Contrasting effects of land-use intensification on carabid beetles occurring in insular (semi-)natural habitats within arable fields

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Abstract

The increase of agricultural fields leads to habitat loss and fragmentation of (semi-)natural habitats (SNHs) that provide refuge sites for a variety of taxa. Carabid beetles are reliable biodiversity indicators and provide important ecosystem services in agricultural landscapes. However, it still remains unclear how carabid beetles inhabiting SNHs respond to increasing arable field cover as a measure of land-use intensification. We predict that the relationship between arable field cover and carabid beetle abundance and species richness is specific to habitat type and species ecology. We tested our predictions in an intensively used agricultural landscape in northeast Germany and sampled carabid beetles at two different insular SNHs within arable fields: grassland patches of wind turbines (novel SNH) and kettle holes (natural SNH). Our multi-spatial-scale analyses revealed that with increasing arable field cover the proportion of arable species increases for both SNH types. However, we found contrasting relationships in species richness and abundance between the SNHs. At the grassland patches around wind turbines, arable field cover negatively affected arable species´ richness and abundance as well as non-arable species´ richness. In contrast, at kettle holes, arable species richness and abundance increased with arable field cover, while non-arable species were not affected. In summary, our study demonstrates that the effect of land-use intensification on carabid beetles is highly dependent on the specific habitat type and species ecology. Our findings highlight the importance of habitat type for managing SNHs within agricultural landscapes while improving our understanding of how land-use intensification affects carabid beetle diversity.

1. Introduction

Agricultural land-use intensification has dramatically increased in the past decades (Tscharntke et al. 2005; Matson et al. 1997). The current management regime of agricultural fields, including the application of pesticides and herbicides, monocultural cultivations and strong disturbances by ploughing, offers only a low habitat quality for many plants and animal taxa (Geiger et al. 2010; Stoate et al. 2001). Especially, land-use intensification in terms of increased arable field cover has led to severe losses of (semi-)natural habitats (SNHs) (Emmerson et al. 2016). As a result, the few remining SNHs, such as hedgerows, ditches, field margins or ponds, play an outstanding role as refuge habitats to maintain biodiversity in agricultural landscapes (Tscharntke et al. 2005; Holland et al. 2009; Schweiger et al. 2005). Previous studies have shown that increasing arable field cover has a negative effect on multiple taxa, highlighting negative consequences of land-use intensification on biodiversity (Gossner et al. 2016; Benton et al. 2002; Sala et al. 2000). However, responses of carabid beetles to land-use intensification still remain ambiguous (Hanson et al. 2016; Winqvist et al. 2014; Caballero-López et al. 2012).

Carabid beetles occur in high abundances in agricultural landscapes (Rusch et al. 2013; Saska et al. 2007; Holland 2002) providing a variety of ecosystem services such as pest control (Kromp 1999) and being able to act as nutrient cycling agents (Gkisakis et al. 2016). Hence, land-use induced changes in carabid beetle abundance and diversity could affect whole food webs and ultimately yield outcomes in agricultural landscapes (Zalewski et al. 2016; Helenius 1990). Previous studies showed that carabid

abundance and diversity in SNHs may show diverse responses to arable field cover (Woodcock et al. 2010; Mayr et al. 2007; Medeiros et al. 2018; Ribera et al. 2001), presumably because species differ in their ecological strategies (Winqvist et al. 2014; Vries et al. 1996; Niemelä et al. 1988). Species that avoid arable fields (henceforth non-arable species) should be negatively affected by land-use intensification, because a higher proportion of arable fields increases isolation of SNH patches within the arable field matrix. As a result, non-arable species should have difficulties to (re-)colonize isolated SNHs in agricultural fields (Hanson et al. 2016; Elek et al. 2014; Rusch et al. 2013; Vries 1996) . In contrast, species that use arable fields at least partly during their life cycle (e.g. foraging, during hibernation, resting; henceforth arable species) should be positively affected by land-use intensification, as they may benefit from adjacent arable fields to their refuge habitats. Further, arable species should be less dispersal-limited than non-arable species in agricultural landscapes, due to their use of agricultural fields as suitable habitats (Hanson et al. 2016; Ribera et al. 2001).

Carabid responses to land-use intensification may further change with the respective refuge habitat. Agricultural landscapes may contain a variety of refuge habitats spanning from near-natural, like kettle holes (Platen et al. 2016), forest patches (Fournier and Loreau 2001) to novel, anthropogenic habitats, like grasslands around wind turbines (Pustkowiak et al. 2018). Since particular properties differ between habitats, like habitat age, habitat complexity and disturbance intensity, habitats may harbor on the one hand different carabid species (Hoffmann et al. 2021; da Silva et al. 2008; Fairchild et al. 2000), but may also modulate the impact of land-use intensification on carabids in the respective habitats. For instance, dispersal limitation of non-arable species may be particularly strong in novel habitats, since species had less time to colonize new patches. Further, newly-established habitats may have a lower habitat quality and thus their functioning as a refuge habitat is limited (Ranjha and Irmler 2013; Frank and Reichhart 2004). As a result, the negative impact of land-use intensification on carabids might be more pronounced in novel habitats.

Our study aims to reveal how carabid beetle abundance and species richness respond to agricultural intensification depending on habitat type and species ecology (arable vs. non-arable species). We compare two fundamentally different insular SNHs in arable fields: kettle holes and grasslands around wind turbines. Kettle holes (also called potholes) are small water bodies (< 1 ha) which have been formed over thousands of years and therefore represent “natural” isolated habitats (Nilsson 1984) found across the whole northern-hemisphere. They are known to be potential hotspots of biodiversity in monotonous arable fields (Platen et al. 2016; Lozada-Gobilard et al. 2019; Boix et al. 2012). In contrast, grasslands on the fundament of wind turbines are man-made structures that are regularly mowed to prevent shrub encroachment. Thus, grassland around wind turbines represent “novel” habitats (Hobbs et al. 2009) with high disturbance intensity. Both kettle holes and grassland around wind turbines can act as refuge habitats, yet, the role of latter for biodiversity, and in particular for carabid beetles, in agricultural landscape remains largely unknown. Due to different habitat properties, we expect that carabid responses to land-use intensification differ between both habitat types. We sampled carabid beetles with pitfall traps in 20 kettle holes and 25 grasslands around wind turbines in an intensively-used agricultural landscape in NE Germany. We distinguished between arable and non-arable species, in order to analyze

how species richness, abundance and proportion of both groups respond to arable field cover around the habitats. Since the effect of landscape parameters on a biological response variable may strongly depend on the spatial scale (Huais 2018; Jackson and Fahrig 2015; Wheatley and Johnson 2009; Graf et al. 2005), we evaluate the effect of land-use intensification on carabid beetle communities across multiple radii (20 – 2000 m).

Specifically, we predict that land use intensification (arable field cover):

i) has a positive effect on arable species irrespective of the habitat, i.e. the proportion of arable to non-arable species as well as arable species richness and abundance increases.

ii) has a negative effect on non-arable species. Especially, in novel habitats (grassland around wind turbines), non-arable species respond stronger to increased arable field cover than non-arable species in natural habitats (kettle holes).

2. Methods

2.1 Study area

Our study was conducted in the “AgroScapeLab Quillow” (www.bbib.org/experimental-platform.html), an agricultural landscape laboratory in the Uckermark (North-eastern Germany; Figure 1). The landscape of Northeast Germany has been shaped by the repeated glaciation during the Pleistocene, resulting in the development of numerous wetlands and small water bodies (40 per km^2), called kettle holes (<1 ha area each) (Kalettka and Rudat 2006). Kettle holes are characterized by a high structural and biological diversity and provide habitats for many diverse species (Platen et al. 2016) being protected by law since 2009 (Bundesnaturschutzgesetz 2009). Besides those water bodies, the landscape is characterized by a high proportion of intensive agricultural land use. 65 % of the landscape is covered by crop fields with maize (*Zea mays L.*), wheat (*Triticum aestivum L.*), and oil-seed rape (*Brassica napus L.*) as the main crops. Forests and grasslands contribute only to a small proportion of the Uckermark (BfN 2012), covering 17 % and 9 % respectively of the catchment area. A modern dominant structure shaping the landscape are the 3900 wind parks which are distributed throughout Brandenburg, Germany (Deutsche Presse-Agentur 2020). In the study area, four wind parks are present with a total of 76 wind turbines.

2.2 Study system

Within the “AgroScapeLab Quillow” landscape we selected 20 kettle holes situated within arable fields ranging in sizes from 0.06 – 0.78 ha (Figure 1). As kettle holes may undergo wet-dry cycles from water marshy outflows to full dry ups, all chosen kettle holes were mostly temporarily flooded. Those partly strong fluctuations in water level may occur in inter- or intra-yearly cycles (Kalettka and Rudat 2006). Moreover, the kettle holes were selected according to similar terrestrial plant community along the water edge without any shrub or tree layer.

The 25 wind turbines selected for this study are from three different wind parks (A, B, C) located within arable fields (Figure 1). The wind turbines are surrounded by a foundation covered with compacted backfill (Currie et al. 2013), a layer of soil and sown with a mixture of grasses, and therefore referred here as grassland patches. The wind turbines in wind park A, which started operating in 2017 (most recent wind park), are surrounded by circular bases being at level with the surrounding area. The wind turbines and grassland patches in wind park B are shaped as square and elevated by about 1.5 – 3.0 m compared to the surrounding landscape. These wind turbines were constructed between 1999 and 2004. The wind turbines in wind park C started operating in 2000 and are surrounded by slightly elevated (30 – 90 cm) circular grassland patches. To keep the wind turbines accessible and free from woody vegetation the green bases are mowed once or twice a year. Furthermore, depending on the sown plant species, age of the structure, construction type, maintenance, and the surroundings, a variety of plant species can be found in those bases. Hence, the vegetation of the grassland patches differs between the wind parks. The grassland patches of wind park A were sown with a mixture of grasses including 45 % of *Festuca brevipila*, 40 % of *Festuca rubra*, and 15 % of *Lolium perenne*. However, many more species are found on the grassland patches of wind park A, which favor open ruderal and mesotrophic conditions. On the grassland patches of wind park B and C common grass species were sown (*Lolium perenne, Dactylis glomerata, Festuca rubra*). The species composition indicated a tendency to dry, ruderal and mesotrophic conditions.

2.3 Carabid sampling

The carabid beetles (*Carabidae*) were captured with pitfall traps designed after Barber (1931). The pitfalls (honey jar with 7.5 cm in diameter) were buried 10 cm in the ground, so that the rim was at the level of the surrounding ground. A saturated saline solution was used as killing and preserving fluid consisting of 300 g NaCl per 1 l water. A drop of dish soap was also added to break the water surface tension. The traps were sheltered from the top with a wire mesh (hole size 3.5 cm), preventing small mammals and amphibians to fall in.

At each kettle hole, five traps were arranged in a transect from the field border to the water body (Figure 2A) to cover the heterogeneity of the kettle holes. At each wind turbine, five traps were buried in the grassland patch arranged in five fixed radii from the wind turbine but randomized in position (Figure 2B). The first one was placed exactly at the field border. The other four were placed in the grassland patch at diminishing distances to the wind turbine. For wind park A, one trap was buried in the gravel ring directly around the wind turbine.

Carabid beetles were caught twice within the vegetation period for 14-day periods, in the time period from 10.05.2019 to 26.05.2019 and from 21.06.2019 to 07.07.2019. The catching periods were split into two points in time to cover a higher range of carabid species due to their differing life cycles. At the end of both catching periods, the contents of the traps were carried to the laboratory and transferred into a solution with 70 % ethanol. Identification of specimens was performed based on Freude et al. (2012). The carabid beetles were further classified into two para-taxonomic groups based on their habitat type

preference in the Northeast plain region of Germany (Gesellschaft für Angewandte Carabidologie e.V. 2021). Latter classification system includes the habitat preference of nine different habitat types such as largely open cultural landscape, dry biotopes that are open or poor in larger woody areas, forest biotopes, swamps, moors and wetlands for all carabid species of Germany. In this study, carabid species were grouped into arable and non-arable species. Species were classified as arable species, if open cultural landscape (including arable fields) were listed as a main habitat type for the species occurrence. Non-arable species refer to species for which open cultural landscapes are not listed as main habitat type. In our study, the non-arable species are found across a variety of habitat types, in particular wetland habitats in kettle holes and dryer habitats at wind turbines (Balthasar 2020; Wedekind 2020).

2.4 Landscape parameters

The surrounding landscape around the kettle holes and wind turbines under investigation was determined to analyze the influence of the arable field cover on carabid beetles. Arable field cover was determined using the percentage of the biotope class “arable fields” within the “Biotopkartierung Brandenburg – Liste der Biotoptypen” (Landesamt für Umwelt, Gesundheit und Verbraucherschutz 2011). Since the scale at which a landscape parameter is determined may have an influence on the outcome (Wheatley and Johnson 2009; Jackson and Fahrig 2015), we estimated arable field cover in percentage for different radii (20 m – 2000 m with 20 m steps) around each sampling sites.

2.5 Statistical analysis

All statistical analyses and graphs were created with R (R Core Team 2021) version 4.1.0 in RStudio 1.4.1717. We included only carabid beetle samples from traps that were not scavenged from wild animals or destroyed by heavy rains leaving a total of 382 traps (217 pitfalls in wind parks and 165 in kettle holes) from 45 sampling sites and two catching periods. For each sampling site the corresponding five traps were pooled together to calculate carabid beetle species richness and abundance (number of individuals) for each catching period.

We fitted Linear Mixed effects Models (LMER, function lmer, R-package lme4, Bates et al. 2015) to determine the effect of arable field cover on carabid beetle abundance, species richness, and proportion of arable to non-arable species. Carabid beetle abundance and richness were both determined for arable species, non-arable species and all species. Furthermore, for each response variable separate models were performed for kettle holes and wind turbines.

We included *agricultural land cover [%]* and *catching period* as fixed effects. For some sampling sites less than five traps were included in the analysis (see above). Thus, the *number of traps* per sampling site were also included as fixed effects. For the models of wind turbines, we included additionally *wind park* (A, B, C) as fixed effect, due to the clumped spatial distribution of wind turbines in the study region. Sampling site ID (for each kettle hole and wind turbine) was included as random effect to account for repetitively sampling within the same kettle hole or wind turbine in two catching periods.

The response variables carabid species richness and abundance were log-transformed prior analyses. The response variables were z-scaled to make effect sizes comparable (Schielzeth 2010). Furthermore, model assumptions (homoscedasticity, normality of residuals, spatial autocorrelation) were checked with the DHARMa package (Hartig 2021). The collinearity between explanatory variables was checked by analyzing the variance-inflation factors (VIF). However, no explanatory variable exceeded a threshold of 3 (Zuur 2009) and thus, no variable was removed. We tested the effect of arable field cover on the response variables for different spatial scales (20 m – 2000 m) using the multifit function (Huais 2018). The model with the lowest AIC (Akaike 1974) and strongest effect was selected for further investigating the effects of the explanatory effects on the response variable. We also determined whether the estimated model coefficient of arable field cover for each spatial scale was statistically significant ($p < 0.05$).

3. Results

A total of 101 carabid beetle species and 9179 carabid beetle individuals were caught. 79 carabid beetle species (3604 individuals) were caught in kettle holes, of which 23 were arable beetle species (816 individuals) and 56 were non-arable beetle species (2788 individuals). Around wind turbines 52 carabid beetle species (5575 individuals) were caught of 28 which were arable beetle species (2411 individuals) and 24 were non-arable beetle species (3164 individuals). The multi-scale analysis showed that arable field cover had similar effects on the proportion of arable to non-arable species as well as on the abundance and species richness of carabid beetle species from 400 m to 2000 m. The strongest effect between arable field cover and the abundance as well as species richness was also always measured between 400 m and 2000 m (Figure 3).

The proportion of arable species was significantly positively influenced by an increase in arable field cover in both kettle holes and around wind turbines (Figure 3C) which is in line with our first Hypothesis. Yet only in kettle holes the abundance and species richness of arable carabid beetle species was positively affected by an increase in arable field cover (Figure 3 & Figure 4). However, around wind turbines, an increase in arable field cover had a significantly negative effect on arable species abundance and no significant effect of arable species richness (Figure 4).

We predict that arable field cover had a negative effect on non-arable species, particularly in grasslands around wind turines (Hypothesis ii). Indeed, on grassland patches around wind turbines non-arable species were significantly negatively affected by an increase of arable field cover. In contrast to this, no significant effect was found by an increase in arable field cover for non-arable species in kettle holes (Figure 3).

In summary, we found stronger differences of the arable field cover effect between both habitat types than between arable and non-arable species. Hereby, the total species richness and abundance showed similar responses within the two ecological groups (Figure 4).

Interestingly, although the three wind parks (A, B, C) had different ages, no differences in carabid beetle richness and proportion of arable species were revealed between the wind parks (Figure 4). However, wind

park A (newest) showed a higher beetle abundance than wind park B and C (older).

4. Discussion

The main objective of this study was to assess how carabid beetles in two different habitats – kettle holes and grassland patches around wind turbines – respond to an increase in arable field cover as a measure of land-use intensification.

In line with our expectations (Hypothesis i), our analyses revealed that an increase in surrounding arable field cover resulted in an increase in the proportion of arable carabid beetle species in both studied habitats. This is consistent with previous findings, observing a change in the trait composition of carabid beetle communities in response to agricultural intensification (Hanson et al. 2016; Birkhofer et al. 2014; Rusch et al. 2013; Caballero-López et al. 2012) . The emerging carabid beetles in arable fields are found to be linked by diet, dispersal and body size (Winqvist et al. 2014; Hendrickx et al. 2009; Schweiger et al. 2005; Tscharntke et al. 2005) . They are generally eurytopic, have high dispersal abilities, are of medium to smaller size (Ribera et al. 2001), and are polyphagous (Holland 2002). An increase in arable field cover is thus more beneficial for such carabid beetle species, utilizing resources and nesting habitats within arable fields, compared to non-arable beetle species avoiding arable fields.

However, while arable species richness and abundance increased with arable field cover in kettle holes confirming hypothesis i, at wind turbines arable species abundance was negatively affected by arable field cover. SNH have been demonstrated to have positive effects on carabid diversity and abundance, also for arable species inhabiting agroecosystems (Della Rocca et al. 2021; Duflot et al. 2016; Hof and Bright 2010; Mayr et al. 2007; MacLeod et al. 2004; Varchola and Dunn 2001) as many beetle species use them for shelter, breeding or dispersal (Holland and Luff 2000) . Since temperate carabid beetles are very sensitive to dehydration (Andersen et al. 1986), kettle holes might serve as essential retreat options for carabid beetles that are frequently found in arable fields, especially during dry seasons. Kettle holes offer higher shelter which are less disturbed and feature a large gradient of soil moisture conditions compared to the more homogenized and disturbed grassland patches around wind turbines. Hence, kettle holes may be particular good refuge habitats for arable species and could attract arable species in an otherwise homogenous land-use intensified landscape. Similar observations, i.e. positive relationship of arable field cover on abundance and species richness, were made for hoverflies in agricultural landscapes as a result of resource concentration (Bergholz et al. 2021; Aguilera et al. 2020; Meyer et al. 2009). In contrast, grasslands around wind turbines might have a poorer habitat quality and hence the increase in arable field cover implies a reduction in the area of other potential SNH. Thus, the different responses of arable beetle species may arise from a higher habitat quality of kettle holes compared to grasslands of wind turbines.

For non-arable beetle species abundance and species richness were negatively affected by arable field cover around wind turbines. Whereas at kettle holes their abundance and species richness were not significantly affected at any spatial scale by an increase in arable field cover. Thus, these findings only

partially support our hypothesis ii, which states that in both habitats non-arable beetle species are negatively influenced by an increase in arable field cover. Yet this observation meets our prediction that in grassland patches around wind turbines non-arable carabid beetles reacted stronger to arable land cover than in kettle holes. Kettle holes were formed over thousands of years and were colonized since then by species adapted to the specific environmental conditions of kettle holes (Platen et al. 2016). Despite, many of these species being capable of flight and proficient at colonizing new sites, they seem to rather stay in their environment than migrate through unsuitable land to find new habitats, as a potential consequence of reproduction-dispersal trade off (Desender 2000). This results into distinct carabid beetle communities at kettle holes even if the kettle holes were in close proximity (Platen et al. 2016; Desender 2000). Similarly, macropterous ground beetles in isolated roadside strips chose to reproduce rather than emigrate by flight which is highly energy costly, forming highly isolated communities (Geipel and Kegel 1989). Such isolated and adapted carabid beetle populations might therefore not be strongly influenced by the surrounding non-suitable arable fields. Wind turbines, on the other hand, represent “novel” anthropogenic habitats (< 20 years). Hence, non-arable species had much less time to colonize wind turbine patches compared to kettle holes. Therefore, the community structure of non-arable species at wind turbines should be shaped by the dispersal ability of species which depends on multiples factors, including the availability of suitable habitats and the survival availability during dispersal (Kotze et al. 2000). Carabid species associated with grassland habitats are often vulnerable to high perturbations and therefore particularly avoid arable fields (Kotze and O'Hara 2003; Vries 1996). In this way, high arable field cover increases the isolation of wind turbines as well as the dispersal barrier leading subsequently to the observed negative effect of land-use intensification on non-arable species.

The role of wind turbines for biodiversity in agricultural landscapes is not yet clear. Many studies have investigated the negative effects of wind turbines on avian species such as bats, birds and even flying insects (Voigt 2021; Grünkorn et al. 2017; Erickson et al. 2001). However, the impacts of grassland patches around wind turbines on ground-dwelling beetles in agricultural landscapes are poorly studied. Dudek et al. (2015) have shown that wind turbines offer overwintering sites for lady beetles, enhancing their survival rates, and Pustkowiak et al. (2018) are claiming that local pollinating insects are positively affected. Still, carabid beetle communities around wind turbines seemed to be more influenced by agricultural intensification than carabid beetles at kettle holes.

We showed that grasslands around wind turbines are dominated by arable carabid beetle species, especially as arable field cover increases, but we also observed species associated with forests and grasslands. We assume that the community structure of carabid beetle species is very much determined by dispersal limitation of non-arable species. However, with increasing habitat age and/or in less intensified agricultural landscapes, dispersal limitation may get less important leading to communities that resembles more those to grasslands than arable fields. Therefore, we see a strong need for studies that investigate wind turbines in different landscape contexts and with different habitat ages, to assess the role of grasslands at wind turbines for maintaining biodiversity and ecosystem functioning of ground-dwelling beetles in agricultural landscapes.

We conclude that the effects of agricultural intensification on ground-dwelling beetles are strongly influenced by the habitats they inhabit. For our study, we chose two insular habitats in an agricultural landscape that span a large gradient from a near-natural undisturbed to a novel and highly disturbed habitat. However, we are confident that differences in the environmental conditions in other refuge habitats, like hedgerows, ditches or forest patches, also influence the outcome of land-use intensification effects on carabid communities. Therefore, our study highlights the need to consider the particular habitat properties to resolve contrasting responses of ground-dwelling beetles to land-use intensification.

Declarations

Author Contributions

Material preparation and data collection were performed by Cathrina Balthasar and Lorenz Wedekind during their Master thesis. Data manipulation and analysis were performed by Thibault Fronville and Kolja Bergholz. The first draft of the manuscript was written by Thibault Fronville and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Declaration of Competing Interest

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

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Figures

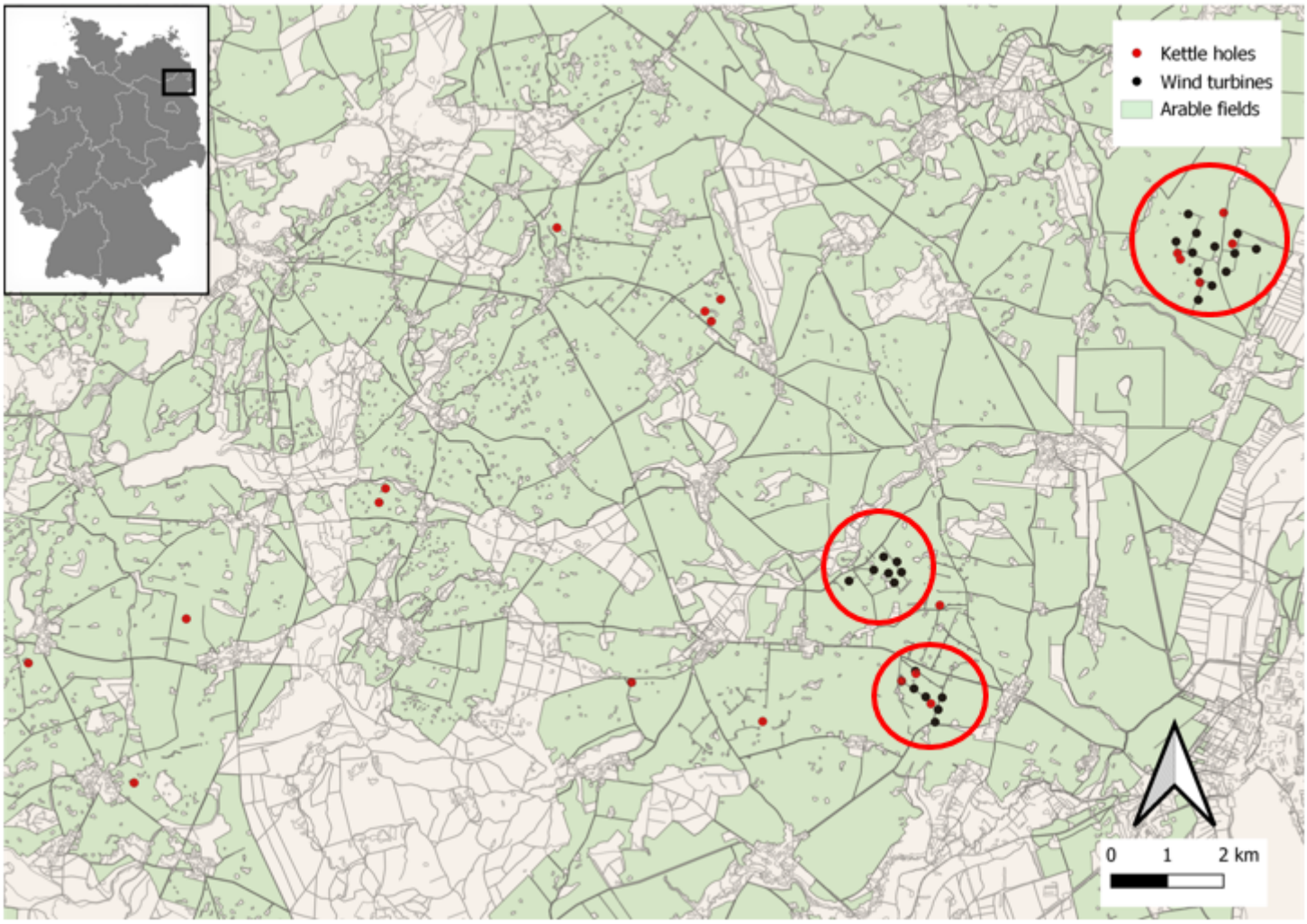

Figure 1

Spatial map showing the location of the study area 'AgroScapeLab Quillow' (Brandenburg, Germany) as well as the pitfall trap locations in the kettle holes (red) and around wind turbines (black). The red circles indicate the locations of the three wind parks. The green area represents the agricultural land cover.

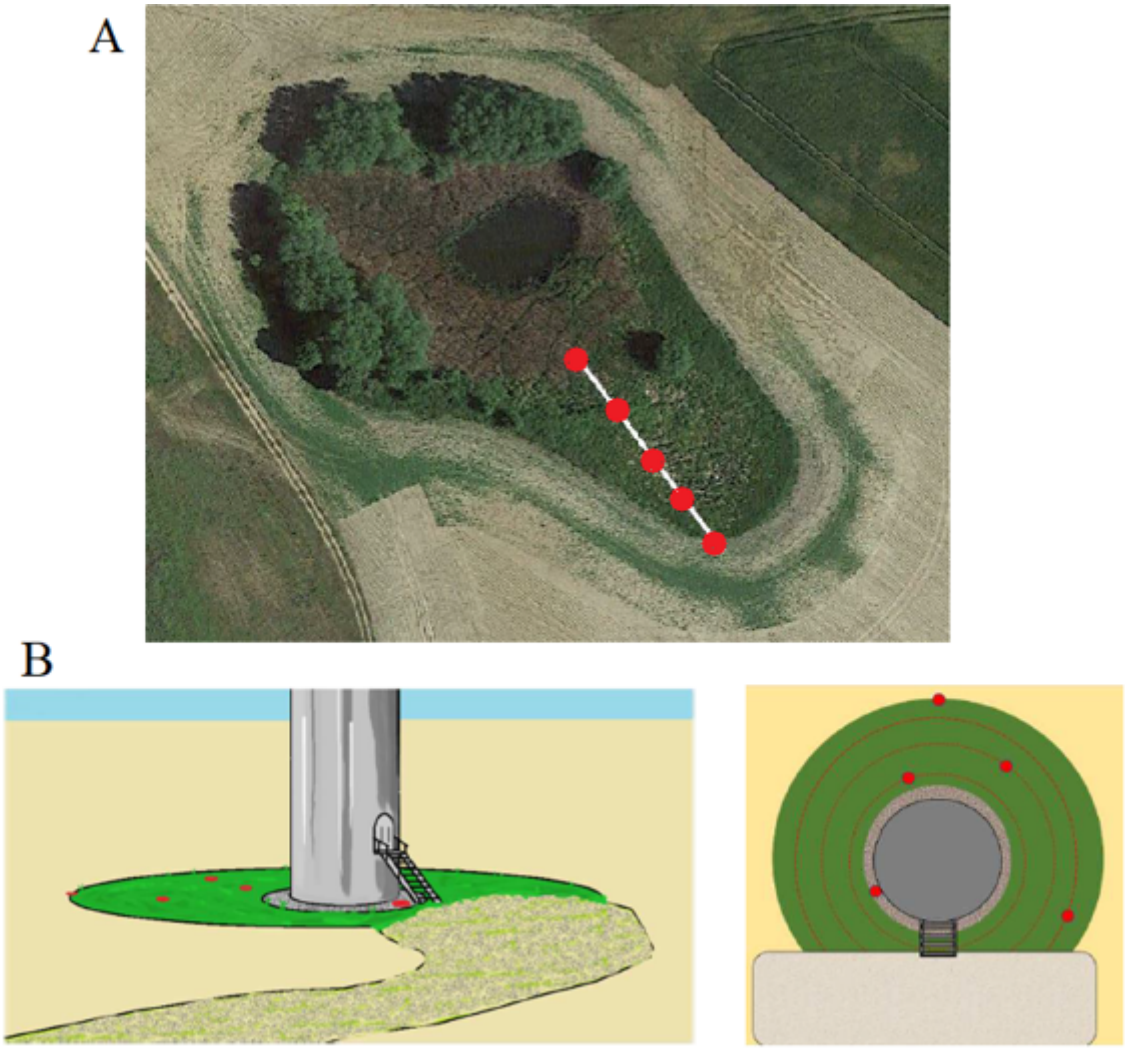

Figure 2

Graphical representation of the studied habitats how the traps were placed in both kettle holes (A) and in the grassland-patches around wind turbines (B). The traps are marked in red.

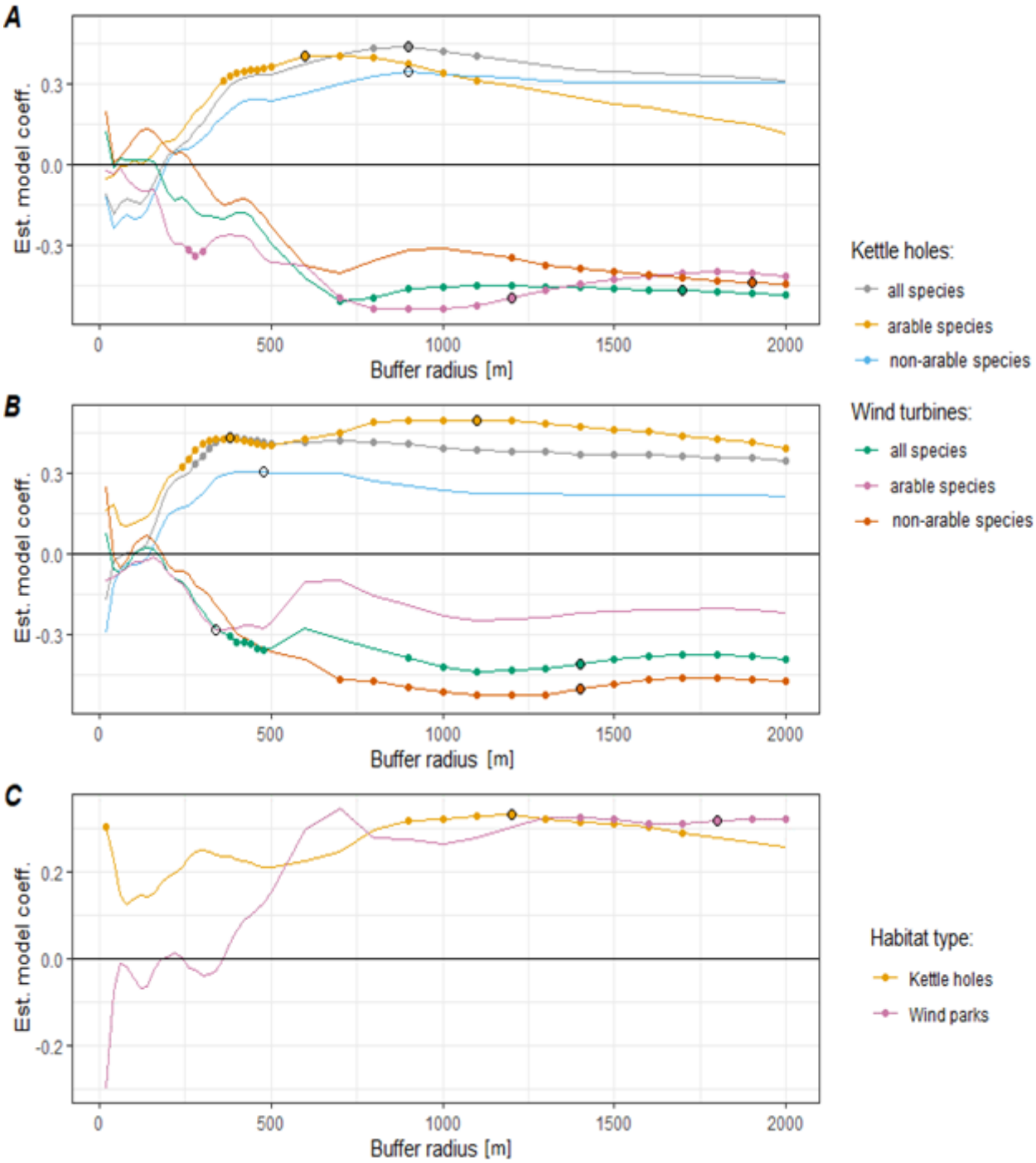

Figure 3

Multi-scale analyses of arable field cover on the response variables A) abundance, B) species richness, C) proportion of arable species. The plots show model coefficients of arable field cover on different scales between 20m and 2000m. The filled dots represent models with significant ($p<0.05$) estimated model coefficients. The black circle indicates the spatial scale at which the statistical model has the lowest AIC. The horizontal black line marks a slope of 0.

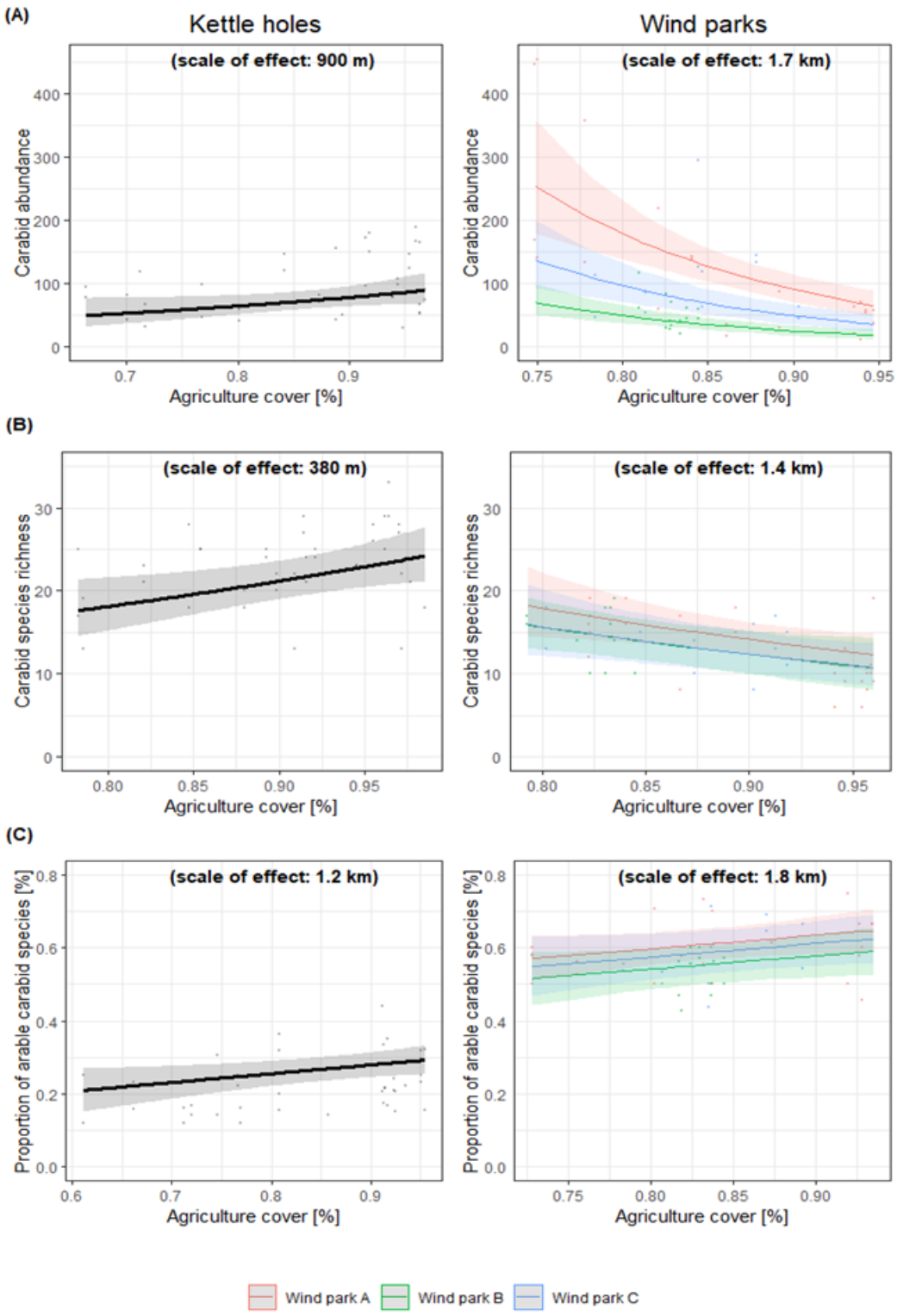

Figure 4

The effect of arable field cover on carabid beetle (A) abundance, (B) species richness and (C) proportion of arable to non-arable species in both habitat types (kettle holes and wind parks). For each response variable, only the spatial scale at which the model expressed the lowest AIC was chosen. The lines depict the mean estimated trend calculated with the corresponding model. Colours represent the different wind

parks (red: Wind Park A; green: Wind Park B; blue: Wind Park C). The dots show the raw data. The ribbons depict the 95 % confidence intervals.