Forest	0.116	0.007			
		Semi-open	0.127	0.011			
		Open	0.108	0.011			
		Sampling year	-	-	1, 20	0.02	0.89
		2013	0.116	0.007			
		2014	0.112	0.009			
Schwäbische Alb	α- diversity	Habitat types	-	-	2, 20	15.32	**<0.001**
		Forest	14.84	1.26			
		Semi-open	24.55	1.78			
		Open	21.07	1.78			
		Sampling year	-	-	1, 20	1.16	0.29
		2013	19.40	1.55			
		2014	21	2.2			
	FD	Habitat types	-	-	2, 20	9.36	**0.001**
		Forest	0.063	0.009			
		Semi-open	0.118	0.013			
		Open	0.112	0.013			
		Sampling year	-	-	1, 20	0.89	0.35
		2013	0.103	0.011			
		2014	0.093	0.015			

Table A2.5: Correlation between environmental or landscape variables and the ground beetle assemblages found in semi-open habitats. P-values have been corrected for multiple testing and are in bold if significant. The proportions of forest, semi-open, open, and other open habitats were measured in a 500 m radius using Google Earth pro aerial photographs.

Environmental variable	Lüneburger Heide		Schwäbische Alb	
	r^2	p-value	r^2	p-value
patch size (ha)	0.01	0.98	0.43	0.35
canopy cover (%)	0.27	0.58	0.01	0.97
distance forest edge (m)	0.42	0.26	0.40	0.35
distance open edge (m)	0.09	0.78	0.45	0.35
% forest	0.30	0.58	0.31	0.46
% semi.open	0.37	0.58	0.69	0.29
% open	0.42	0.58	0.48	0.35
% other.open	0.35	0.58	0.86	**0.007**
% all.open	0.42	0.58	0.45	0.35

Table A2.6: Ground beetles species point-biserial correlation coefficient (rpb) and corrected p-value for forest, semi-open, and open habitats or combination of in the Lüneburger Heide. Significant values are in bold.

Species	r_{pb}	p.value
Forest habitat		
Abax parallelepipedus	0.515	**0.007**
Amara brunnea	0.311	0.219
Amara makolskii	0.405	**0.049**
Carabus auronitens	0.527	**0.012**
Carabus violaceus	0.643	**0.002**
Cychrus caraboides	0.651	**0.001**
Leistus rufomarginatus	0.301	**0.007**
Loricera pilicornis	0.415	**0.048**
Nebria brevicollis	0.271	0.593
Notiophilus biguttatus	0.397	0.071
Pterostichus oblongopunctatus	0.57	**0.008**
Forest and Semi-open habitat		
Amara convexior	0.241	0.373
Carabus convexus	0.443	0.062
Carabus hortensis	0.211	0.658
Carabus problematicus	0.322	0.267
Harpalus latus	0.379	0.136
Notiophilus palustris	0.406	0.085
Pterostichus niger	0.459	**0.050**
Pterostichus strenuus	0.344	0.226
Syntomus truncatellus	0.306	0.314
Semi-open habitat		
Amara lunicollis	0.39	0.103
Amara similata	0.528	**0.010**

Species	r_{pb}	p.value
Bembidion lampros	0.283	0.411
Calathus micropterus	0.272	0.419
Leistus ferrugineus	0.371	0.146
Pterostichus quadrifoveolatus	0.266	0.753
Trechus obtusus	0.27	0.441
Open and semi-open habitat		
Amara equestris	0.413	0.084
Bradycellus harpalinus	0.343	0.209
Calathus erratus	0.324	0.216
Harpalus rufipes	0.425	0.069
Microlestes minutulus	0.372	0.148
Nebria salina	0.493	**0.027**
Notiophilus aquaticus	0.32	0.275
Oxypselaphus obscurus	0.247	0.496
Pterostichus nigrita	0.313	0.386
Pterostichus rhaeticus	0.12	1.000
Synuchus vivalis	0.269	0.381
Open habitat		
Amara tibialis	0.434	0.067
Bembidion nigricorne	0.544	**0.001**
Bradycellus caucasicus	0.248	0.596
Bradycellus ruficollis	0.708	**<0.001**
Calathus fuscipes	0.261	0.5532
Calathus melanocephalus	0.503	**0.011**
Carabus arcensis	0.482	**0.001**
Carabus cancellatus	0.295	0.621
Carabus nemoralis	0.233	0.640
Carabus nitens	0.382	0.100
Cicindela campestris	0.536	**0.003**
Cymindis humeralis	0.418	**0.044**
Cymindis vaporariorum	0.639	**0.002**
Dyschirius globosus	0.286	0.348
Harpalus rubripes	0.434	**0.044**
Olisthopus rotundatus	0.382	**0.004**
Poecilus cupreus	0.509	**0.004**
Poecilus lepidus	0.798	**<0.001**
Poecilus versicolor	0.463	**0.023**
Pterostichus diligens	0.177	0.716
Pterostichus vernalis	0.469	**0.004**
Syntomus foveatus	0.3	0.303

Table A2.7: Ground beetles species point-biserial correlation coefficient (rpb) and corrected p-value for forest, semi-open, and open habitats or combination of in the Schwäbische Alb. Significant values are in bold.

Species	r_{pb}	p.value
Forest habitat		
Abax ovalis	0.629	**<0.001**
Abax parallelepipedus	0.701	**<0.001**
Carabus auronitens	0.575	**<0.001**
Carabus coriaceus	0.583	**0.008**
Carabus irregularis	0.506	**0.001**
Cychrus attenuatus	0.582	**0.018**
Harpalus rufipes	0.233	1.000
Loricera pilicornis	0.520	0.082
Molops piceus	0.595	**0.005**
Pterostichus aethiops	0.295	1.000
Pterostichus burmeisteri	0.644	**0.002**
Pterostichus niger	0.309	0.200
Pterostichus oblongopunctatus	0.509	**<0.001**
Pterostichus pumilio	0.439	**0.024**
Pterostichus strenuus	0.279	1.000
Trechus quadristriatus	0.163	1.000
Trichotichnus laevicollis	0.365	**0.004**
Trichotichnus nitens	0.448	0.078
Forest and Semi-open habitat		
Abax parallelus	0.41	0.101
Carabus auratus	0.224	0.642
Molops elatus	0.351	0.218
Semi-open habitat		
Carabus granulatus	0.454	**0.015**
Carabus nemoralis	0.509	**0.030**
Cicindela campestris	0.377	0.221
Nebria brevicollis	0.257	0.512
Notiophilus aestuans	0.183	1.000
Notiophilus biguttatus	0.418	0.098
Notiophilus palustris	0.444	0.079
Panagaeus bipustulatus	0.58	**0.015**
Pterostichus madidus	0.437	0.068
Pterostichus melanarius	0.207	0.746
Open and semi-open habitat		
Amara eurynota	0.2	0.735
Amara lunicollis	0.341	0.294
Badister bullatus	0.544	**0.014**
Bembidion lampros	0.36	0.198
Carabus monilis	0.264	0.356
Carabus problematicus	0.216	0.607

Species	r_{pb}	p.value
Harpalus dimidiatus	0.446	0.098
Ophonus puncticeps	0.281	0.581
Pterostichus ovoideus	0.488	**0.046**
Synuchus vivalis	0.444	0.063
Open habitat		
Amara aenea	0.369	0.144
Amara communis	0.407	0.096
Amara convexior	0.577	**0.011**
Amara familiaris	0.511	**0.026**
Brachinus crepitans	0.396	0.134
Bembidion properans	0.307	0.127
Calathus fuscipes	0.571	**0.012**
Cymindis humeralis	0.296	0.306
Dyschirius globosus	0.3	0.340
Harpalus latus	0.369	0.067
Harpalus rubripes	0.497	**0.033**
Microlestes maurus	0.307	0.461
Ophonus azureus	0.372	0.144
Ophonus cordatus	0.483	0.081
Ophonus puncticollis	0.503	**0.030**
Poecilus cupreus	0.694	**<0.001**
Poecilus versicolor	0.488	**0.034**

Chapter III

3. Vegetation features and habitat specialisation matter for semi-open corridors and their management: a perspective on ground beetles (Coleptera Carabidae and Cicindelidae)

Estève Boutaud, Dorothea Nolte, Thorsten Assmann, and Claudia Drees

Manuscript to be submitted

A close view of a semi-open area from within the glade.

Abstract

Increasing connectivity is widely advocated in conservation to mitigate the harmful effects of fragmentation and enable species to respond to environmental change. Semi-open areas appear suitable as corridors for ground beetles and are more advantageous than traditional corridors because of their ability to increase connectivity without increasing fragmentation. Nonetheless, whether species could effectively use semi-open areas as corridors depends on both the corridor quality and the species' habitat preferences and specialisation. In this study, we investigated the effects of vegetation structures and landscape attributes on generalist and specialist ground beetle taxonomic diversity as well as the activity density in eight semi-open areas in two Central European landscapes. In both study landscapes, habitat preference determined the responses of ground beetles to environmental variables. Species associated with open and forest habitats displayed opposite microhabitat preferences. Open habitat species richness and activity-density increased in the heathland or grassland glades, characterised by the presence of heather and bare soil or the absence of leaf litter. In contrast, forest habitat species richness and activity-density increased in the forest-like patches characterised by the presence of bilberry, moss, and leaf litter. Furthermore, as habitat specialisation increased, so did the importance of microhabitat structures. In conclusion, to be effective, in particular for habitat specialist ground beetles, semi-open corridors must simultaneously provide high-quality vegetation structure within both the forest-like patches and the glades that constitute them. This will necessitate the implementation of differential management for glades and treed patches, similar to existing management recommendations for classical corridors.

3.1 Introduction

Ecological corridors can ensure the dispersal of organisms in fragmented landscapes (Gilbert-Norton *et al.*, 2010), however, not all linear structures in a landscape effectively function as a corridor. The quality of a corridor, namely its ability to provide organisms with appropriate structures, resources, and suitable abiotic conditions, is critical for its performance for many taxa, including invertebrates (e.g. Charrier *et al.*, 1997; Haddad & Tewksbury, 2005; Noordijk *et al.*, 2011). Corridor quality affects, for example, the number of species and individuals, mortality, as well as the movement rate of dispersing organisms (Haddad & Tewksbury, 2005). Corridor quality and the underlying features responsible for it have been investigated in traditional corridors such as hedgerows (e.g. Charrier *et al.*, 1997; Lövei & Magura, 2017) or trackways, grassy strips, or road verges (e.g. Söderström & Hedblom, 2007; Noordijk *et al.*, 2011; Bertoncelj & Dolman, 2013; Habel *et al.*, 2020). However, these corridors, even when quality has been optimised, come with the disadvantage of simultaneously acting as a barrier for non-target species (e.g. Mauremooto *et al.*, 1995; Dover & Settele, 2009).

Semi-open areas are more advantageous than traditional corridors due to their ability to increase connectivity without increasing fragmentation for species from both forest and open habitats that could use them simultaneously (Eggers *et al.*, 2010; Travers *et al.*, 2020). This property of semi-open corridors is certainly linked with their unique and intermediate structure, which consists of a mosaic of forest-like patches dominated by trees or shrubs embedded in a matrix of open heathland or grassland (Garbarino & Bergmeier, 2014; Boutaud *et al.*, 2022). Semi-open areas are suitable as corridors for ground beetles (Eggers *et al.*, 2010; Boutaud *et al.*, 2022) and plants (Travers *et al.*, 2020). However, optimising the connectivity potential of semi-open corridors requires an understanding of the features susceptible to affecting their quality. Few studies have considered the effect of vegetation and landscape structures on the presence and abundance of a particular invertebrate group in semi-open areas. Considering the prevalence of trees, which are considered keystone structures in many habitats (Prevedello *et al.*, 2018), those studies mainly focused on woody structural features and found in both Swedish wood-pastures and Mediterranean Dehesa that many invertebrate assemblages respond to the proportion of treed and open patches (David *et al.*, 1999; Söderström *et al.*, 2001; García-Tejero & Taboada, 2016).

The suitability of corridors depends not only on habitat quality but also on the species' ecology. Studies on traditional corridors, in particular, have shown that species habitat preference and specialisation influence corridor suitability (e.g. Noordijk *et al.*, 2011; Bertoncelj & Dolman, 2013; Habel *et al.*, 2020). In their study, David et al. (1999) found that while saprophagous macroarthropods effectively responded to the proportion of open and forest-like patches in semi-open areas, the nature of the response depended on the species' habitat preference. Species of open habitats dominated the open vegetation patches, which were characterised by the absence of trees and shrubs. Species preferring forest habitats avoided the open patches, which in turn dominated the forest-like patches while avoiding the open-like ones. This indicates that the species found in semi-open areas may not be randomly distributed but instead seek patches most similar to their original habitat. Moreover, habitat specialists require high-quality corridors, whereas less-specialised species can use a larger range of corridor quality (Söderström & Hedblom, 2007; Noordijk *et al.*, 2011; Habel *et al.*, 2020). However, to our knowledge, the effect of either habitat preference or specialisation on the response of invertebrates to semi-open corridor quality have so far not been considered.

The composition of the surrounding landscape influences invertebrate assemblages in many habitats. The proportion of other habitats, such as forests or arable lands, in the surrounding landscape had varying effects depending on whether species richness or assemblages of semi-open areas were considered. While landscape elements explained little variation in species richness, they did have a systematic influence on invertebrate assemblages (Söderström *et al.*, 2001). Furthermore, it has been proposed that mass-effect is a key driver of the high diversity found in semi-open areas (Boutaud *et al.*, 2022). Considering the limited amount of evidence, further investigations are needed.

When assessing the quality of a corridor, measuring variations in moisture, temperature, the amount of prey, or the number of seeds are tedious processes, thus, proxies more suitable for use by stakeholders can be used as an alternative. Such proxies could be vegetation structures. Ground beetles' responses to vegetation structures are believed to be linked with the vegetation-altering microclimatic conditions or resources (Thiele, 1977; Diehl *et al.*, 2012; Stoutjesdijk & Barkman, 2014). Additionally, those responses depend on the species' habitat preference, with open habitat species preferring drier and warmer conditions while forest species prefer moister and cooler conditions (Thiele, 1977). Ground beetle species found in semi-open areas could be further divided based on habitat specialisation. Four groups of species could be distinguished: stenotopic species associated with open or forest habitats and less stenotopic species associated with both open or forest habitats, and semi-open areas (Boutaud *et al.*, 2022).

Ground beetles make effective use of various types of corridors, such as hedgerows, linear trackways, and road verges (Gilbert-Norton *et al.*, 2010) and have already been used as a model organism to study corridor quality (e.g. Noordijk *et al.*, 2011; Bertoncelj & Dolman, 2013; Lövei & Magura, 2017). The ability of ground beetles to respond to variations in microclimatic, structural, and resource features in the environment (Lövei & Sunderland, 1996; Antvogel & Bonn, 2001; Koivula, 2011) leads to a diverse array of responses to varied vegetation features (Table A3.1). Features such as trees or shrubs that create moister and shadier conditions in their vicinity would be preferred by forest species while being avoided by open habitat ones. In addition to the presence of trees and shrubs as well as their densities, features of the field layer found in semi-open habitat corridors could influence the presence and activity of ground beetles. On the one hand, bare soil and the presence of dwarf shrubs such as heather have been observed to benefit many open habitat species, particularly thermophilic ones (Cameron & Leather, 2012), whereas leaf litter or mosses provide suitable cooler, moister environments for various forest species (Heliölä *et al.*, 2001). On the other hand, other features could trigger more diverse responses from ground beetles. Grass, for example, can provide resources such as seeds for some species of open habitats but has also been shown to reduce the mobility of other species by impeding the movement of ground beetles and affecting large-bodied species typical of forest habitats (Greenslade, 1964). As such, ground beetles appear to be a good model organism for evaluating the effects of the structure and composition of semi-open areas and their potential as corridors.

Our primary objective is to analyse the importance of local habitat structures, landscape attributes of potential relevance from a management perspective, and habitat specialisation on taxonomic diversity and abundance of ground beetle assemblages found in semi-open areas. For this, we studied 16 semi-open areas in two landscapes in Germany, using ground beetles as indicators. Specifically, we hypothesise that 1) ground beetle species will show different and contrasting preferences for the vegetation structures associated with either the forest-like patches or the open vegetation glades as well as the landscape features in accordance with their habitat preference, resulting in a non-random distribution of the species. Second, 2) we expect stenotopic species to be more sensitive to environmental features than than less specialised species.

3.2 Materials and methods

3.2.1 Study landscapes and habitat characteristics

The study was conducted in two landscapes in Germany. The first landscape, the Lüneburger Heide (hereafter Heide), is located in the north-western German lowland (70 – 170 m.a.s.l.; 53.1675 N, 9.91345 E), has a suboceanic climate (mean annual precipitation: 854 mm, mean annual temperature: 9 °C), and podzol is the predominant soil type (Keienburg & Prüter, 2004). The semi-open areas in this landscape are a mosaic, with the open patches made up of heathland dominated by heather (Calluna vulgaris), and forest-like patches made up of shrubs, single trees, or groups of trees (Betula pendula, Quercus robur, Pinus sylvestris). The semi-open structures resulted either from a combination of trees and shrubs encroaching and extensive sheep and goat grazing (about 1 animal per hectare) on former heathland, or they were established by forest thinning followed by extensive grazing. The second landscape, the Schwäbische Alb (hereafter Alb), is located in a low mountain range in south-west Germany (450 – 1 000 m.a.s.l.; 48.2983 N, 9.24926 E), has a subcontinental climate (mean annual precipitation: 750 mm, mean annual temperature: 7 °C), and limestone-derived rendzic leptosol soil (Beinlich & Plachter, 1995). The semi-open areas comprise a mosaic with open patches constituted of semi-dry calcareous grassland dominated by the grass *Bromus erectus,* with shrubs (*Juniperus communis)* and trees (*Quercus robur and Sorbus aucuparia*) isolated or in small groups. The semi-open structure resulted from a combination of tree encroachment and extensive sheep grazing (about 3.5 to 4.6 animals per hectare). More details about the studied landscapes and plant composition can be found in Boutaud *et al.* (2022) and Travers *et al.* (2020).

3.2.2 Ground beetle sampling

In each landscape, we selected eight semi-open areas (> 2 km apart), of which we surveyed half of them in 2013–2014 and the other half in 2014–2015. Each semi-open area was in the direct vicinity of open and forest habitats. A row of five pitfall traps with a distance of 10 m between traps was used in each semi-open area. In total, 40 traps were used in each landscape (8 sites x 5 traps). In the Heide, traps were serviced year-round from January 2013 to February 2014 and from March 2014 to January 2015 every three weeks (except for extended trapping periods caused by snow cover in winter). In the Alb, traps were serviced every three weeks from April to September in 2013 and 2014. This resulted in 18 collection events per site in the Heide in 2013–2014 (720 traps collected in total), 15 in 2014–2015 (600 traps), and, in the Alb, eight collection events in both years (320 traps per year). As pitfall traps, we used transparent plastic cups (500 ml, 10 cm in diameter) filled with 150 ml of Renner solution (Renner, 1982) and set flush with the ground. To reduce disturbance by sheep, an acrylic glass roof was added in the Alb, 3 to 4 cm above the trap. Ground beetles were counted and identified to species level in the laboratory using standard literature (Müller-Motzfeld, 2006), and nomenclature followed Schmidt *et al.* (2016). The ground beetle habitat association was based on Boutaud *et al.* (2022), and the following categories were considered for analysis: (I) species associated with open and (II) species associated with forest habitats with a high degree of habitat specialisation, as well as (III) species associated with both open habitats and semi-open areas (hereafter species of open & semi-open habitats) and (IV) species of forest habitats and semi-open areas (hereafter species of forest & semi-open habitats), for which the degree of habitat specialisation is lower.

Table 3.1: Environmental variables within the semi-open habitats in the Lüneburger Heide and Schwäbische Alb, with the mean values and standard deviation (in parenthesis) presented for the 40 pitfall traps considered in each landscape. If the variables were recorded in both landscapes, we used Wilcoxon two-sided tests, for which we provide the W and associated p values. Significant values are in bold.

Environmental variables	Lüneburger Heide	Schwäbische Alb	W	p-value
Vegetation				
Bare soil cover (%)	2.1 (5.1)	7.4 (12.1)	474	**<0.001**
Bilberry cover (%)	17.1 (28.7)	-	-	-
Tree canopy cover (%)	20.4 (33.6)	26.3 (37)	682	0.22
Deadwood cover (%)	2.1 (5.3)	0.7 (2.8)	910	0.12
Distance to the nearest tree (m)	4.8 (2.3)	2.9 (2)	1157	**<0.001**
Grass cover (%)	15.9 (23)	33.9 (14.4)	301	**<0.001**
Herbaceous cover (%)	1.4 (4.7)	34.2 (10.4)	8.5	**<0.001**
Heather cover (%)	35.4 (36.2)	-	-	-
Moss cover (%)	13.9 (13.9)	10 (10)	888	0.40
Plant litter cover (%)	11.1 (20.7)	3.5 (8.2)	1007	**0.024**
Landscape				
Distance to forest edge (m)	66.3 (31.1)	77.6 (64.3)	845	0.67
Distance to open edge (m)	50.9 (24.9)	28.7 (13.6)	129	**<0.001**

3.2.3 Environmental variables

To describe the condition surrounding the pitfall traps, a set of vegetation variables was recorded. We visually estimated the aerial covers (sensu Fehmi, 2010) of eight parameters in a 1 m radius around each pitfall trap (Table 3.1). The following ground covers were considered: cover of grass, herbaceous, heather, bilberry, moss, bare soil, plant litter, and deadwood. For the plant cover, we considered all plants with similar structures together and thus estimated the cover of all species of grasses, mosses, and non-woody herbaceous together. For the woody vegetation, dwarf shrubs were split into two groups between heather (*Calluna vulgaris*) and bilberry (*Vaccinium myrtillus*). The estimated covers were described to the nearest 5%. In addition, tree canopy cover was similarly estimated as the percentage of tree crowns directly above each pitfall trap. Using a measuring tape, the distance to the closest tree was measured and rounded to the nearest centimetre. The surveys were conducted once for each region, in July 2014 for the Alb and in September 2014 for the Heide.

To take into account the potential influence of the surrounding landscape, we measured the distances to the open or forest habitat edges as the distance between a given trap and the limit of the tree crowns at the forest or semi-open habitat edges using the measuring tool in Google Earth Pro (version 7.3.4.8248). We also measured the proportion of the main habitat types in the surrounding landscape in a 250 m buffer around each pitfall trap line as well as the size of the semi-open areas, however, those variables were strongly correlated with either of the distances to the habitat edges and as such were not used for the analyses (Fig. A3.1). All 12 variables were chosen for their simplicity to measure, making them more suitable and likely to be used by practitioners and stakeholders. Both landscapes were notably different due to the vegetation of the glades, which were dominated by either dwarf shrubs or grass and herbaceous plants. Additionally, the Heide had less bare soil and more litter cover, greater distances to the nearest tree, and shorter distances to the open habitat compared to the Alb (Table 3.1).

3.2.4 Statistical analyses

Due to the activity of large mammals, 37 traps (1.9%) in the Heide and 55 traps (5.7%) in the Alb were lost. The missing information was replaced by the average catch value corresponding to the remaining undisturbed traps at the given site, habitat, and trapping interval. Prior to statistical analyses, we pooled the catches for each pitfall trap over the entire trapping period. Statistical analyses were performed using the software R, version 4.2.1 (R Core Team, 2022), and the package ggplot2 was used for the graphics (Wickam, 2016).

We investigate the effects of the vegetation and landscape variables on carabid beetle assemblages using non-metric multidimensional scaling (NMDS), for each landscape separately (function “metaMDS”). We omitted carabid species with fewer than five individuals recorded per landscape. Three dimensions were considered to reduce the stress value, and we used Horn dissimilarity measures, which give more weight to rarer species (Jost *et al.*, 2011). Using the function “envfit” (5000 permutations), we checked whether the environmental variables correlated with the ordination axes. The obtained p-values from “envfit” were corrected using the false discovery rate (function “p.ajust” ; Benjamini & Hochberg, 1995). We presented the information about species diversity and activity-density using a modified multidiversity index (see Allan *et al.*, 2014), calculated as the combined average proportional rarefied species richness and standardised activity-density (see equation A3.1) across habitat association groups. Both species richness and activity density values were further standardised for each habitat association group by scaling them to the maximum observed value across all traps separately for each landscape to avoid giving higher weight to species-rich groups. The multidiversity index values could theoretically range from 0 to 1. A value of 0 will indicate that both the species richness and activity-density of all four association groups were equal to 0, while a value of 1 indicates that they were the highest across all traps.

As the number of individuals per trap was unequal, we used rarefaction to calculate the rarefied species richness for each trap. Using the function “rrarefy”, we rarefied the assemblage of each trap, separately for each landscape, to 75 individuals for the Heide and 44 for the Alb before determining the number of species (function “specnumber”) belonging to each of the four habitat association groups. The rarefaction was repeated 1000 times for each trap, and the mean species richness over the 1000 rarefied assemblages was used for analysis. Both ordination and rarefaction functions are part of the vegan package (Oksanen *et al.*, 2019). We also standardised the activity-density to ensure that all species contributed equally. For each species and trap, the sum of the activity density across all species was used as the total activity-density (hereafter standardised activity density), and here also we omitted carabid species with fewer than five individuals recorded per landscape. The standardised activity-densities were calculated for each habitat association group separately.

Linear mixed effects models (package lme4: Bates *et al.*, 2015) were used to investigate the relationship between vegetation and landscape features and rarefied species richness as well as standardised activity densities of open, forest, open & semi-open, and forest & semi-open habitats associated species. When the relationship between the response variable and an explanatory variable appeared to be hump-shaped, the quadratic term was introduced in the model. We used site id as a random effect and removed it when simpler linear models performed equally well (using likelihood ratio tests from package lmerTest). Variance inflation factor was used ("VIF" value below 5 from car package Fox & Weisberg, 2019) to ensure that multicollinearity between explanatory variables was not present in the model. For each model, we first built a full model, which was then simplified by removing non-significant fixed terms (> 0.1) one by one. F and p-values were interpreted using Satterthwaite's approximations to determine denominator degrees of freedom as implemented in the package lmerTest (Kuznetsova *et al.*, 2017). Model validation was carried out graphically, and when assumptions were violated, the response variables were transformed using the bestNormalize package (Peterson, 2021).

3.3 Results

In total, we sampled 8668 carabid beetles belonging to 73 species in the Heide. The number of species associated with forest, open, forest & semi-open, and open & semi-open habitats were 12, 19, 7, and 10, respectively. We found 11 species with fewer than five individuals. In the Alb, we recorded 3518 carabid beetles belonging to 74 species, of which 13, 17, 3, and 10 species were associated with forest, open, forest & semi-open, and open & semi-open habitats, respectively, and 12 species with fewer than five individuals recorded.

For the Heide, the pitfall trap assemblages with the highest multidiversity index values are aggregated in the centre-right of the ordination along the first axis (Fig. 3.1a and b). Ground beetle species are also separated along axis 1, where the species associated with open and open & semi-open habitats are located on the right while species associated with the forest and forest & semi-open are on the left (Fig. 3.1c and d). In addition, species associated with open and open & semi-open habitats as well as assemblages with a high value of the multidiversity index showed a positive correlation with increasing bare soil cover and a trend with heather and distance to the nearest tree. Species associated with forest and forest & semi-open habitats showed a positive correlation with increasing distance to the open habitat and a trend with bilberry and deadwood cover (Table A3.2).

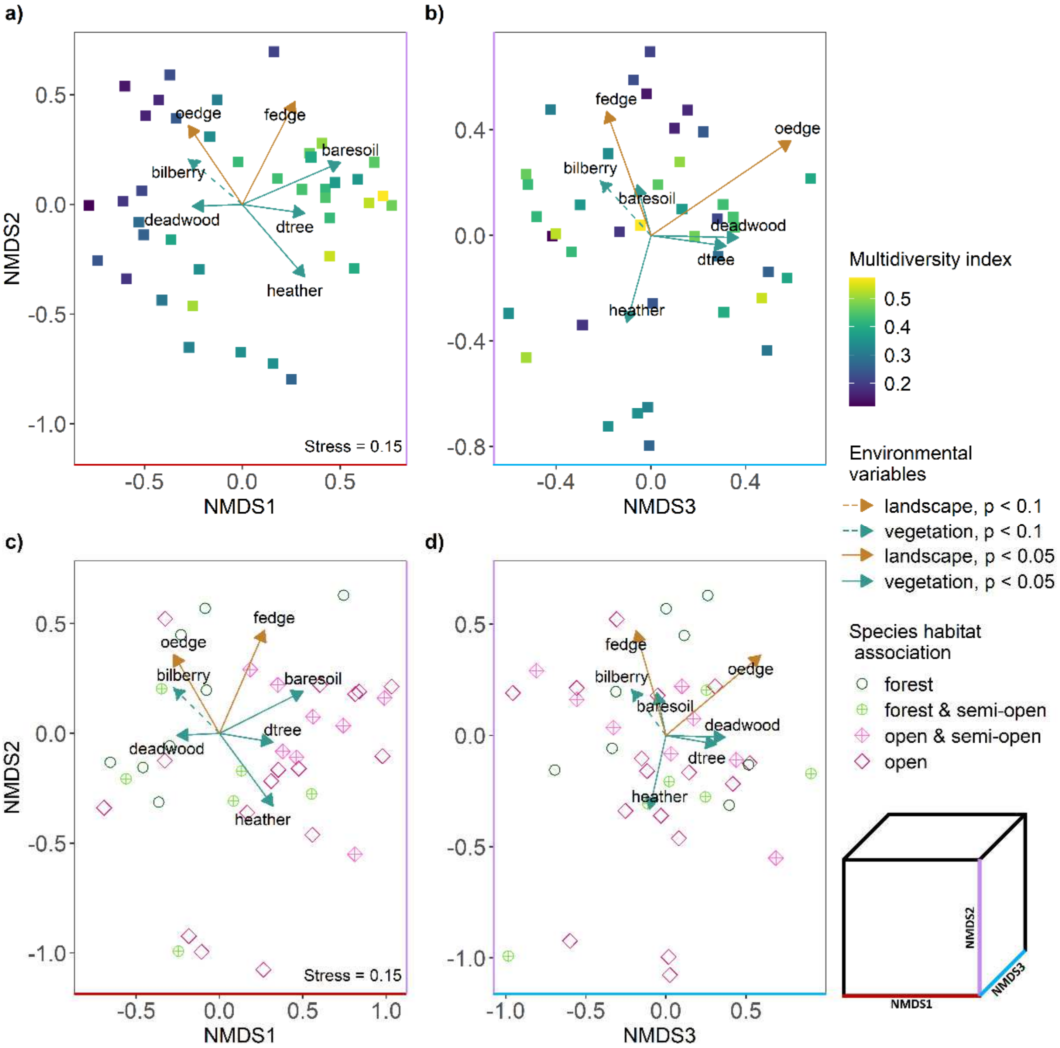

Figure 3.1: Non-metric multidimensional scaling of ground beetle assemblages in semi-open habitats in the Lüneburger Heide. Trap assemblages (filled squares, a and b) are coloured according to the multidiversity index values (see material and method). Species associated with forest (dark green circle), forest & semi-open (light green circle plus), open (dark purple diamond), and open & semi-open (lavender diamond plus) are displayed (c and d). Arrows indicate significant (solid line) or near significant (dashed line) vegetation (blue-green) and landscape (light brown) variable effects. heather: heather cover; bilberry: bilberry cover; dwood: deadwood cover; baresoil: bare soil cover; dtree: distance to the nearest tree, fedge: distance to the forest habitat edge; oedge: distance to the open habitat edge.

In the Alb, the pitfall trap assemblages with the highest multidiversity index values are clustered near the centre of the ordination (Fig. 3.2a and b) and associated with intermediate values of all the environmental variables. Ground beetle species were separated along axis 2 between open and open & semi-open habitat-associated species, which were located in the upper half, while forest and forest & semi-open habitat-associated species are found in the lower half (Fig. 3.2c and d). Furthermore, species associated with open and open & semi-open habitats showed a positive correlation with increasing bare soil cover, while species associated with forest and forest & semi-open habitats showed a positive correlation with increasing litter and moss cover as well as increasing distance to the forest edge (Table A3.2).

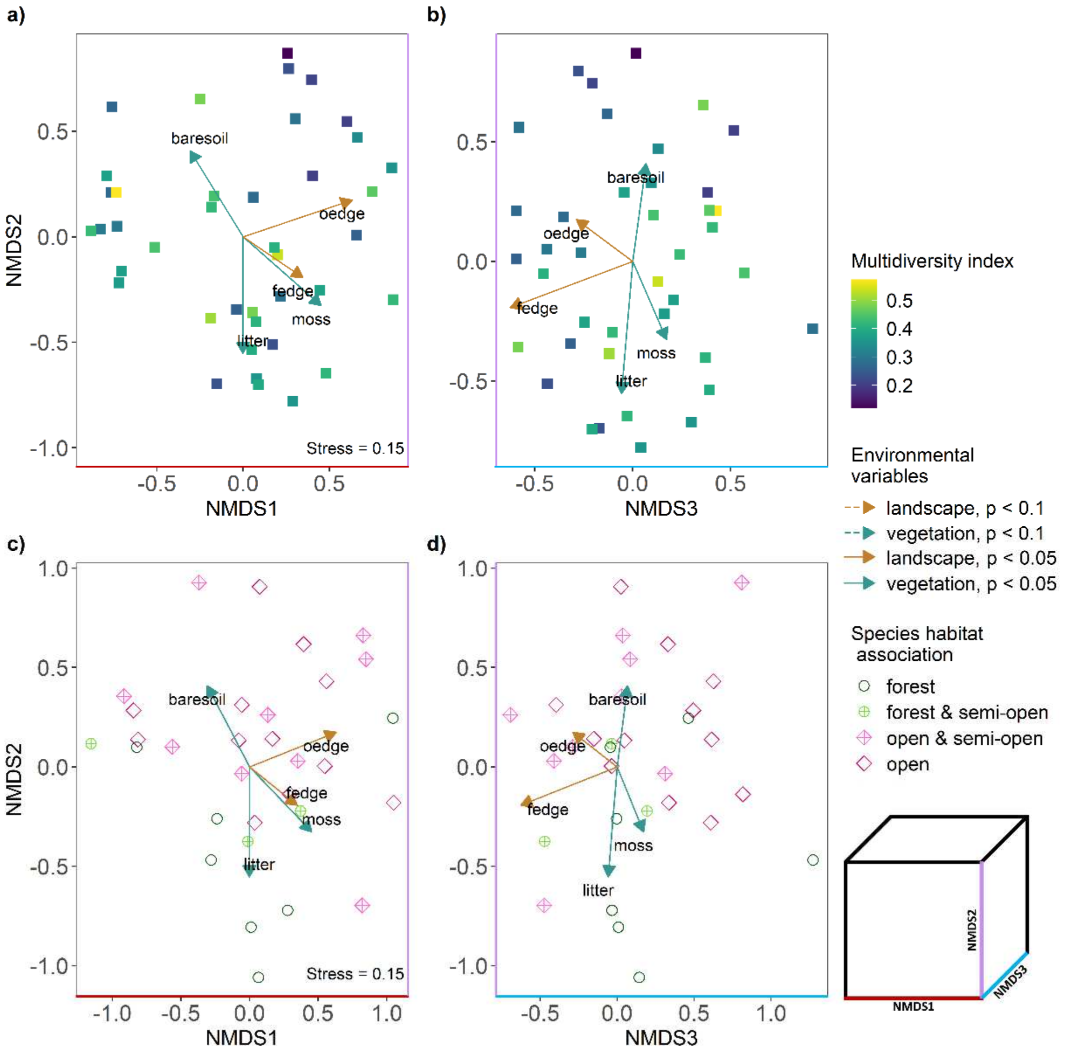

Figure 3.2: Non-metric multidimensional scaling of ground beetle assemblages in semi-open habitats in the Schwäbische Alb. Trap assemblages (filled squares, a and b) are coloured according to the multidiversity index values (see material and method). Species associated with forest (dark green circle), forest & semi-open (light green circle plus), open (dark purple diamond), and open & semi-open (lavender diamond plus) are displayed (c and d). Arrows indicate significant (solid line) or near significant (dashed line) vegetation (blue-green) and landscape (light brown) variable effects. litter: litter cover; moss: moss cover; baresoil: bare soil cover; fedge: distance to the forest habitat edge; oedge: distance to the open habitat edge.

In the Heide, species richness of the different habitat association groups responded mainly to vegetation features except for species associated with forest & semi-open habitats that responded negatively to increasing distance to the forest edge (Fig. 3.3e, Table 3.2 and Table A3.3). In addition, environmental variables explained a higher portion of the variance in species richness of association groups with the highest habitat specialisation than that of association groups with lower habitat specialisation (Table 3.2). The species richness of species associated with open habitats showed significant positive relationships with heather, bare soil, and moss covers (Fig. 3.3a, b, c, and Table 3.2). The richness of species associated with forest habitat showed significant positive relationships with bilberry and bare soil cover (Fig. 3.3f, g, and Table 3.2).

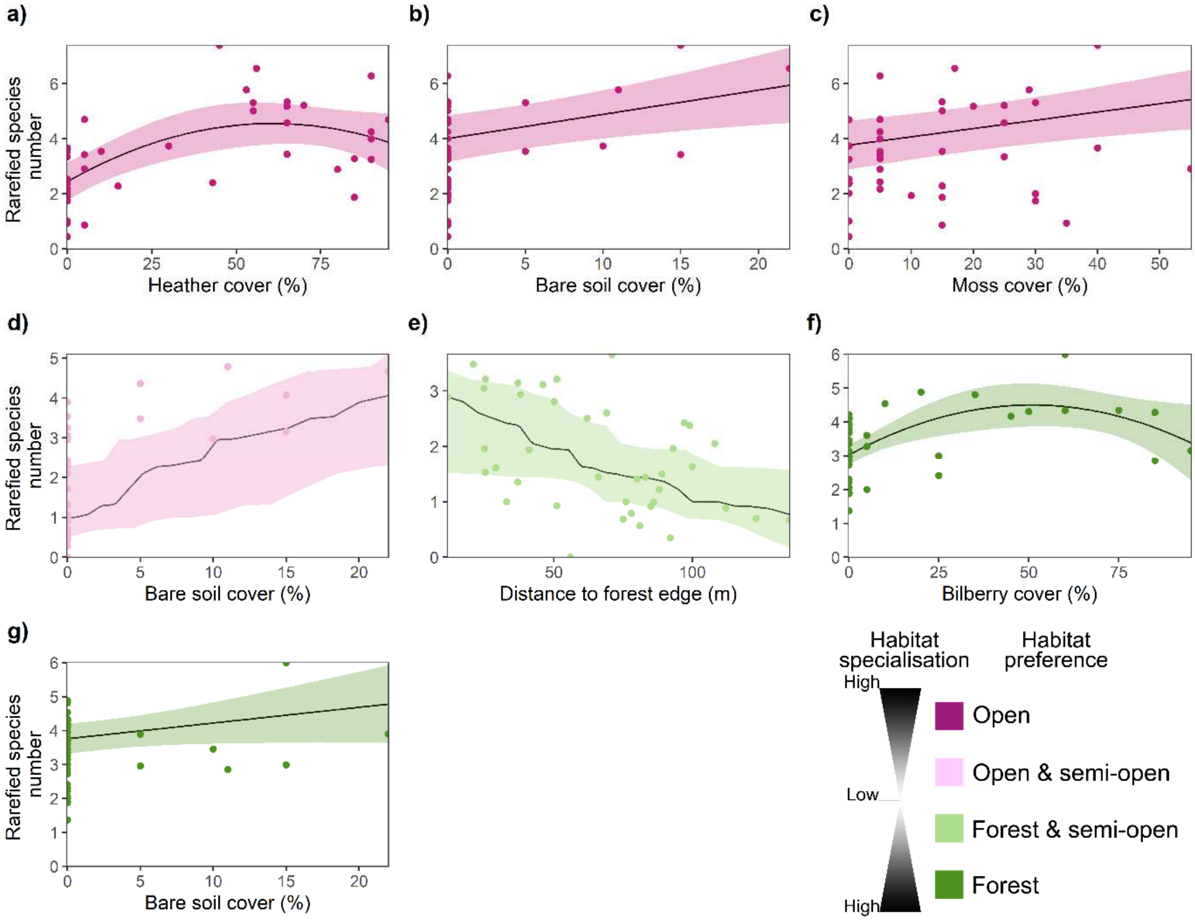

Figure 3.3: Relationships between ground beetle rarefied species richness and environmental features of the Lüneburger Heide semi-open areas for species associated with open (dark purple), forest (dark green), open & semi-open (lavender), and forest & semi-open (light green) habitats. Black regression lines indicate significant ($P \leq 0.05$) relationships, while long dashed lines indicate a trend ($p < 0.1$), and shaded areas correspond to 95 percent confidence intervals. Means and confidence intervals are based on the back-transformed values estimated by the model when the original response variables were transformed. Points represent observed values per trap.

Table 3.2: Results (estimate, standard error (se), degrees of freedom (Df), t-values, and p-values) of the final linear and linear mixed-effects models for the effect of vegetation and landscape features on the rarefied species richness of species associated with open, forest, open & semi-open, and forest & semi-open habitats for the Lüneburger Heide. The R^2 column provides adjusted R^2 for linear models as well as both marginal and conditional R^2 for mixed effect models. Statistically significant p-values are in bold.

Environmental predictors	Model	R^2	Estimate	se	Df	t-value	p-value
Open	Mixed, untransformed	0.54/0.79					
Intercept			3.46	0.32	6.64	10.93	**<0.001**
Heather cover			2.51	0.64	31.03	3.93	**<0.001**
Heather cover^2			-1.77	0.66	31.30	-2.69	**0.011**
Moss cover			0.42	0.14	29.69	3.02	**0.005**
Bare soil cover			0.45	0.17	21.47	2.75	**0.001**
Open & semi-open	Mixed, OrderNorm	0.14/0.56					
Intercept			0.01	0.23	6.18	0.06	0.95
Bare soil cover			0.34	0.12	37.31	2.79	**0.008**
Forest & semi-open	Mixed, OrderNorm	0.19/0.51					
Intercept			0.00	0.23	6.51	0.00	0.99
Distance to forest edge			-0.45	0.21	12.84	-2.19	**0.048**
Forest	Linear, untransformed	0.27					
Intercept			3.40	0.14	1	25.02	**<0.001**
Bilberry cover			1.67	0.50	1	3.31	**0.002**
Bilberry cover^2			-1.32	0.50	1	-2.62	**0.013**
Bare soil cover			0.24	0.14	1	1.73	**0.093**

The activity-density of the different habitat association groups responded mainly to vegetation features except for species associated with open habitats that responded negatively to increasing distance to the open edge (Fig. 3.4b, Table 3.3, and Table A3.4). In addition, environmental variables explained a higher portion of the variance in activity-density of habitat specialists than that of less specialised association groups (Table 3.3). The activity-density of species associated with open habitats showed significant positive relationships with distance to the nearest tree and a trend with heather cover (Fig. 3.4a, c, and Table 3.3). The activity-density of species associated with forest habitat showed significant positive relationships with bilberry and deadwood cover (Fig. 3.4g, h, and Table 3.3). For species associated with open & semi-open habitats, a negative relationship trend with increasing grass cover was found (Fig. 3.4d) while the activity-density of species associated with forest & semi-open habitats negatively responded to increasing grass cover and showed a trend with bilberry cover (Fig. 3.4 g, h, and Table 3.3).

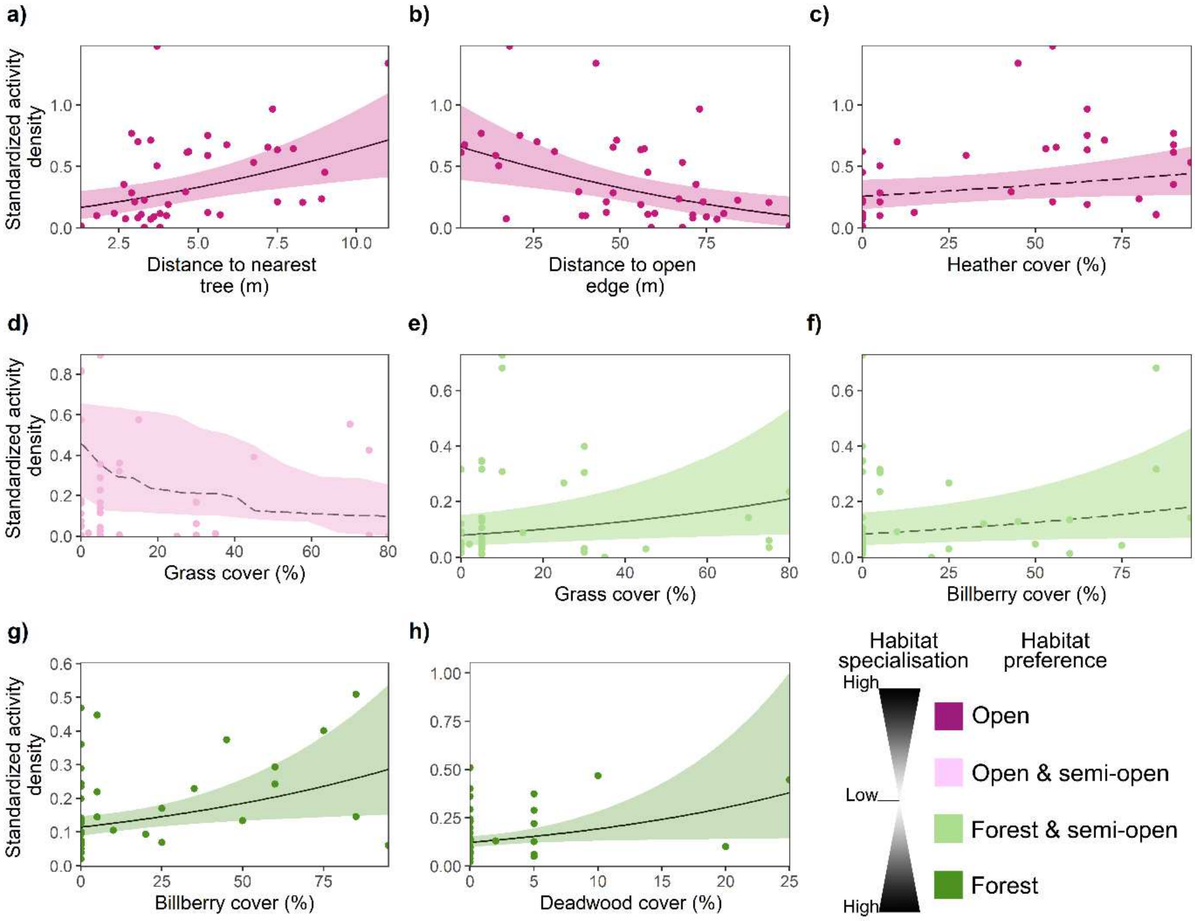

Figure 3.4: Relationships between ground beetle standardized activity-density and environmental features of the Lüneburger Heide semi-open areas for species associated with open (dark purple), forest (dark green), open & semi-open (lavender), and forest & semi-open (light green) habitats. Black regression lines indicate significant ($p \leq 0.05$) relationships, while long dashed lines indicate trends ($p< 0.1$), and shaded areas correspond to 95 percent confidence intervals. Means and confidence intervals are based on the back-transformed values estimated by the model when the original response variables were transformed. Points represent observed values per trap.

In the Alb, similarly to the Heide, species richness of the different habitat association groups responded mainly to vegetation features, except for species associated with forest habitats. The species richness of species associated with open and open & semi-open habitats showed significant negative relationships with litter cover (Fig. 3.5a, b, Table 3.4, and Table A3.5). The richness of species associated with forest habitat showed significant positive relationships with litter and moss cover (Fig. 3.5e, f, and Table 3.4) and a significant negative relationship with distance to the open edge (Fig. 3.5g and Table 3.4). Similarly, the richness of species associated with forest & semi-open habitats positively responded to increasing moss cover but negatively to increasing distance to the nearest tree (Fig. 3.5c, d, and Table 3.4).

Table. 3.3: Results (estimate, standard error (se), degrees of freedom (Df), t-values, and p-values) of the linear and linear mixed-effects models for the effect of vegetation and landscape features on standardised the activity-density of species associated with open, forest, open & semi-open, and forest & semi-open areas for the Lüneburger Heide. R^2 column provides adjusted R^2 for linear models as well as both marginal and conditional R^2 for mixed effect models. Statistically significant p-values are in bold.

Environmental predictors	Model	R^2	Estimate	se	Df	t-value	p-value
Open	Mixed, square root	0.47/0.64					
Intercept			0.57	0.05	6.46	11.38	**<0.001**
Distance to nearest tree			0.10	0.03	35.41	3.09	**0.004**
Distance to open edge			-0.13	0.04	17.91	-3.00	**0.008**
Heather cover			0.06	0.04	35.39	1.75	0.089
Open & semi-open	Mixed, OrderNorm	0.04/0.65					
Intercept			0.01	0.30	6.95	0.05	0.96
Grass cover			-0.20	0.11	33.53	-1.74	0.091
Forest & semi-open	Mixed, Log_{10}	0.08/0.65					
Intercept			-2.34	0.32	6.81	-7.23	**<0.001**
Grass cover			0.28	0.13	32.33	2.22	**0.036**
Bilberry cover			0.23	0.13	33.17	1.76	0.09
Forest	Linear, Log_{10}	0.15					
Intercept			-2.00	0.11	1	18.43	**<0.001**
Bilberry cover			0.28	0.11	1	2.47	**0.018**
Deadwood cover			-1.32	0.11	1	2.14	**0.0392**

Except for species associated with forest and forest and semi-open habitats, the activity density of the different habitat association groups responded primarily to vegetation features (Table A3.6). The activity-density of species associated with open habitats showed significant positive relationships with distance to the nearest tree and negative significant relationships with moss and litter covers (Fig. 3.6a, b, c, and Table 3.5). The activity-density of species associated with forest habitat showed, on the contrary, significant positive relationships with litter and moss covers (Fig. 3.6f, g, and Table 3.5) and negative significant relationships with distance to the open edge (Fig. 3.6h and Table 3.5). The activity-density of species associated with open & semi-open habitats showed an increasing trend with increasing distance to the nearest tree (Fig. 3.6d and Table 3.5) while the activity-density of species associated with forest & semi-open habitats negatively responded to increasing distance to the open edge (Fig. 3.6e and Table 3.5).

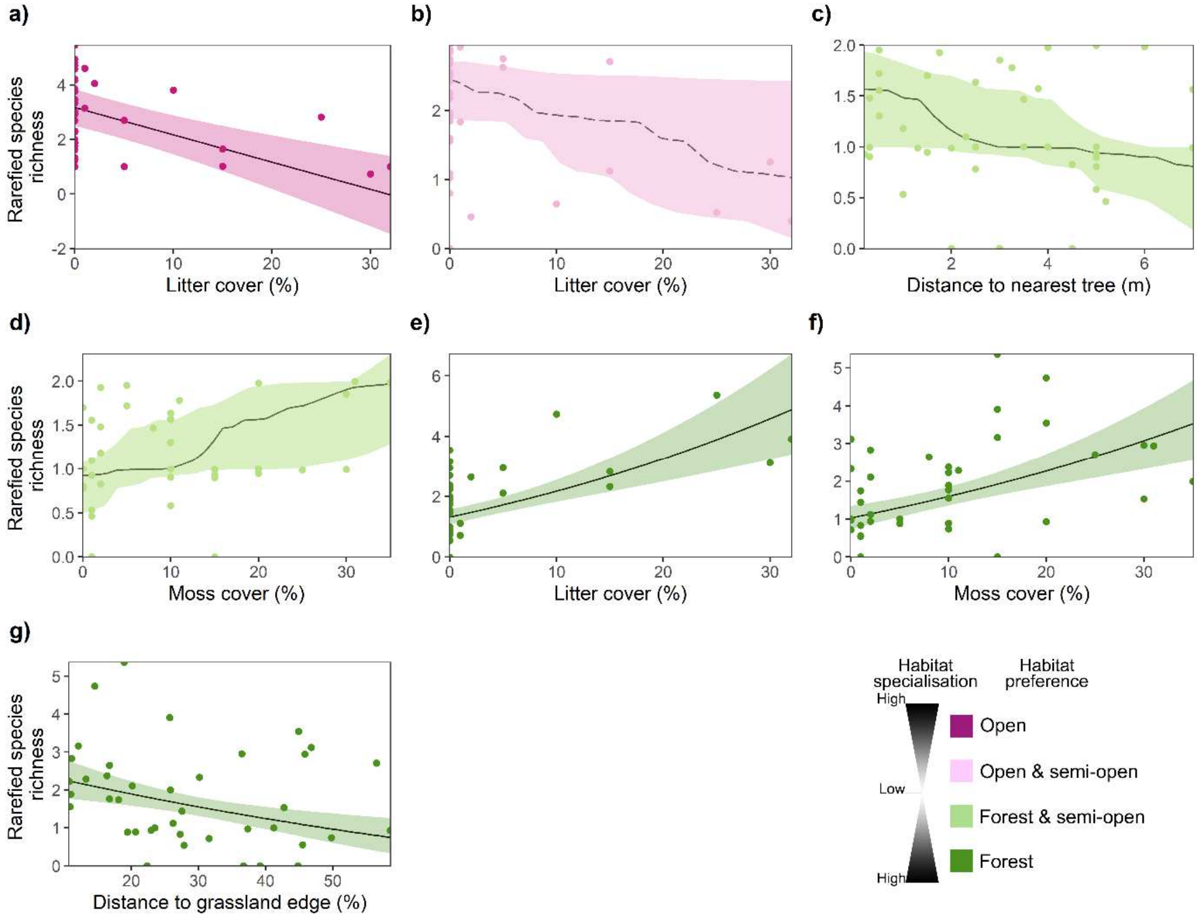

Figure 3.5: Relationships between ground beetle rarefied species richness and environmental features of the Schwäbische Alb semi-open areas for species associated with open (dark purple), forest (dark green), open & semi-open (lavender), and forest & semi-open (light green) habitats. Black regression lines indicate significant ($P \leq 0.05$) relationships, and shaded areas correspond to 95 percent confidence intervals. Means and confidence intervals are based on the back-transformed values estimated by the model when the original response variables were transformed. Points represent observed values per trap.

Table .3.4: Results (estimate, standard error (se), degrees of freedom (Df), t-values, and p-values) of the linear and linear mixed-effects models for the effect of vegetation and landscape features on the rarefied species richness of species associated with open, forest, open & semi-open, and forest & semi-open habitats for the Schwäbische Alb. R² column provides adjusted R² for linear models as well as both marginal and conditional R² for mixed effect models. Statistically significant p-values are in bold.

Environmental predictors	Model	R²	Estimate	se	Df	t-value	p-value
Open	Linear, untransformed	0.29/0.58					
Intercept			2.82	0.33	5.99	8.44	**<0.001**
Litter cover			-0.82	0.19	36.37	-4.40	**<0.001**
Open & semi-open	Mixed, OrderNorm	0.08/0.33					
Intercept			0.00	0.22	6.48	0.00	1.00
Litter cover			-0.28	0.15	37.87	-1.93	0.061
Forest & semi-open	Mixed, OrderNorm	0.25/0.74					
Intercept			0.01	0.30	6.37	0.02	0.99
Distance to nearest tree			-0.42	0.11	32.44	-3.82	**<0.001**
Moss cover			0.58	0.21	26.03	2.75	**0.010**
Forest	Linear, untransformed	0.57					
Intercept			1.08	0.06	1	17.46	**<0.001**
Litter cover			0.33	0.06	1	5.35	**0.001**
Moss cover			0.30	0.06	1	4.69	**0.001**
Distance to open edge			-0.22	0.06	1	-3.37	**0.002**

Table 3.5: Results (estimate, standard error (se), degrees of freedom (Df), t-values, and p-values) of the linear and linear mixed-effects models for the effect of vegetation and landscape features the on standardised activity-density of species associated with open, forest, open & semi-open, and forest & semi-open areas for the Schwäbische Alb. R² column provides adjusted R² for linear models as well as both marginal and conditional R² for mixed effect models. Statistically significant p-values are in bold.

Environmental predictors	Model	R²	Estimate	se	Df	t-value	p-value
Open	Mixed, Box-cox	0.35/0.77					
Intercept			-1.16	0.19	5.35	-6.12	**0.001**
Litter cover			-0.35	0.08	31.62	-4.64	**<0.001**
Distance to nearest tree			0.27	0.08	30.51	3.71	**<0.001**
Moss cover			-0.40	0.14	23.08	-2.97	**0.007**
Open & semi-open	Mixed, square root	0.06/0.49					
Intercept			0.43	0.05	6.77	7.69	**<0.001**
Litter cover			0.05	0.02	35.80	1.78	0.084
Forest & semi-open	Mixed, square root	0.13/0.46					
Intercept			0.24	0.03	6.71	7.52	**<0.001**
Distance to open edge			-0.05	0.02	24.67	-2.00	0.06
Forest	Linear, orderNorm	0.63					
Intercept			0.01	0.09	40	0.09	0.92
Distance to open edge			-0.60	0.10	40	-6.18	**<0.001**
Litter cover			0.50	0.09	40	5.38	**<0.001**
Moss cover			0.25	0.10	40	2.51	**0.017**

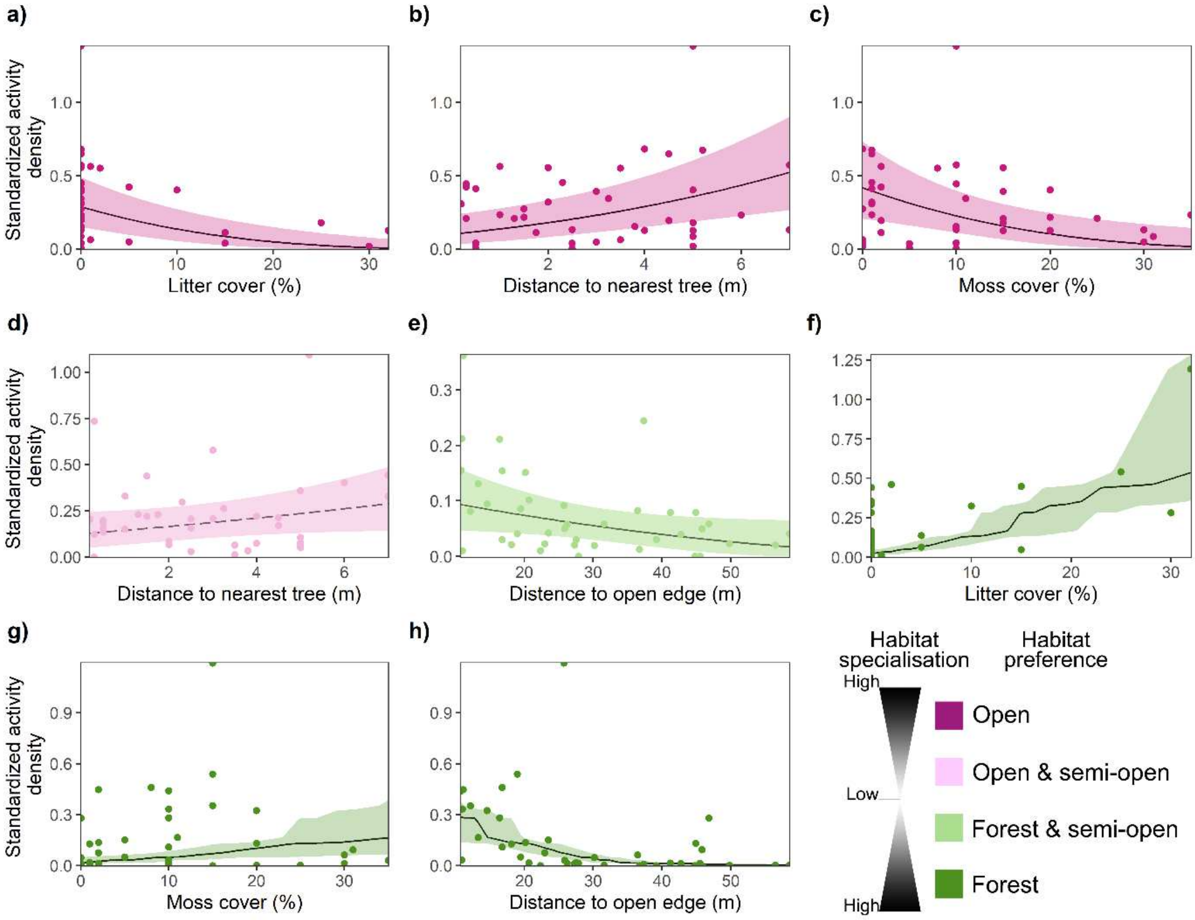

Figure 3.6: Relationships between ground beetle standardised activity-density and environmental features of the Schwäbische Alb semi-open areas for species associated with open (dark purple), forest (dark green), open & semi-open (lavender), and forest & semi-open (light green) habitats. Black regression lines indicate significant ($P \leq 0.05$) relationships, and shaded areas correspond to 95 percent confidence intervals. Means and confidence intervals are based on the back-transformed values estimated by the model when the original response variables were transformed. Points represent observed values per trap.

3.4 Discussion

Our results provide evidence that the distribution of carabid beetles in semi-open areas is influenced by both the local vegetation structures and, to a lesser extent, by the landscape features, resulting in a non-random distribution of the species and their activity-densities. Furthermore, in both studied landscapes, species broadly associated with open habitats displayed microhabitat preferences that were opposite to the preferences of species broadly associated with forest habitats. In addition to habitat preference, the species' habitat specialization further modulated the influence of the environmental variables, with the specialist species being more sensitive to the environment while the more generalist species were less influenced or, at times, barely responded to it.

3.4.1 Effect of microhabitat vegetation structures

In both landscapes studied, species associated with open and semi-open habitats preferred microhabitats in semi-open areas with characteristics most similar to those found in adjacent woodlands or grasslands. In the Heide, high-quality open-like microhabitats were characterised by higher heather and bare soil cover and, in the Alb, by a low cover of leaf litter as well as wider glades, as indicated by the increased distance from the nearest tree in both landscapes. In contrast, species associated with forests and forest and semi-open habitats preferred forest-like microhabitats within semi-open areas. Those microhabitats were characterised in the Heide by the increased cover of bilberry and dead wood and, in the Alb, by higher leaf litter and moss cover. These preferences are in agreement with the ecology of both species groups. Heathland and dry grassland species are known to prefer, in both their habitats and classical open corridor types such as road verges or trackways, areas with sparse heather or grass vegetation (e.g. Eversham & Telfer, 1994; Vermeulen, 1994b; Bertoncelj & Dolman, 2013) as well as avoiding getting close to standing trees or into treed habitats where leaf litter is commonly found (e.g. Molnár *et al.*, 2001; Taboada *et al.*, 2004; Noordijk *et al.*, 2011). Similarly, forest species have been shown to have a preference for areas where bilberry, leaf litter, moss, or deadwood are present, all of which are typical elements found within the species' original habitats or dedicated corridors such as hedgerows (e.g. Heliölä *et al.*, 2001; García-Tejero & Taboada, 2016; Lövei & Magura, 2017).

Semi-open corridors can accommodate species of both open and forest habitats with even species of both groups found within the same traps simultaneously (Eggers *et al.*, 2010). However, our results, in agreement with our first hypothesis, highlight that species associated with open habitats appeared to be to some extent restricted to the open-like glades found within semi-open areas. The forest species were partly restricted to the forest-like patches, which they likely use as stepping stones. Similarly, restricted distributions within semi-open areas have been found for saprophagous macroarthropods (David *et al.*, 1999). Similar small-scale changes and restrictions in the distribution of many taxa have been found notably in the context of forest grassland edges (e.g. Lacasella *et al.*, 2015), thus it is likely that such patterns will be commonly encountered for many arthropod taxa found within semi-open areas.

3.4.2 Effect of landscape features

We found limited evidence that landscape features influenced the taxonomic richness or activity-density of ground beetles in both landscapes. This is in agreement with the finding of Söderström et al. (2001) for ground beetles found in Swedish semi-open areas. In their study and similarly in ours, it appears that the surrounding landscapes have limited importance in explaining the variation in ground beetle species richness and activity-density compared to local microhabitat conditions. Ground beetle species have varying dispersal abilities, however, even for species with limited abilities, the distances to our sampling locations in the semi-open areas fall well within the range of what such taxa could reach within one activity season (e.g. Baars, 1979; Rijnsdorp, 1980; Vermeulen, 1994a; Völler *et al.*, 2018). As such, the absence of landscape effects is likely a by-product of our study design, which reduces our ability to highlight landscape effects. However, we found in the Alb negative relationships for forest-associated groups with distance to the grassland edges, which is rather surprising and even counterintuitive. A similar increase in species number and activity-density have been found in transition areas between forest and grassland. Such increases result from the accumulation of forest-dwelling individuals along the edge between the two habitats (Lacasella *et al.*, 2015). As such, in our semi-open areas, when the distance to the open grassland is small, individuals associated with forest habitats increase in abundance close to the edge, resulting in higher activity-density and species richness.

3.4.3 Influence of habitat specialisation and climate conditions

Studies on the effect of habitat fragmentation on invertebrates have long recognised the importance of habitat specialisation; however, Habel et al. (2020) only recently found evidence that specialist butterfly species require higher-quality corridors when compared to generalists. Following our second hypothesis, we found that specialist ground beetles associated with both forest or grassland and heathland habitats responded more sensitively to vegetation structure quality than less specialised species. Consequently, the same corridor with identical vegetation structures is likely to affect species differently depending on the species' habitat specialisation. Furthermore, vegetation structure and composition seem to be key components of corridor quality for invertebrates.

In addition to habitat specialization, the responses of species differed between the landscapes. The open-associated species responded more sensitively to vegetation structures in the Heide than in the Alb while the opposite was found for the forest-associated species. Differences in climatic conditions between the two studied landscapes may be the driver for this pattern. In the Alb, the sub-continental climate results in generally drier and warmer conditions, while in the Heide, the oceanic climate leads to cooler and moister conditions. Consequently, the species associated with open habitats, which prefer drier and warmer microclimates (Thiele, 1977), are less dependent on the vegetation structure to create suitable microclimatic conditions in the Alb than they are in the Heide. For the species associated with forest habitats, which prefer cooler and moister conditions (Thiele, 1977), the opposite is found, with a lesser influence of the vegetation structures in the Heide compared to the Alb.

3.5 Implication for semi-open corridors management

While corridors have remained a controversial conservation solution, there is now clear evidence pointing to their effectiveness (Gilbert-Norton *et al.*, 2010). However, information remains limited concerning corridor structures and associated management strategies that take into account the needs of habitat specialists and species with limited dispersal abilities, such as ground beetles (Haddad & Tewksbury, 2005; Habel *et al.*, 2020). Our results show that species responded differently to the same environmental features, and in particular, the presence of high-quality vegetation structures in semi-open areas is critical for the more specialised species. In addition to habitat specialisation, the prevailing climatic conditions where the corridors are established also need to be taken into consideration.

Concerning semi-open corridors, the main aim of corridor management should be to produce high-quality habitat structures to ensure that one corridor might effectively serve a broad variety of species that depend on contrasting microhabitat conditions. This will require establishing management strategies that will ensure the presence of high-quality glades of heathland or grassland with a suitable amount of typical structures like bare soil as well as high-quality forest-like patches embedded within them with associated tree shading and leaf litter. As such, differential management between the different elements of semi-open corridors will be required. Specific management practises similar to existing management recommendations for classical corridors and having demonstrated their effects on other invertebrate taxa could be directly applied (e.g. Berg *et al.*, 2013; Pedley *et al.*, 2013). However, the presence of mature trees will certainly require additional mechanical removal of their saplings to keep the glades truly open when grazing alone is not sufficient. Furthermore, in oceanic climates, priority should be given to the quality of open-like glades, whereas in more continental climates, priority should be given to forest-like patches.

We conclude that semi-open areas could be valuable elements to integrate into conservation planning. They may even be able to meet the needs of endangered specialist species if these corridors are managed in such a way that high-quality vegetation structures are maintained or established. If management is inappropriate or even nonexistent, the resulting low quality of such corridors will undermine their effectiveness, although they will nevertheless remain well accepted by species with low habitat specialisation but will be of no or very limited importance for more specialised species.

Acknowledgement

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Appendix 3

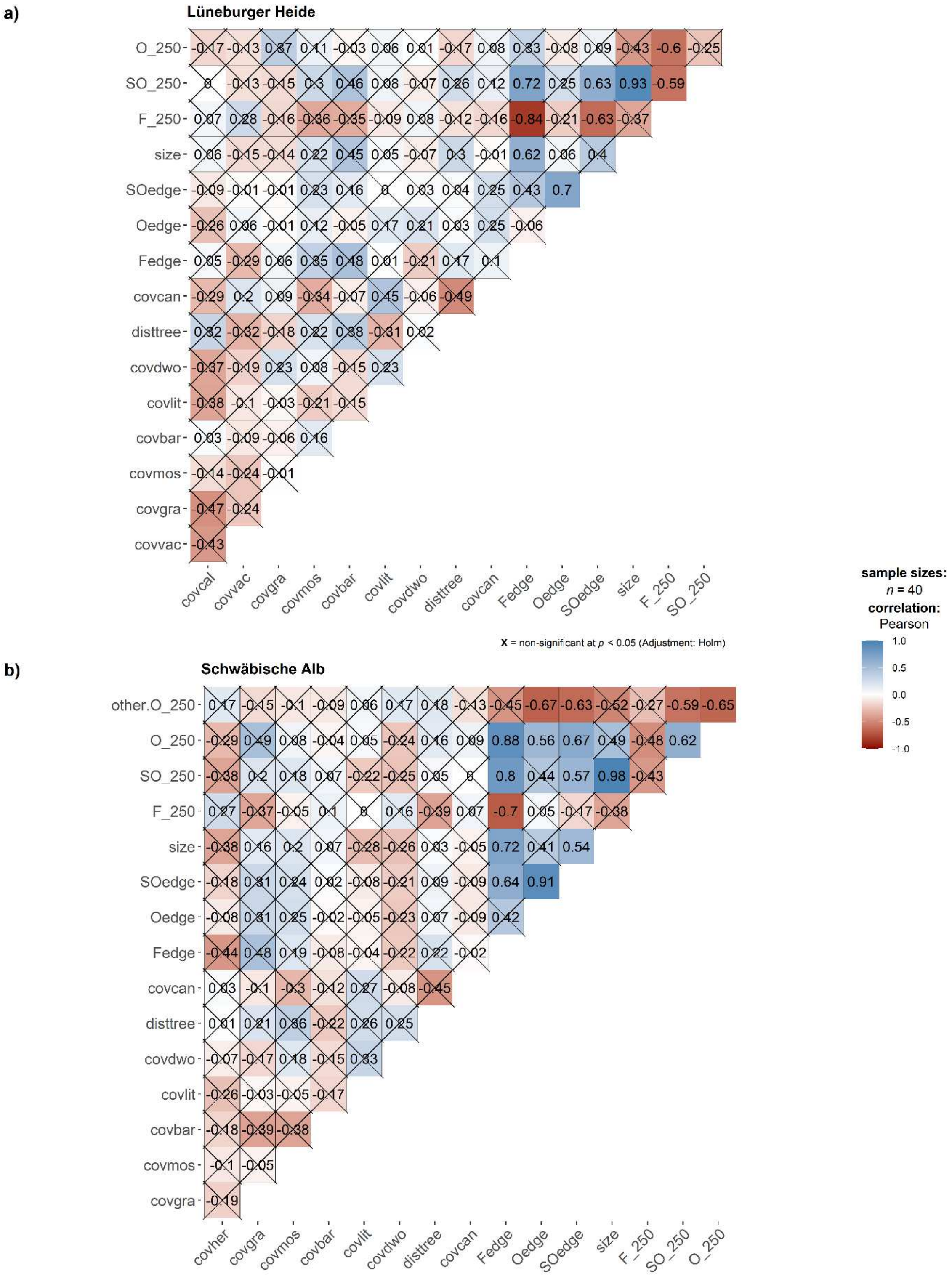

Figure. A3.1: Correlation matrix of the vegetation and landscape features for the Lüneburger Heide (a) and the Schwäbische Alb (b). Values in the cells show Pearson correlation coefficients. The correlations are non-significant if the cell is crossed out. Positive correlation are in blue, while negative correlation are in red.

Equation 3.1: Multidiversity index

$$\mathrm{MI} = \left(\frac{\mathrm{SRo}}{\mathrm{maxSRo}} + \frac{\mathrm{SRoso}}{\mathrm{maxSRoso}} + \frac{\mathrm{SRf}}{\mathrm{maxSRf}} + \frac{\mathrm{SRfso}}{\mathrm{maxSRfso}} + \frac{Ao}{maxAo} + \frac{Aoso}{maxAoso} + \frac{Af}{maxsAf} + \frac{Afso}{maxsAfso}\right)/8$$

where SR stands for rarefied species richness, A for standardised activity density, and o, oso, f, and fso for the open, open & semi-open, forest, and forest & semi-open habitat association groups, respectively. Each component of the index was standardised by dividing by the highest observed (max) value.

Table A3.1: Vegetation feature used in the analyses and their assumed effect on microclimation, structure and resource conditions affecting ground beetles.

Vegetation features	Microclimate	Structure	Resources	References
bare soil	absence of vegetation result in drier and hotter conditions	lack of shelter expose species to predation		Cameron & Leather (2012)
billberry	indicate cooler, shaded, moist conditions			Heliölä *et al.* (2001)
deadwood	shelter from harshe conditions			Heliölä *et al.* (2001)
distance to tree	provide shade and buffer conditions			Söderström *et al.* (2001); García-Tejero & Taboada (2016)
grass		inpede movement	provide seeds	Greenslade (1964); Schirmel & Buchholz (2011)
heather	increase shade and humidity but also indicate sun expose locations			Gimingham (1972); Schirmel & Buchholz (2011)
herbaceous		Shelter from predator	provide seeds and preys	Cameron & Leather (2012); Taboada *et al.* (2008)
moss	increase moisture and indicate shaded conditions			Vogels et al. (2005); Schirmel et al. (2011); Heliölä et al.(2001)
plant litter		Shelter (in particular for forest litter dweller)		Cameron & Leather (2012); Heliölä *et al.* (2001); García-Tejero & Taboada (2016); Taboada et al. (2004); Molnár et al. (2001)
tree canopy	provide shade and buffer conditions			Molnár et al. (2001)

References for table A3.1:

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Table A3.2: Correlations (r^2) with the three axes of the ground beetle ordination and associated p-values for vegetation and landscape features in Lüneburger Heide and Schwäbische Alb. Features are sorted by decreasing correlation coefficients, and p-values were corrected using the false discovery rate. Statistically significant p-values are in bold, and trends are in italic.

Vegetation and landscape features	r^2	p-values
Lüneburger Heide		
Distance to open edge (m)	**0.55**	**0.009**
Distance to forest edge (m)	**0.33**	**0.009**
Bare soil cover (%)	**0.29**	**0.009**
Deadwood cover (%)	*0.20*	*0.06*
Heather cover (%)	*0.22*	*0.06*
Distance to nearest tree (m)	*0.20*	*0.07*
Bilberry cover (%)	0.16	0.13
Moss cover (%)	0.07	0.50
Grass cover (%)	0.05	0.62
Schwäbische Alb		
Distance to forest edge (m)	**0.55**	**0.004**
Distance to open edge (m)	**0.51**	**0.004**
Moss cover (%)	**0.34**	**0.005**
Litter cover (%)	**0.31**	**0.008**
Bare soil cover (%)	**0.27**	**0.010**
Grass cover (%)	0.13	0.22
Herbaceous cover (%)	0.11	0.25
Distance to the nearest tree (m)	0.06	0.54

Table A3.3: Results of the linear and linear mixed-effects models for the effect of vegetation and landscape features on rarefied species richness of species associated with open, forest, open & semi-open, and forest & semi-open habitats in the Lüneburger Heide. P-values for the model correspond to the LRT for the mixed effect. Statistically significant p-values are in bold.Df: degree of freedom.

Environmental parameters	Model	Df	F value	p-value
Open	Mixed, untransformed		3.80	**0.05**
Deadwood cover		1, 26.63	0.01	0.93
Litter cover		1, 27.84	0.28	0.60
Distance to forest edge		1, 14.50	0.58	0.45
Grass cover		1, 30.99	1.03	0.31
Distance to open edge		1, 19.72	1.93	0.17
Distance to nearest tree		1, 29.80	2.46	0.12
Open & semi-open	Mixed, OrderNorm		5.65	**0.017**
Distance to open edge		1, 13.91	0.00	0.99
Heather cover		1, 30.86	0.06	0.80
Distance to nearest tree		1, 28.14	0.17	0.63
Deadwood cover		1, 31.58	0.46	0.50
Moss cover		1, 29.41	0.55	0.46
Grass cover		1, 33.83	0.97	0.33
Distance to forest edge		1, 15.77	1.86	0.19
Forest	Linear, untransformed		0.17	0.67
Moss cover		1, 40	0.13	0.71
Distance to forest edge		1, 40	0.10	0.75
Deadwood cover		1, 40	1.00	0.32
Grass cover		1, 40	1.86	0.18

Environmental parameters	Model	Df	F value	p-value
Distance to open edge		1, 40	2.56	0.11
Distance to nearest tree		1, 40	2.70	0.10
Forest & semi-open	Mixed, OrderNorm		7.69	**0.005**
Distance to nearest tree		1, 27.38	0.02	0.87
Bilberry cover		1, 30.03	0.07	0.79
Moss cover		1, 28.52	0.10	0.75
Deadwood cover		1, 31.58	0.26	0.61
Distance to open edge		1, 22.19	0.46	0.50
Bare soil cover		1, 33.37	1.59	0.21
Grass cover		1, 34.81	2.27	0.14

Table A3.4: Results of the linear and linear mixed-effects models for the effect of vegetation and landscape features on standardised activity-density of species associated with open, forest, open & semi-open, and forest & semi-open habitats in the Lüneburger Heide. P-values for the model correspond to the LRT for the mixed effect. Statistically significant p-values are in bold.Df: degree of freedom.

Environmental parameters	Model	Df	F value	p-value
Open	Mixed, square root		7.36	**0.007**
Deadwood cover		1, 28.01	0.00	0.96
Distance to forest edge		1, 12.12	0.22	0.65
Grass cover		1, 31.66	0.23	0.63
Moss cover		1, 30.60	2.87	0.10
Bare soil cover		1, 34.93	2.84	0.10
Open & semi-open	Mixed, OrderNorm		12.20	**<0.001**
Distance to nearest tree		1, 28.94	0.00	0.95
Deadwood cover		1, 29.74	0.01	0.92
Moss cover		1, 28.46	0.16	0.69
Heather cover		1, 32.39	0.52	0.48
Distance to forest edge		1, 16.67	0.77	0.39
Distance to open edge		1, 28.85	1.32	0.26
Bare soil cover		1, 35.04	1.80	0.19
Forest	Linear, Log_{10}		1.18	0.28
Distance to open edge		1, 40	0.00	0.95
Grass cover		1, 40	0.36	0.55
Distance to forest edge		1, 40	0.84	0.36
Moss cover		1, 40	1.98	0.17
Bare soil cover		1, 40	2.30	0.14
Distance to nearest tree		1, 40	1.78	0.19
Forest & semi-open	Mixed, Log_{10}		7.69	**0.005**
Distance to nearest tree		1, 27.17	0.09	0.77
Moss cover		1, 27.45	0.10	0.75
Distance to open edge		1, 24.09	0.31	0.58
Deadwood cover		1, 30.55	0.72	0.40
Bare soil cover		1, 31.94	0.80	0.38
Distance to forest edge		1, 17.60	2.54	0.12

Table A3.5: Results of the linear and linear mixed-effects models for the effect of vegetation and landscape features on rarefied species richness of species associated with open, forest, open & semi-open, and forest & semi-open habitats in the Schwäbische Alb. P-values for the model correspond to the LRT for the mixed effect. Statistically significant p-values are in bold.Df: degree of freedom.

Environmental parameters	Model	Df	F value	p-value
Open	Linear, untransformed		3.39	0.06
Bare soil cover		1, 30.86	0.01	0.92
Distance to nearest tree		1, 31.28	0.03	0.87
Distance to forest edge		1, 6.36	0.69	0.43
Distance to open edge		1, 18.34	0.26	0.61
Moss cover		1, 9.47	0.83	0.38
Grass cover		1, 32.04	1.08	0.30
Herbaceous cover		1, 36.37	2.14	0.15
Open & semi-open	Mixed, OrderNorm		7.56	**0.006**
Herbaceous cover		1, 30.38	0.10	0.76
Distance to nearest tree		1, 28.27	0.05	0.83
Distance to forest edge		1, 5.27	0.38	0.56
Distance to open edge		1, 25.10	0.21	0.65
Grass cover		1, 34.82	0.50	0.49
Bare soil cover		1, 28.80	1.19	0.28
Moss cover		1, 10.81	2.85	0.12
Forest	Linear, Yeo-Johnson		1.11	0.29
Distance to nearest tree		1, 40	0.08	0.78
Distance to forest edge		1, 40	0.28	0.59
Herbaceous cover		1, 40	0.58	0.45
Grass cover		1, 40	0.45	0.50
Bare soil cover		1, 40	0.37	0.54
Forest & semi-open	Mixed, OrderNorm		12.03	**<0.001**
Herbaceous cover		1, 30.98	0.10	0.75
Litter cover		1, 30.65	0.46	0.50
Distance to forest edge		1, 8.41	1.25	0.30
Grass cover		1, 33.25	1.68	0.20
Bare soil cover		1, 32.14	1.19	0.28
Distance to open edge		1, 31.30	2.85	0.10

Table A3.6: Results of the linear and linear mixed-effects models for the effect of vegetation and landscape features on standardised activity-density of species associated with open, forest, open & semi-open, and forest & semi-open habitats in the Schwäbische Alb. P-values for the model correspond to the LRT for the mixed effect. Statistically significant p-values are in bold.Df: degree of freedom.

Environmental parameters	Model	Df	F value	p-value
Open	Mixed, Box-cox		9.7	**0.002**
Herbaceous cover		1, 30.35	0.06	0.80
Distance to open edge		1, 28.18	0.10	0.75
Grass cover		1, 30.54	0.52	0.47
Distance to forest edge		1, 6.34	0.52	0.50
Bare soil cover		1, 28.79	1.94	0.17
Open & semi-open	Mixed, square root		6.63	**0.011**
Distance to forest edge		1, 6.76	0.00	0.94
Distance to open edge		1, 18.44	0.00	0.96
Grass cover		1, 32.92	0.03	0.87

Environmental parameters	Model	Df	F value	p-value
Litter cover		1, 33.38	0.18	0.67
Moss cover		1, 14.92	0.68	0.42
Bare soil cover		1, 34.32	0.46	0.50
Herbaceous cover		1, 34.00	0.27	0.61
Forest	Linear, orderNorm		2.44	0.12
Distance to forest edge		1, 40	0.01	0.91
Grass cover		1, 40	0.08	0.78
Distance to nearest tree		1, 40	0.04	0.85
Herbaceous cover		1, 40	0.56	0.46
Bare soil cover		1, 40	1.19	0.28
Forest & semi-open	Mixed, square root		8.16	**0.004**
Herbaceous cover		1, 31.00	0.01	0.92
Distance to forest edge		1, 7.55	0.07	0.79
Distance to nearest tree		1, 30.40	0.16	0.69
Bare soil cover		1, 29.54	0.31	0.58
Grass cover		1, 34.52	0.46	0.50
Moss cover		1, 14.80	0.93	0.35
Litter cover		1, 36.45	1.26	0.27

Chapter IV

4. The pace of range expansion: a long-term study on the flightless ground beetle *Carabus hortensis* (Coleoptera: Carabidae)

Eva Völler Estève Boutaud Thorsten Assmann

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Figure 4.1: Drawing of the habitus of *Carabus hortensis* (left) and typical mixed forest habitat where the species can be found within the Lüneburger Heide.

Abstract

Range shifts are predicted for numerous species due to climate change, and therefore understanding species dispersal is more crucial than ever. For some species, their low dispersal capabilities may prevent them from reaching new, suitable habitats, thus threatening their survival. This is of particular concern for those ground beetles which are flightless and depend on a specific type of habitat. However, studies on ground beetle dispersal rates are rare. We investigated the shift in distribution range of Carabus hortensis in northwestern Germany over a span of 22 years. We found that this species disperses on average 127 m per year with low variation between years. Although C. hortensis' movement (locomotory) activity is not different or lower than that found in similar ground beetles, its dispersal rate is rather low. We speculate that this slow range expan- sion may be due to a long individual development time from egg to teneral and suggest that in the face of climate change, conservation actions, like assisted migration, may be an option for such slow dispersing species.

4.1 Introduction

Dispersal is essential for species to cope with environmental changes and local extinction processes (Den Boer, 1990; Clobert *et al.*, 2001). Particularly in times of climate change, dispersal ability is a key trait for species survival (e.g. Peterson *et al.*, 2002; Thomas *et al.*, 2004). It has been shown that species have shifted or expanded their distribution ranges in reaction to climate change (Parmesan *et al.*, 1999; Thomas & Lennon, 1999). These successful dispersers are often generalists with advantageous dispersal traits. There are species which are less successful in dispersing, species with more disadvantageous dispersal traits, and such that are stenotopic, and therefore have fewer potential habitats to colonise. A better understanding of dispersal rates of such species is important in the face of global environmental change, to help predict species' responses to changing environmental conditions and to develop appropriate conservation actions. Such knowledge of dispersal rates may contribute to understand the distribution and occurrence of species, and data of dispersal ability are needed to model population dynamics or species responses to today's challenges like habitat loss, climate change and species introductions (Kokko & López-Sepulcre, 2006).

Dispersal takes place at different rates in different species (Clobert *et al.*, 2012). To elucidate how fast insect species disperse or to predict dispersal ability, many studies related the power of dispersal to morphological traits such as body or wing size (Jenkins *et al.*, 2007; Sekar, 2012; Stevens *et al.*, 2012) or to life history traits such as adult lifetime or larval growth rate (Stevens *et al.*, 2013). Although these studies contribute to our understanding as to why some species disperse better or worse, there are fewer studies that empirically investigated the rate of dispersal (Ronce, 2007). However, the most accurate and reliable way to determine the dispersal ability of a species is to observe its dispersal rate under natural conditions over many years. Other methods, like mark-release-recapture or radio-tracking, can measure dispersal only during short time intervals. As beetle movement varies due to e.g. satiation or temperature (Růžičková & Veselý, 2016), dispersal ability can only be roughly estimated with such methods.

Ground beetles are often categorized by the level of hindwing development, a trait which is a good predictor of flight ability (Homburg *et al.*, 2014b). Studies that are dealing with the dispersal of ground beetles mostly focused on these categories (Zalewski & Ulrich, 2006; Wamser *et al.*, 2012). Brachypterous species that disperse by walking have the lowest dispersal ability in comparison to macropterous species that are mostly able to fly or dimorphic species, which harbour individuals that are either able to fly or flightless (Den Boer, 1970). Yet, brachypterous species are of special interest as they offer the possibility to study ongoing dispersal processes in species with low dispersal power. Low power of dispersal does not necessarily mean that species are or will become endangered, but under conditions of global climate change and niche shifts, low dispersal power may be disadvantageous for species survival. *Carabus hortensis* is medium-frequent within Central Europe (Nolte *et al.*, 2017) and was recorded in 125 out of 217 grid cells covering Germany (grid based on the topographical map 1:100,000 (TM100); Trautner *et al.*, 2014). This species is not listed as threatened in Germany (Schmidt *et al.*, 2016), but protected due to the Federal Ordinance on the Conservation of Species (BArtSchV, 2013), as all species belonging to the genus *Carabus*, which are all not able to fly (except for two dimorphic species without flight records; Turin *et al.*, 2003).

We investigated the dispersal rate of the brachypterous ground beetle *C. hortensis* in northern Germany. Our study took place in the nature reserve Lüneburger Heide, located approximately 40 km south of Hamburg, a region in which *C. hortensis* occurs only in the eastern parts. We analysed presence–absence data of *C. hortensis* collected over a time span of 22 years to estimate the pace of range expansion in this species and therefore its dispersal power. In this study, dispersal is defined by the detection of a westward range expansion in an area of unfragmented forest. To the best of our knowledge there are no studies which investigated the dispersal rates of ground beetles empirically over such a long time and in a continuous habitat.

4.2 Materials and methods

4.2.1 Study area

Our study was carried out in the nature reserve Lüneburger Heide, located in the lowlands of northern Germany (Lower Saxony). This region would naturally be dominated by forests, but human land use since the Middle Ages has almost completely eradicated the forests in the area (Tempel, 1994). Approximately 250 years ago most of the Lüneburger Heide area was deforested, with only small patches of woodlands, mostly located next to farmyards, remaining (Kost, 1970; Keienburg & Prüter, 2006). Since the middle of the nineteenth century, large areas were reforested either actively or due to natural succession after the abandonment of heathlands and arable fields. Today, the landscape consists of a matrix of forests, heathlands and arable fields. Patches of ancient forests, areas which have been continuously wooded for more than 250 years, are embedded within recent forest stands (Fig. 4.2). Thus, colonization of the area could only have begun less than 250 years ago, starting from ancient forests located in the east of the area. In ancient forests the species survived during deforestation (Assmann, 1999). Dispersal is only taking place in a westward direction as here suitable and continuous forest habitat is available, while in the other directions unsuitable habitat, like heathland, arable fields and settlements are found (Fig. 4.2).

4.2.2 Study species

We investigated the dispersal rate of the 22–30 mm long ground beetle *C. hortensis* Linnaeus, 1758 (Coleoptera: Carabidae; Fig. 4.1). As this species is brachypterous, it disperses by walking only. It is a predatory species that is restricted to but eurytopic within forests (Lindroth, 1985; Turin *et al.*, 2003). *Carabus hortensis* is active from mid-July to the end of October (Günther & Assmann, 2000). Larvae and a large proportion of adults hibernate (Kádár *et al.*, 2015). Its geographical distribution range encompasses large areas of Northern, Central and Eastern Europe from Finland to Russia and the Balkan Peninsula (Turin *et al.*, 2003). This species is widespread within Germany but is missing in the western parts of the county (Trautner, 2017).

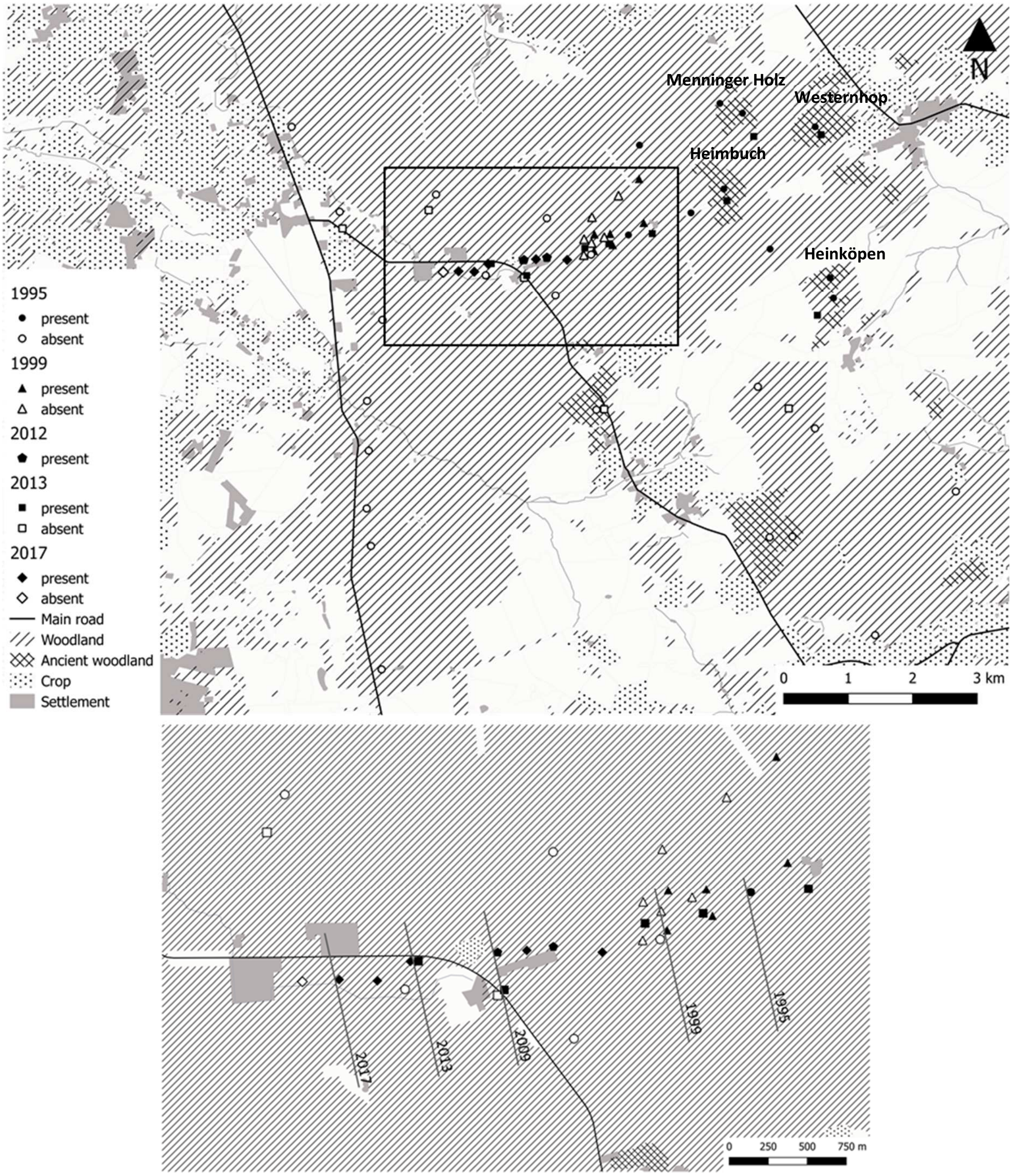

Figure 4.2: Study site in the Lüneburger Heide. Black symbols indicate presence, white symbols no records of C. hortensis. Circles represent sampling sites in 1994 and 1995, triangles 1999, pentagons 2009, squares 2013 and diamonds 2017. The intensively sampled area in the box is magnified below and the western-most distribution limits for each study year are indicated with a line. Ancient woodlands are named.

4.2.3 Trapping

To detect how far westwards C. hortensis occurs in the Lüneburger Heide, we set baited pitfall traps which contained a small piece of cellulose soaked in red wine (Assmann & Janssen, 1999). A transect of at least eight traps, 10 m apart, was installed at each sampling site during all six sampling campaigns, 1994–1995, 1999, 2009, 2013 and 2017 (Fig. 4.2). Trapping was conducted in late summer (August–September) and traps were emptied within 24–48 h. Beetles were immediately released at the site after counting. Initially, in 1994 and 1995, sampling sites were spread all over the area, to characterise the distribution of the species within the Lüneburger Heide. In the following years, the dispersal front was monitored by locating new sampling sites west of the previously known distribution edge.

4.2.4 Dispersal rate

In 1978, during the first study with pitfall traps in the forests of the nature reserve, *C. hortensis* was not found (sites in the Menninger Holz and west of it; G.A. Lohse, Hamburg, pers. comm.). We found this species first in 1994; in the subsequent year, we observed a westward dispersal (Assmann *et al.*, 2001). Based on trapping in subsequent years (1999, 2009, 2013 and 2017) beyond the known dispersal front of 1995, we could determine the westward colonisation progress of *C. hortensis*. Additional traps at sites where *C. hortensis* had already been recorded reconfirmed its presence and served as proof that the species was active during the trapping campaign.

4.3 Results

We first found *C. hortensis* in 1994 in the nature reserve Lüneburger Heide. It occurred in ancient forests, like the Menninger Holz, Westernhop, Heimbuch and Heinköpen, but also in recent forests (Fig. 4.2). By examining 30 sampling sites, we could define its westwards migration limit in 1995 at a site where we sampled in 1994 without success (Assmann *et al.*, 2001) (Fig. 4.2). During subsequent years the migration limit shifted to the west: in 1999, we found *C. hortensis* 540 m further westwards of the distribution limit detected in 1995. By 2009 the species was present 1140 m further to the west, compared to 1999, and in 2013 it was found 514 m westwards of the catches from 2009. In 2013 the most western individuals were found close to a site where traps were set in 1994 and 1995, but *C. hortensis* was not caught (Fig. 4.2). In 2017, the species was found 522 m westwards of the catches from 2013. Overall *C. hortensis* dispersed on average 127 m/year (Table 4.1).

Table 4.1: Westward migration of C. hortensis in the nature reserve Lüneburger Heide.

Year	Dispersal distance (m), since last census	Dispersal distance (m/year), since last census
1994	First detection in the area	-
1995	Detection of the expansion edge	-
1999	540	135
2009	1140	114
2013	514	128.5
2017	522	130.5

At sites at the edge of the distribution limit, *C. hortensis* was always found in low numbers (e.g. two individuals in 1995 and 2013, one individual in 2009 and 2017) compared to more eastern sites where *C. hortensis* was well established (133 ± 47 (sd) individuals/ten traps during four nights of trapping). Moreover, at the most westward sampled site where *C. hortensis* was found in 2013 only two individuals were caught (ten traps, six nights of trapping), while ten individuals were caught at this site in 2017 (ten traps, two nights of trapping), indicating a well-established population at this site 4 years later.

4.4 Discussion

Although it is known that dispersal ability varies among closely related ground beetle species, e.g. linked to specific traits such as wing development (Zalewski & Ulrich, 2006) or body size (Gutiérrez & Menéndez, 1997), real dispersal rates in single species investigated under natural conditions are rarely documented. By tracing the dispersal front of *C. hortensis* over 22 years, we found that this species disperses an average of 127 m per year at a constant rate.

It is often assumed that variation in dispersal ability among species is likely to correlate with the species movement rate (Brouwers & Newton, 2009). According to Szyszko *et al.* (2004a), *C. hortensis* moves between 0.85 and 2.35 m/h, depending on whether the movement rate was measured in a pine forest or in a beech forest.

Skłodowski (1999) found that *C. hortensis* moves 3.88 m/day. This measured rate is similar to those of other *Carabus* species of a similar size. For example, *C. cancellatus* moves 3.69 m/day and forest-dwelling individuals of *C. nemoralis* 2.54 m/day (Skłodowski, 1999). However, as movement rates vary throughout the activity period or due to feeding state, prey density (Szyszko *et al.*, 2004b), ground texture (Skłodowski, 1999) and temperature (Růžičková & Veselý, 2016), information on movement rates of ground beetles vary considerably across studies. Moreover, movement rates do not reflect straight movement in one specific direction (Baars, 1979) and do not indicate if beetles leave their home range or establish at a new site. Thus, knowing that *C. hortensis* movement rate is comparable with that of other ground beetle species does not imply that it disperses at the same rate.

Trying to compare dispersal rates of species that are also a brachypterous, stenotopic forest species of similar size to *C. hortensis*, we only found credible dispersal rates for *Carabus auronitens*. Drees *et al.* (2008) investigated the recolonization of woodlands in north-western Germany by *C. auronitens* after reforestation and defragmentation. Using population genetics methods, Drees *et al.* (2008) found that the site of investigation was recolonised from refuges located 12–15 km away. These refuges were not connected to the study site by forest until the early nineteenth century, and by 1923 *C. auronitens* had already colonised the study area. Thus, in less than 23 years *C. auronitens* dispersed at least 12 km, giving a dispersal rate of more than 500 m per year. Niehues *et al.* (1996) found a similar dispersal rate of 650 m per year of *C. auronitens*. Thus, *C. auronitens* disperses at least four times faster than *C. hortensis*. However, *C. auronitens* may have dispersed through inhospitable habitats, like non-forest patches. Dispersal distances in unsuitable habitats are usually larger than in suitable habitats, as shown for butterflies (Nowicki *et al.*, 2014). Also carabid species showed more directed movement in unsuitable habitats, compared to random walk in suitable habitats. Directed movement implies walking longer distances in one direction and therefore contributes strongly to dispersal (Baars, 1979). Both types of locomotory movement are reported for *Carabus auronitens* (Niehues *et al.*, 1996). Although *C. hortensis*' movement rate is similar to that of comparable ground beetles, it disperses much slower than *C. auronitens*.

To successfully disperse, it is not sufficient to move beyond the distribution edge, it is also essential to establish a population at a new site (Den Boer, 1970). Two requirements of population establishment are aggregating behaviour, as a prerequisite to find mates (Brandmayr, 1992) and a rapid population growth (Hockmann *et al.*, 1992) to minimize the chances of random local extinction (Lande *et al.*, 2003). *Carabus hortensis* has a strong aggregating behaviour (Rosenkranz, 2000), but there are no data about the population growth rate in this species. However, individual development time, the time between the appearance of the first eggs laid and the detection of first tenerals, lasts 9–10 months (Turin *et al.*, 2003; Kádár *et al.*, 2015). This long developmental period makes the population rather vulnerable to random events (Kádár *et al.*, 2015). Moreover, Allee effects might additionally reduce initial population growth (Stephens *et al.*, 1999). Thus, slow population growth rather than low movement rate may be limiting the dispersal rate of *C. hortensis*. However, dispersal in other brachypterous forest species is rarely investigated and there are no standard values for fast or slow dispersal.

To put our results into perspective, we tried to estimate the dispersal rate of the species from its possible northern-most Pleistocene refuge to the northern border of its current distribution (Habel *et al.*, 2010). The probable location is in Slovenia around Ljubljana, as permafrost approximately reached this far southwards (Tzedakis *et al.*, 2013). The recent northernmost distribution is around Lycksele/Sweden (Turin *et al.*, 2003). The shortest distance beeline between these two locations is approximately 2000 km. If *C. hortensis* dispersed about 127 m per year, it would have needed about 15,000 years to cover this distance, which is about the time since the end of the last glaciation (Quante, 2010). However, as a walk following a straight line is unlikely, this is probably an underestimate, and the existence of so far unknown northern refuges (Homburg *et al.*, 2013; Drees *et al.*, 2016) cannot be excluded.

In general, ground beetles have shown marked altitudinal and latitudinal shifts, which have been linked to climate change (Hickling *et al.*, 2006; Brandmayr & Pizzolotto, 2016). During 25 years, the northern limit in Great Britain of the distribution ranges of several carabid species has shifted approximately 50 km northwards (Hickling *et al.*, 2006). These studies however, refer to flight active carabids with a high power of dispersal, while the estimated dispersal rate of *C. hortensis* is more than an order of magnitude lower: our data indicated a dispersal over 25 years of only 3.2 km. This suggests that brachypterous ground beetles may not be able to compensate for changes in climate solely by natural dispersal. Excluding changes in the species' power of dispersal, e.g. by selection for more effective colonizers (Laparie *et al.*, 2013), active intervention via conservation measures such as assisted migration may be an option (Fuchs *et al.*, 2010). For brachypterous ground beetle species, assisted migration has been shown to be an effective method to establish populations outside of the current distribution ranges (Malausa & Drescher, 1991; Vigna Taglianti *et al.*, 2000), and has already been suggested as a conservation strategy for low dispersing *Carabus* species under global change conditions (Homburg *et al.*, 2014a).

Concluding, this study clearly indicates that dispersal power may be a limiting factor and should be taken into account, especially for the long-term conservation under global change conditions. Many studies model future species distributions using climatic data and recent geographic distribution data but do not account for slow dispersal which may limit possible future distributions (Peterson *et al.*, 2002; Thomas *et al.*, 2004). Thus it is important to empirically investigate dispersal rates of natural populations.

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Chapter V

5. *Notiophilus quadripunctatus* Dejean, 1826: Range expansion in northern Central Europe

Notiophilus quadripunctatus Dejean, 1826: Ausbreitung im nördlichen Mitteleuropa

Estève Boutaud, Wolfgang Schacht, and Thorsten Assmann

Accepted by Angewandte Carabidologie

Abb 5.1: Drawing of the habitus of *Notiopphilus quadripunctatus* (left) and typical scarified heathland site where the species was found within the Lüneburger Heide (right).

Kurzfassung: Eigene Nachweise sowie in Literatur und Internet verfügbare Daten zum Vorkommen des Laufkäfers *Notiophilus quadripunctatus* Dejean, 1826 werden zusammengefasst und ausgewertet. Damit lässt sich die Ausbreitung der Art in Mitteleuropa abschätzen und verstehen. Offensichtlich hat die flügeldimorphe Art ihr Verbreitungsgebiet mit einer Geschwindigkeit von maximal ca. 50 km/Jahr in der nördlichen Hälfte Mitteleuropas erweitert. Die neu gegründete Population im Naturschutzgebiet Lüneburger Heide besteht ausschließlich oder ganz überwiegend aus geflügelten Individuen. Daher erfolgte die Ausbreitung wahrscheinlich über Flugaktivität. Die durch Ganzjahres-Fallenfänge dokumentierte Phänologie zeigt eine deutliche Winteraktivität in den Sandheiden des Naturschutzgebietes Lüneburger Heide.

Abstract: Using information from own catches, the data available in the literature, and online databases, the occurrence of the ground beetle *Notiophilus quadripunctatus* Dejean, 1826 is summarised and evaluated. This allows the spread of the species in Central Europe to be estimated and understood. Apparently, the wing dimorphic species has expanded its range in the northern half of Central Europe at a maximum rate of about 50 km/year. The newly established population in the Lüneburg Heath nature reserve consists exclusively or predominantly of winged individuals. Therefore, the spread probably occurred via flight activity. The phenology documented by year-round trapping shows clear winter activity in the sandy heaths of the Lüneburg Heath nature reserve.

5.1 Einleitung

Der sich abzeichnende Klimawandel hat im letzten Jahrzehnt in Deutschland zu Durchschnittstemperaturen geführt, die mehr als ein Grad Celsius über dem langjährigen Mittel liegen (Deutscher Wetterdienst, 2021). Erstmeldungen thermophiler Insektenarten nördlich ihrer bisher bekannten Verbreitungsgebiete lassen sich darauf zurückführen, so auch von Laufkäferarten (Schacht, 2016). Teils erfolgten allerdings lediglich Beobachtungen einzelner Individuen, und es bleibt offen, ob es sich um bereits etablierte Populationen oder um nach Norden verschleppte oder verdriftete Einzeltiere handelt. Als Beispiel kann hier *Polistichus connexus* (Geoffroy in Fourcroy, 1785) gelten, für den bislang lediglich zwei Einzelfunde aus Niedersachsen vorliegen (Schacht, 2019; Theunert, 2020).

Eine weitere dieser sich ausbreitenden Arten ist *Notiophilus quadripunctatus* Dejean, 1826, von der oft gleichfalls nur einzelne Individuen gefunden werden (z. B. Heijerman & Aukema, 2014; Chittaro & Marggi, 2016). Die sichere Determination von *N. quadripunctatus* war in der Vergangenheit aufgrund der Variationsbreite wichtiger Unterscheidungskriterien nicht immer zuverlässig (Horion, 1941; Muilwijk & Felix, 2004). Alte Meldungen, wie beispielsweise von Horion erwähnt, sind daher, wenn überhaupt, mit Vorsicht einzubeziehen. Mittlerweile liegen gute Darstellungen zur Differenzierung der Art von anderen Vertretern der Gattung vor (Hemmann & Trautner, 2002; Heijerman & Aukema, 2014; Raupach *et al.*, 2020) Auch wenn dies das Risiko einer Fehlbestimmung verringern sollte, könnten Entomologen, die mit der Art nicht vertraut sind oder denen unbekannt ist, dass sie in ihren Untersuchungsgebieten vorkommt, sie dennoch als *N. biguttatus* erfassen. Daher kann eine bessere Kenntnis der tatsächlichen Verbreitung der Art und ihrer Ausbreitungsrate dazu beitragen, Fehlbestimmungen zu vermeiden.

Der Käfer kommt von Nordafrika (Algerien, Marokko und Tunesien) über Süd- (Portugal, Spanien und Italien) bis Westeuropa (Vereinigtes Königreich, ein Großteil Frankreichs und Belgien) vor. Vor Anfang 2000 gab es zuverlässige Nachweise für das Vorkommen der Art in Mitteleuropa nur für den westlichen und südwestlichen Teil Belgiens (Desender et al. 2008). So war der schwerpunktmäßig *atlantisch-*westmediterran verbreitete *N. quadripunctatus* zunächst aus Deutschland wie auch aus anderen mitteleuropäischen Ländern unbekannt. Die Erstfunde für den Südwesten Mitteleuropas stammen vom Beginn dieses Jahrhunderts: Der Käfer trat im Jahr 2001 sowohl im Elsass als auch in Baden-Württemberg auf (Hemmann & Trautner, 2002; Schott, 2019). Inzwischen sind etablierte Populationen in Baden-Württemberg nachgewiesen (Fritze, 2017; Oellers *et al.*, 2022). Nach zahlreichen Funden in den letzten Jahren aus Nordrhein-Westfalen (Hannig, 2015, 2016a, 2016b, 2018, 2020) und den Niederlanden (z. B. Heijerman & Aukema, 2014) konnten wir die Art nun auch in Nord-Niedersachsen feststellen. Durch Ganzjahres-Fallenfänge können wir nicht nur deren Etablierung belegen, sondern auch die Phänologie sowie Hinterflügelausbildung bestimmen. Zusammen mit Nachweisen aus Nordrhein-Westfalen liegen damit umfangreiche Daten zur Ausbreitungsbiologie vor.

5.2 Material und Methode

Wir haben die uns zur Verfügung stehende Literatur für Mitteleuropa gemäß Definition von Müller-Motzfeld (2006) ausgewertet. Zusätzlich herangezogen wurden die Internet-basierte Datenbank von ColeoWeb (Bleich *et al.*, 2023), die überprüfbaren Nachweise von Observations.org (Observation.org, 2023), Obervation.be (Observations.be, 2023), Waarneming.nl (Waarneming.nl, 2023) und Kerbtier.de (Benisch, 2023). Umfangreiche eigene Funde liegen aus dem Naturschutzgebiet (NSG) Lüneburger Heide vor.

5.2.1 Bodenfallen-Untersuchungen im NSG Lüneburger Heide

Die Untersuchungsflächen lagen im zentralen Bereich des NSG zwischen den Orten Schneverdingen und Undeloh. Es handelte sich um trockensandige Heidehabitate, dominiert von Besenheide (*Calluna vulgaris*). Unterschiede zwischen den einzelnen Flächen bestanden lediglich hinsichtlich Pflegemanagement, Lebensraumgeschichte und dem Alter des *Calluna*-Bestandes. Insgesamt wurden 42 Flächen beprobt. 15 über den Zeitraum von April 2018 bis März 2021 und 27 von April 2019 bis März 2021. Die Nachweise erfolgten durch klassische Bodenfallen (sogenannte Barberfallen). Die transparenten Plastikbecher hatten einen Öffnungsdurchmesser von 10 cm und ein Volumen von 500 ml. Als Fangflüssigkeit wurde Renner-Lösung verwendet (Renner 1982). Alle Untersuchungsflächen wurden mit je fünf Bodenfallen im Abstand von 10 m ausgestattet. Die Fallen wurden von April bis September etwa alle zwei Wochen geleert und im Winterhalbjahr einmal pro Monat. Im Winter 2021-2022 wurde eine weitere Fläche mit 10 Bodenfallen beprobt (Öffnungsdurchmesser 8 cm, Volumen 300 ml). Die Fallen wurden von Anfang November bis Mitte Dezember zur Hälfte mit Ethylenglykol gefüllt. Von Mitte Dezember bis Ende Februar wurde halbgesättigte Kochsalzlösung verwendet (180 g Kochsalz pro liter Wasser). Die Fallen wurden alle drei bis vier Wochen geleert. Am 14.6.2021 wurde ein Exemplar von *Notiophilus quadripunctatus* mit einem Streifkescher erhalten.

5.2.2 Hinterflügel-Ausbildung

In Anlehnung an Lindroth (1992) prüften wir, ob die Individuen makropter oder brachypter waren. Käfer wurden als makropter klassifiziert, wenn die Flügel länger und breiter als die entsprechenden Elytren waren. Wir haben maximal 40 Individuen pro Stichprobenjahr (von April bis März) überprüft, sofern diese verfügbar waren. Dabei wurde ein gleicher Anteil von männlichen und weiblichen Tieren berücksichtigt.

5.3. Ergebnisse

5.3.1 Faunistik

Aus der Literaturrecherche, Datenbankabfragen und eigenen Untersuchungen ergaben sich insgesamt mehr als 200 Fundorte von *N. quadripunctatus* in vier mitteleuropäischen Ländern (Abb. 5.2 und Tab. 5.1).

Fragwürdige Angaben liegen für Österreich im südlichsten Kärnten (Hölzel, 1951) aus den Jahren 1948, 1949 und 1950 vor sowie ein 1992 für Liechtenstein gemeldetes Exemplar (Brandstetter & Kapp, 1997). Da keine weiteren Meldungen aus diesen Ländern vorliegen und die Art im Paläarktenkatalog weder für Österreich noch für Liechtenstein geführt wird (Bousquet, 2017), müssen die Angaben stark in Zweifel gezogen werden. Insbesondere erscheinen die Angaben unwahrscheinlich, da Nachweise aus Italien ausschließlich aus südlichen Regionen stammen (Pesarini & Monzini, 2010; Casale *et al.*, 2021). Beide Angaben werden im Folgenden nicht übernommen und bleiben in Abb. 5.2 unberücksichtigt. Aus Dänemark, Skandinavien, Polen und Tschechien liegen keine Meldungen vor. Diese Länder gehören nicht zum derzeitigen Verbreitungsgebiet (Bousquet, 2017).

Im Detail ergibt sich für die vier zum Verbreitungsgebiet zählenden Länder folgender Überblick Die Länder werden dabei entsprechend der beobachteten Ausbreitungsrichtung von Westen nach Osten betrachtet:

Aus Belgien war die Art schon vor 1950 bekannt. Bis 2007 war sie wohl auf den südlichen und westlichen Teil des Landes beschränkt (Desender *et al.*, 2008). Seit 2007 kommt der Käfer weiter nördlich bis zur Grenze der Niederlande und östlich bis zur Grenze nach Luxemburg vor (Abb. 5.2).

Aus Luxemburg ist die Art unseres Wissens allerdings nicht bekannt und wird in der Laufkäfer-Checkliste von Braunert & Gerend (1997) nicht angeführt. Die Art wurde jedoch in Belgien nur wenige Kilometer von der Grenze entfernt sowie in den benachbarten deutschen Bundesländern gefunden. Eine Besiedlung von Luxemburg ist damit wahrscheinlich, auch wenn der Nachweis noch aussteht.

Tabelle 5.1: Jahr der Erstmeldung mit Literaturquellen für Meldungen von *Notiophilus quadripunctatus* Dejean, 1826 aus verschiedenen mitteleuropäischen Ländern, wo die Art in der letzten zwei Jahrzehnten neu nachgewiesen wurde (in chronologischer Reihenfolge).

Table 5.1: Year of first detection and literature sources for records of *Notiophilus quadripunctatus* Dejean, 1826 from various Central European countries where the species was newly discovered in the last two decades (sorted in chronological order).

Länder	Jahr der Erstmeldung	Literaturquellen
Deutschland, Baden-Württemberg	2001	Hemmann & Trautner 2002; Schanowski & Schiel 2004; Schanowski 2013; Oellers et al. 2022
Frankreich, Elsaß	2001	Schott 2019
Deutschland, Nordrhein-Westfalen	2011	Hannig 2015, 2016a, 2016b, 2018, 2020
Niederlande, Limburg	2012	Heijerman & Aukema 2014
Schweiz, Jura	2015	Chittaro & Marggi 2016
Deutschland, Rheinland Pfalz	2016	Kitt & Kielhorn 2017
Deutschland, Hessen	2016	Ulrich Schaffrath unveröffentlicht
Deutschland, Niedersachsen	2018	Diese Publikation
Deutschland, Saarland	2019	Lillig & Eisinger 2022
Deutschland, Schleswig-Holstein	2023	Benisch 2023
Deutschland, Sachsen-Anhalt	2023	Bleich et al. 2023

Niederlande: Die ersten gesicherten Nachweise stammen aus dem Winter 2012/13 im südlichsten Teil des Landes in der Provinz Limburg (Heijerman & Aukema, 2014), alle älteren Nachweise waren wahrscheinlich falsch bestimmt (vgl. Muilwijk & Felix, 2004). Die Art wurde inzwischen mehrfach in der Provinz Limburg nachgewiesen und breitet sich innerhalb dieser weiter nach Norden aus (Muilwijk *et al.*, 2015). Insgesamt scheint sich *N. quadripunctatus* weiter nach Norden auszubreiten, und die Art wurde in den letzten Jahren in den Provinzen Nordbrabant, Süd-Holland, Gelderland und Overrijssel nachgewiesen (Abb. 5.2).

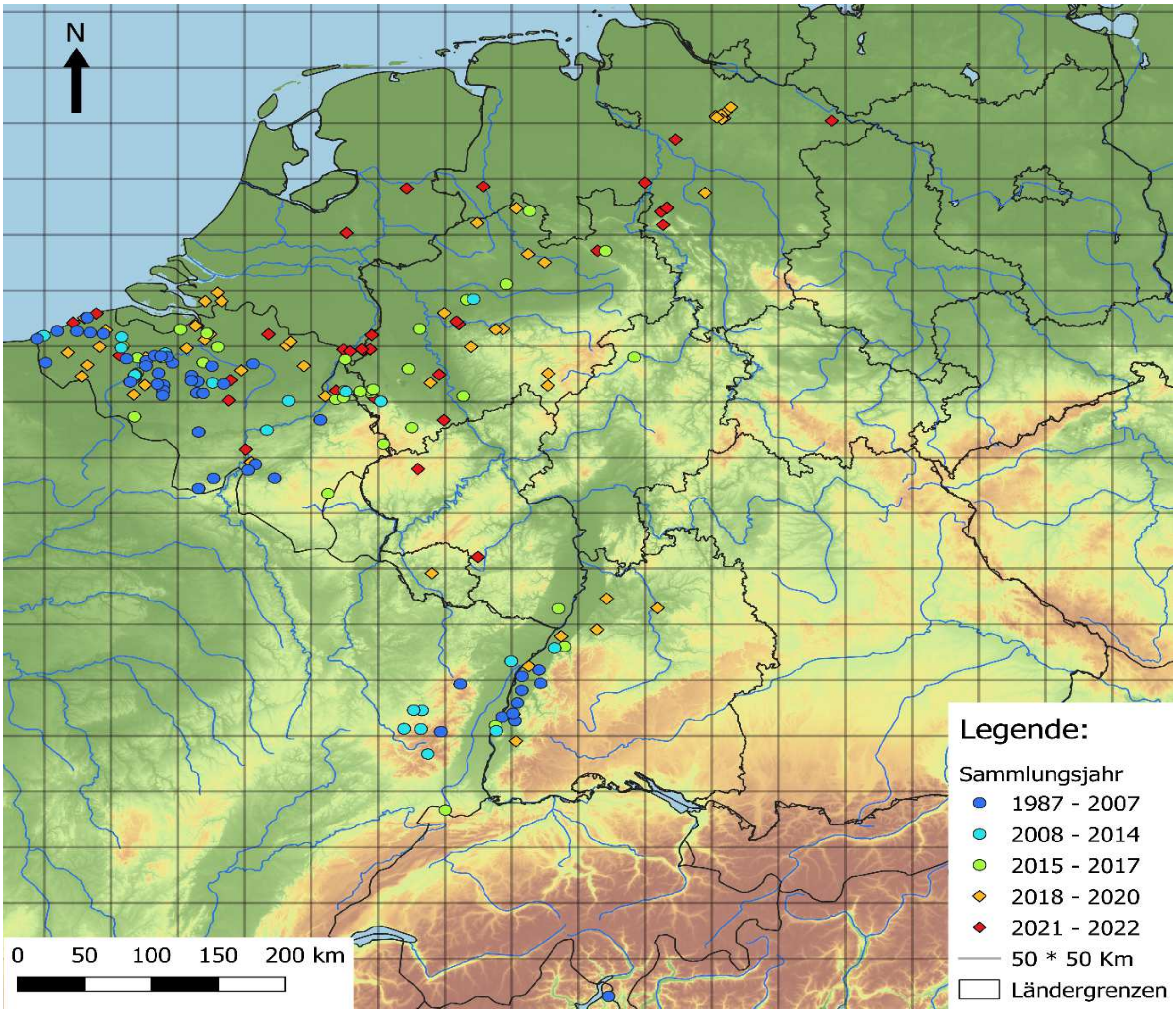

Abbildung 5.2: Aktuelle Nachweise von *Notiophilus quadripunctatus* in Mitteleuropa. Jeder Punkt entspricht mindestens einem Nachweis, der entweder in der Literatur oder in einer Online-Datenbank (Coleoweb.de, Observations.org/be, Waarneming.nl, Kerbtier.de) zu finden ist. Die Farbe zeigt das früheste Jahr eines Nachweises an dem betroffenen Ort an.

Figure 5.2: Distribution of observation of *Notiophilus quadripunctatus* in Central Europe. Each point corresponds to at least one observation found either in the literature or in an online database (Coleoweb.de, Observations.org/be, and Waarneming.nl, Kerbtier.de). The color indicates the earliest year of a detection at the location.

Frankreich, Elsass: *N. quadripunctatus* gilt als in den meisten Teilen Frankreichs vorkommend, jedoch ist die Art im nordöstlichen Teil sehr selten (Jeannel, 1941; Bonadona, 1971). Aus dem Elsass ist die Art erst seit 2001 bekannt (Schott, 2019) und seitdem an zahlreichen Orten in der Region zu finden (Abb. 5.2).

Schweiz: *N. quadripunctatus* wurde erstmals 2015 aus dem Kanton Jura gemeldet, der nahe der Grenze zum Elsass und Baden-Württemberg liegt (Chittaro & Marggi, 2016). Darüber hinaus wurde bei der Überprüfung in Sammlungen vorhandener Serien von *N. biguttatus* ein Exemplar von *N. quadripunctatus* aus dem Tessin entdeckt, das im Jahr 1987 gesammelt worden war. Dies könnte darauf hinweisen, dass die Art auch in Norditalien vorkommt. Allerdings stammen die nördlichsten italienischen Nachweise der Art aus Ligurien (Pesarini & Monzini, 2010; Casale *et al.*, 2021).

Deutschland: *N. quadripunctatus* war bis zum Jahr 2018 aus fünf Bundesländern bekannt: Baden-Württemberg, Nordrhein-Westfalen, Rheinland-Pfalz, Hessen und Saarland. Die Art wurde erstmals 2001 an verschiedenen Standorten in Baden-Württemberg nachgewiesen (Hemmann & Trautner, 2002; Fritze, 2017; Oellers *et al.*, 2022). Da der Käfer auch in Nordrhein-Westfalen zunächst 2011 bei Aachen und 2014 bei Dortmund (Hannig, 2015) sowie darüber hinaus (u. a. Westfälische Tieflandbucht (Hannig, 2016a, 2016b, 2018)) und bei Bielefeld (Hannig, 2020) nachgewiesen wurde, spricht diese Abfolge für eine Ausbreitung in nordöstlicher Richtung. Im Jahr 2016 wurde der Käfer sowohl in Rheinland-Pfalz (Kitt & Kielhorn, 2017) als auch in Hessen nachgewiesen (Nationalpark Kellerwald Edersee, 2016 Schaffrath unveröffentlicht) sowie 2019 erstmals im Saarland (Lillig & Eisinger, 2022; Abb. 5.2).

Deutschland, Niedersachsen: Seit mehreren Jahrzehnten erfolgen im NSG Lüneburger Heide intensive Studien zu Laufkäfern mit Barberfallen, die oft über mehr als eine Vegetationsperiode aufgestellt wurden (s. Schacht, 2020). Das betrifft auch Heide-Lebensräume (z.B. Boutaud *et al.*, 2022). Dabei wurde *N. quadripunctatus* erstmals im Herbst 2018 nachgewiesen und seitdem regelmäßig (Tab. 5.2). Der zurzeit östlichste Nachweis aus Niedersachsen erfolgte 2021 im Wendland (Benisch, 2023) während der nördlichste 2023 in Schleswig-Holstein nördlich von Hamburg erfolgte (Benisch, 2023). Im Jahr 2023 wurde der Käfer erstmals auch in Sachsen-Anhalt im Harz nachgewiesen (Bleich *et al.*, 2023; Abb. 5.2 und Tab. 5.1).

Tabelle 5.2: Geschlecht, Individuenzahl und Fangzeiten von *Notiophilus quadripunctatus* Dejean, 1826, gesammelt an verschiedenen Fundorten in der Lüneburger Heide. Die Koordinaten des genauen Standortes sind in coleoweb.de zu finden.

Table 5.2: Sex, number of individuals and sampling period of *Notiophilus quadripunctatus* Dejean, 1826, collected from different localities in the Lüneburg Heath. The coordinates of the exact location can be found in coleoweb.de.

Kreis, Ort	Datum	Anzahl	Leg./det.
Landkreis Harburg, Undeloh	28.x.2019 - 31.iii.2020	9 ♂ / 5 ♀	leg. und det. E. Boutaud
Landkreis Heidekreis, Bispingen	28.x.2019 - 31.iii.2020	5 ♂ / 2 ♀	leg. und det. E. Boutaud
	14.vi.2021	1 ♂	leg. und det. W. Schacht
Landkreis Heidekreis, Schneverdingen	02.x.2018 - 17.xi.2018	3 ♂	leg. und det. E. Boutaud
	02.x.2019 – 02.iv.2020	38 ♂ / 23 ♀	leg. und det. E. Boutaud
	30.ix.2020 - 12.iii.2021	5 ♂ / 2 ♀	leg. und det. E. Boutaud
	1.xi.21 – 23.ii.2022	2 ♂ / 3 ♀	leg. und det. W. Schacht

5.3.2 Phänologie und Hinterflügel-Ausbildung

Aus den Untersuchungen im NSG Lüneburger Heide zwischen 2018 und 2022 resultierten insgesamt 93 Individuen von *N. quadripunctatus*. Die weitaus meisten in den Bodenfallen gefangenen Individuen waren im Winterhalbjahr aktiv (Abb. 5.3 und Tab. 5.2), mit einem Maximum von Dezember bis März. Alle 46 (26 männliche und 20 weibliche) auf ihre Hinterflügelausbildung überprüften Individuen erwiesen sich als makropter. Unterschiede zwischen den Geschlechtern traten somit nicht auf.

5.3.3 Ausbreitung

Die Luftliniendistanz von Aachen, wo die Art 2011 erstmals nachgewiesen wurde, und der Lüneburger Heide, wo die Art erstmals 2018 auftrat, beträgt ca. 350 km. Das bedeutet rechnerisch eine Ausbreitungsgeschwindigkeit von ca. 50 km pro Jahr. Die Entfernung zwischen der Lüneburger Heide und dem Fundort im Wendland beträgt ca. 75 km. Diese Distanz wurde jedoch rechnerisch in einem Zeitraum von 3 Jahren zurückgelegt. Damit ergibt sich für diesen Abschnitt der Ausbreitung eine Geschwindigkeit von ca. 25 km pro Jahr.

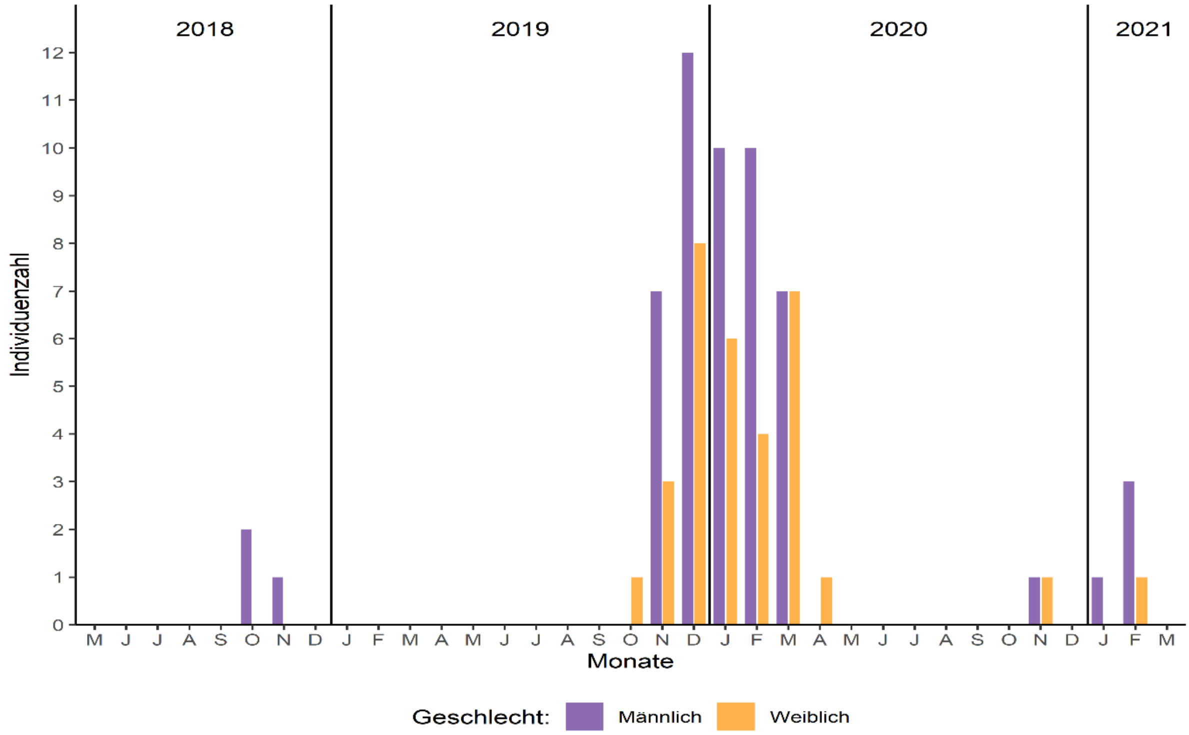

Abbildung 5.3: Phänologie von *Notiophilus quadripunctatus* in der Lüneburger Heide.

Figure 5.3: Phenology of *Notiophilus quadripunctatus* in Lüneburg Heath.

5.4. Diskussion

Im Rahmen der Untersuchungen im NSG Lüneburger Heide konnte die Ausbildung einer Population von *N. quadripunctatus* im nordöstlichen Niedersachsen sicher nachgewiesen werden. Die vorgefundene Individuenzahl bestätigt nicht nur die Ansiedlung, sondern zeigt auch, dass der Käfer in zusagenden Habitaten eine hohe Dichte erreichen kann. Von vielen Fundstellen wird dagegen nur eine begrenzte Anzahl von Exemplaren gemeldet. Die Art gilt dort als selten und in den meisten Teilen ihres Verbreitungsgebiets als nur lokal vorkommend (z.B. Luff, 1998; Muilwijk *et al.*, 2015). Als Ursache ist hier die besondere Phänologie der Art anzunehmen, die sich zumindest im nördlichen Mitteleuropa überwiegend als winteraktiv herausstellte. Aufnahmen von Käferzönosen werden vielfach in der Zeit von November bis März unterbrochen. Gerade in dieser Zeitspanne fanden wir aber das Aktivitätsmaximum. Es ist daher von einer deutlichen Unterkartierung des Käfers auszugehen.

Die Kombination der verfügbaren Informationen aus der veröffentlichten Literatur und von Citizen Scientists über Datenbanken zur Verfügung gestellten Nachweisen zeigt deutlich, dass die Art ihr Verbreitungsgebiet mit einer Geschwindigkeit von bis zu 50 km pro Jahr nach Nordosten ausgedehnt hat und vermutlich weiter ausdehnen wird.

5.4.1 Winteraktivität

Winteraktivität von anderen Laufkäfern ist bekannt, insbesondere aus den (sub-) atlantischen Heiden. Arten mit typischem Winterreproduktionstyp (s. den Boer & den Boer-Daanje, 1990) wie *Bradycellus spp.*, *Amara infima* (Duftschmidt, 1812) oder *Bembidion nigricorne* Gyllenhal, 1827 wurden zusammen mit *N. quadripunctatus* nachgewiesen. Allerdings ist noch unklar, ob sich die *Notiophilus*-Arten einem eindeutigen Reproduktionstyp zuordnen lassen (den Boer, 1986; Ernsting *et al.*, 1992). Auch von den Kanarischen Inseln wird berichtet, dass diese Käfer im Winter die Laufkäfergemeinschaften dominieren (Wallon *et al.*, 2023). Da der Großteil der hier für Mitteleuropa zusammengestellten Nachweise ebenfalls aus dem Winterhalbjahr stammt, sind wir der Meinung, dass sich die Angaben zur Fortpflanzungsrhythmik bei (1998) nicht direkt auf das nördliche Mitteleuropa übertragen lassen. Eine gezielte Suche nach *N. quadripunctatus* muss zwingend die Wintermonate einbeziehen.

5.4.2 Ausbreitung

Die ersten Abschätzungen zur Ausbreitungsgeschwindigkeit von *N. quadripunctatus* von 50 beziehungsweise 25 km/Jahr deuten auf eine relativ schnelle Nordost-Ausbreitung. Diese Geschwindigkeit übertrifft deutlich diejenigen bodengebundener brachypterer Laufkäfer (z.B. Carabus hortensis, siehe Völler *et al.*, 2018).

Viele nordwärts gerichtete Ausbreitungen bei Laufkäfern werden als Folge des Klimawandels gedeutet. Das gilt besonders für die in Großbritannien festgestellten Bewegungen der südlichen oder nördlichen Verbreitungsgrenzen von Laufkäferarten. Diese verlagerten sich um ca. 50 km in einem Zeitraum von 25 Jahren (Hickling *et al.*, 2006). Damit scheint sich *N. quadripunctatus* deutlich schneller auszubreiten.

Besonders spektakuläre Verschiebungen der nördlichen Verbreitungsgrenze von Laufkäfern in Skandinavien stellte Lindroth (1972) bereits vor 50 Jahren vor. So überwand *Stenolophus mixtus* (Herbst, 1784) in 25 Jahren eine Distanz von ungefähr 600 km. Damit handelt es sich um eine durchschnittliche Ausbreitungsgeschwindigkeit von 24 km/Jahr, die am unteren Rand des von uns für *N. quadripunctatus* ermittelten Bereiches liegt. Obwohl ein anthropogener Klimawandel zu Lindroths Zeit weniger in der öffentlichen Diskussion präsent war, postulierte dieser Carabidologe bereits die Arealverschiebungen als Folge einer Klimaerwärmung (Lindroth, 1972). Vor diesem Hintergrund lassen sich auch die Arealveränderungen von *N. quadripunctatus* als Folge des Klimawandels deuten.

Die Ausbreitung von Laufkäfern hängt bei dimorphen Arten hauptsächlich vom Vorhandensein makropterer Individuen ab (Den Boer, 1970). In Anbetracht der Tatsache, dass alle aus dem NSG Lüneburger Heide untersuchten Individuen voll entwickelte Flügel besaßen, ist es wahrscheinlich, dass die schnelle Ausbreitung von *N. quadripunctatus* in Mitteleuropa durch den Flug erfolgte. Belege für eine Ausbreitung in großen Höhen durch Wind wurden für mehrere Laufkäfer gemeldet, darunter die eng verwandte dimorphe Art *Notiophilus biguttatus*. Die Fähigkeit dieser Art, in großer Höhe zu fliegen ermöglicht eine Ausbreitung über viele Kilometer in nur wenigen Stunden (Chapman *et al.*, 2005). Obwohl eine derartige Ausbreitung bislang nicht speziell für *N. quadripunctatus* dokumentiert wurde, steht die gefundene hohe Ausbreitungsgeschwindigkeit mit einem analogen Verhalten in Einklang.

Unterstützt wird die Ausbreitung der Art auch durch die Euryökie, ist sie doch neben Heiden aus sehr unterschiedlichen Lebensräumen nachgewiesen worden wie Äckern, Ruderalflächen, Wäldern, Obstbaumanlagen und Kiesgruben (Hemmann & Trautner, 2002; Heijerman & Aukema, 2014; Muilwijk *et al.*, 2015; Fritze, 2017). Sie ist damit nicht auf selten anzutreffende Trittsteinhabitate angewiesen. Im Lebensraum Calluna-Heide scheint die Art positiv auf Heidemanagement mit Reduktion der Phytomasse, insbesondere durch Abbrennen, Mähen, Schoppern und mechanischer Entfernung der Moose (Kombination aus Plaggen und Mähen) zu reagieren: Von 42 im Jahr 2019 in der Lüneburger Heide beprobten Fangstellen konnte die Art auf 11 zwei Jahre zuvor gepflegten Flächen nachgewiesen werden. Im Folgejahr 2020 wurde die Art nur noch auf 3 dieser Flächen erhalten. Diese Abnahme ließe sich zwar auch durch natürliche Schwankungen der Populationsstärke erklären. Aufgrund der relativ großen Zahl untersuchter Flächen zeichnet sich aber eine Präferenz der Art für besonders vegetationsarme Heideflächen ab, die höhere Bodentemperaturen erreichen. Dies steht im Einklang mit einer aus dem mediterranen Verbreitungsschwerpunkt zu schließenden Thermophilie. Die Auswirkungen des Heidemanagements auf *N. quadripunctatus* und die übrige Laufkäferfauna werden an anderer Stelle ausführlicher analysiert (Boutaud et al. in Vorbereitung).

Durch gezielte Suche in Heiden und anderen Lebensräumen lässt sich überprüfen, ob und in welcher Form eine Ausbreitung von *N. quadripunctatus* erfolgt. Dazu ist es wichtig, in zeitlichen Abständen dieselben Lebensräume erneut aufzusuchen. Dadurch lässt sich zwar nur die jeweilige Existenz der Art belegen. Aussagen bezüglich Häufigkeit sind nur eingeschränkt, die Feststellung des Fehlens ist formal nicht möglich. Allerdings haben Erstnachweise und insbesondere zahlreiche reproduzierende Individuen eine größere Aussagekraft, wenn an denselben Stellen zuvor die Art nicht nachgewiesen wurde. Langzeituntersuchungen an festgelegten Orten über mehrere Dekaden, wie sie aus den Niederlanden oder von manchen anderen Fangstellen bekannt sind (z. B. Kotze *et al.*, 2011), liefern dabei die besten Belege für Veränderungen von Laufkäferfaunen.

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Article overview and authors’ contribution to articles

Thesis title: “*Contribution of semi-open areas to the long-term conservation of insects: a perspective on ground beetles (Coleoptera: Carabidae and Cicindelidae)”*

This cumulative dissertation including four articles that have either been published, submitted for publication or are close to submission for publication in international peer-reviewed journals. These articles are the result of the collaborative work of several authors.

The following table gives an overview of the contribution of all co-authors for each of the articles presented in this thesis.

Table 6.1.: Overview of the articles in this thesis, of my and co-authors contribution as well as publication status.

Chapter	II	III	IV	V
Contribution and weighting factor	predominant contribution, 1.0	predominant contribution, 1.0	equal contribution, 1.0	predominant contribution, 1.0
Publication status	Published in Biodiversity and conservation	Manuscript prepared for submission	Published in Journal of insect conservation	Under review for Angewandte Carabidologie
Specific contribution of all co-authors				
Conceptualization	TA	TA	TA	TA, **EB**
Methodology:	TA	**EB**, TA	TA, EV	**EB**, TA
Formal analysis	**EB**, DN, CD	**EB**, DN, CD	**EB**	**EB**
Visualization	**EB**	**EB**	**EB**	**EB**
Investigation	**EB**, IH, DN	**EB**, DN	EV, **EB**	**EB**, WS
Writing original draft	**EB**	**EB**	EV	**EB**
Writing - review and editing	**EB**, DN, IH, TA, CD	**EB**, DN, TA, CD	EV, TA, **EB**	**EB**, TA, WS

Authors and co-authors contribution: CD = Claudia Drees, DN = Dorothea Nolte, **EB = Estève Boutaud**, EV = Eva Völler, IH = Ingmar Harry, TA = Thorsten Assmann, WS = Wolfgang Schacht.

Declaration (according to § 16 of the guideline for cumulative dissertations)

I avouch that all information given in this appendix is true in each instance and overall.

Lüneburg, 20.01.2013

Explanatory Notes

Author status

According to § 12 and 14 of the guideline for cumulative dissertations in Sustainability Science Dr. rer. Nat. (24. Januar 2012)

- Single author = own contribution amounts to 100%.
- Co-author with predominant contribution = wn contribution is greater than the individual share of all other co-authors and is at least 35%.
- Co-author with equal contribution = (1) own contribution is as high as the share of other co-authors, (2) no other co-author has a contribution higher than the own contribution, and (3) the own contribution is at least 25%.
- Co-author with important contribution = own contribution is at least 25%, but is insufficient to qualify as single authorship, predominant or equal contribution.
- Co-author with small contribution = own contribution is less than 20%.

Weighing Factor

Single author	1.0
Co-author with predominant contribution	1.0
Co-author with equal contribution	1.0
Co-author with important contribution	0.5
Co-author with small contribution	0

List of publications

Refereed Journal Articles

2023 **E. Boutaud**, D. Walmsley, J. Daniels, W. Härdtle, and Vicky Temperton, Effect of scarification, a novel heathland management method, on ground beetles assemblages (in preparation).

E. Boutaud, D. Nolte, T. Assmann, C. Drees, Vegetation features and habitat specialisation matter for semi-open corridors and their management: a perspective on ground beetles (Coleptera Carabidae and Cicindelidae) (to be submitted).

E. Boutaud, W. Schacht, T. Assmann, Notiophilus quadripunctatus Dejean, 1826: Ausbreitung im nördlichen Mitteleuropa. *Angewandte Carabidologie* (under review).

2022 **E. Boutaud**, D. Nolte, I Harry, T. Assmann, C. Drees, Conservation value of semi-open habitats for ground beetles (Coleoptera: Carabidae, Cicindelidae) in Central Europe. *Biodivers. Conserv*. **31**, 1469-1489.

2021 S. Grabener, **E. Boutaud**, S. Hein, F. Luck, C. Schmid-Egger, T. Scholz, K. Ullrich, P. Zumstein, T. Assmann, W. Härdtle, C. Drees, Möglichkeiten der Optimierung von Blühstreifen zum Insektenarten-Schutz in Agrarlandschaften-eine Fallstudie aus dem Nordwestdeutschen Tiefland. *Natur und Landschaft.* ***12***, 561-569.

T. Assmann, **E. Boutaud**, J. Buse, C. Drees, A.-L.-L. Friedman, I. Harry, E. Orbach, I. Renan, C. Schmidt, K. Schmidt, D. W. Wrase, P. Zumstein, The ground beetle tribe Platynini Bonelli, 1810 (Coleoptera: Carabidae) in the southern Levant: dichotomous and interactive identification keys, ecological traits and distribution. *Zookeys.* ***1044***, 449-478.

T. Assmann, **E. Boutaud**, J. Buse, C. Drees, A.-L.-L. Friedman, A. Hetzel, E. Orbach, I. Renan, C. Reuter, D.W. Wrase, The Caterpillar Hunting Beetles (Coleoptera: Carabidae: Calosoma Weber, 1801) in the southern Levant. *Isr. J. Entomol.* ***50***, 133-158.

2020 M. Hülsmann, **E. Boutaud**, J. Buse, K. Frank, A. Schuldt, T. Assmann, Habitat continuity matters: Ancient woodlands tend to have higher biomass and catching rate of dung beetles, mainly driven by one large species. *Acta Oecologica*. **102**, 103501.

2019 K. Homburg, C. Drees, **E. Boutaud**, D. Nolte, W. Schuett, P. Zumstein, E. von Ruschkowski, T. Assmann, Where have all the beetles gone? Long-term study reveals carabid species decline in a nature reserve in Northern Germany. *Insect Conserv. Divers.* **12**, 268–277.

D. Nolte, **E. Boutaud**, D. J. Kotze, A. Schuldt, T. Assmann, Habitat specialization, distribution range size and body size drive extinction risk in carabid beetles. *Biodivers. Conserv.* **28**, 1267–1283.

M. Hülsmann, **E. Boutaud**, J. Buse, A. Schuldt, T. Assmann, Land-use legacy and tree age in continuous woodlands: weak effects on overall ground beetle assemblages, but strong effects on two threatened species. *J. Insect Conserv.* **23**, 623–633.

2018 T. Assmann, **E. Boutaud**, J. Buse, J. Gebert, C. Drees, A.-L.-L. Friedman, F. Khoury, T. Marcus, E. Orbach, I. Renan, C. Schmidt, P. Zumstein, The tiger beetles (Coleoptera, Cicindelidae) of the southern Levant and adjacent territories: from cybertaxonomy to conservation biology. *Zookeys*. **734**, 43–103.

E. Völler, **E. Boutaud**, T. Assmann, The pace of range expansion: a long-term study on the flightless ground beetle Carabus hortensis (Coleoptera: Carabidae). *J. Insect Conserv.* **22**, 163–169.

2017 T. Assmann, **E. Boutaud**, C. Drees, T. Marcus, D. Nolte, W. Starke, H. Terlutter, E. Völler, P. Zumstein, Two new Lebistina Motschulsky, 1864 species from Kenya and Tanzania (Coleoptera, Carabidae, Lebiini). *African Invertebr.* **58**, 9–21.

2015 T. Assmann, K. Austin, **E. Boutaud**, J. Buse, V. Chikatunov, C. Drees, R. F. F. L. Felix, A. L. L. Friedman, F. Khoury, T. Marcus, I. Renan, C. Schmidt, D. W. Wrase, The ground beetle supertribe zuphiitae in the southern levant: (Coleoptera, carabidae). *Spixiana*. **38**, 237–262.

T. Assmann, **E. Boutaud**, J. Buse, V. Chikatunov, C. Drees, A. L. L. Friedman, W. Härdtle, K. Homburg, T. Marcus, I. Renan, D. W. Wrase, The ground beetle tribe Cyclosomini s.l. in Israel (Coleoptera, Carabidae). *Spixiana*. **38**, 49–69.

2013 J. Fleury, C. Bouget, **E. Boutaud**, M. Binon, Nouvelle contribution à la connaissance de l'entomofaune du domaine des Barres (Nogent-sur-Vernisson, Loiret) (Coleoptera). *L'Entomologiste*. **69**, 329–344.

Books

2016 T. Assmann, **E. Boutaud**, P. Finck, W. Härdtle, D. Matthies, D. Nolte, G. von Oheimb, U. Riecken, E. Travers, K. Ullrich, Halboffene Verbundkorridore: ökologische Funktion, Leitbilder und Praxis-Leitfaden. *Naturschutz und Biol. Vielfalt*, 296 pp.

Conferences participation

Papers Presented

2022 Effect of traditional lowland heathland management methods – mowing, burning, and choppering – on ground beetles assemblages. 17th European Heathland Workshop.

Effect of a novel heathland management method, scarification, on ground beetles assemblages. 17th European Heathland Workshop.

Effect of a novel heathland management method, scarification, on ground beetles assemblages. 20th European Carabidologist Meeting.

Biomass and body length in a changing world: can climate change be blamed for insect decline in ground beetles? 20th European Carabidologist Meeting.

2020 Effect of a novel heathland management method, scarification, on ground beetles assemblages. 23. Jahrestagung der GAC.

2019 Life-history traits matter for dispersal into semi-open habitat corridors. 19th European Carabidologist Meeting.

2018 Unravelling the Gordian knot of conflicting habitat corridors: Semi-open habitats and their benefits for habitat connectivity. 21st European Congress of Entomology.

Geringe Auswirkungen der ehemaligen Landnutzung und des Baumalters auf die Laufkäferpopulationen in einem großen Waldgebiet. 21. Jahrestagung der GAC.

2017 Modelling ground beetle dispersal into semi-open habitat: dispersal functions and implication for conservation. 18th European Carabidologists Meeting.

Modelling ground beetle dispersal into semi-open habitat: dispersal functions and implication for conservation. 20. Jahrestagung der GAC.

2016 Cutting the Gordian knot of conflicting habitat corridors: Semi-open habitats and their benefits for habitat connectivity. 4th International Symposium of Carabidology.

2015 Pushing connectivity in landscapes: species-specific life history traits and locomotory behaviour as tools to design semi-open corridors. 17th European Carabidologists Meeting.

Dispersal of stenotopic forest ground beetles through semi-open corridors. 19. Jahrestagung der GAC.

2013 Excessive gene flow despite differences in male genitalia: A contribution to the lock and key hypothesis in Carabidae. 16th European Carabidologists Meeting.

2012 Excessive gene flow despite differences in male genitalia: A contribution to the lock and key hypothesis in Carabidae. 42nd Annual Meeting of the Ecological Society of Germany.

Estève Boutaud

Hiermit erkläre ich, dass ich mich noch keiner Doktorprüfung unterzogen oder mich um Zulassung zu einer solchen beworben habe.

Ich versichere, dass die Dissertation mit dem Titel „*Contribution of semi-open areas to the long-term conservation of insects: a perspective on ground beetles (Coleoptera: Carabidae and Cicindelidae)*" noch keiner Fachvertreterin bzw. Fachvertreter vorgelegen hat, ich die Dissertation nur in diesem und keinem anderen Promotionsverfahren eingereicht habe und, dass diesem Promotionsverfahren keine endgültig gescheiterten Promotionsverfahren vorausgegangen sind.

Ich versichere, dass ich die eingereichte Dissertation „*Contribution of semi-open areas to the long-term conservation of insects: a perspective on ground beetles (Coleoptera: Carabidae and Cicindelidae)*" selbstständig und ohne unerlaubte Hilfsmittel verfasst habe. Anderer als der von mir angegebenen Hilfsmittel und Schriften habe ich mich nicht bedient. Alle wörtlich oder sinngemäß anderen Schriften entnommenen Stellen habe ich kenntlich gemacht.

Lüneburg, 20.01.2023

Estève Boutaud