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A plant–pollinator metanetwork along a habitat fragmentation gradient

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Abstract

To understand how plant–pollinator interactions respond to habitat fragmentation, we need novel approaches that can capture properties that emerge at broad scales, where multiple communities engage in metanetworks. Here we studied plant–pollinator interactions over 2 years on 29 calcareous grassland fragments selected along independent gradients of habitat size and surrounding landscape diversity of cover types. We associated network centrality of plant–pollinator interactions and grassland fragments with their ecological and landscape traits, respectively. Interactions involving habitat specialist plants and large-bodied pollinators were the most central, implying that species with these traits form the metanetwork core. Large fragments embedded in landscapes with high land cover diversity exhibited the highest centrality; however, small fragments harboured many unique interactions not found on larger fragments. Intensively managed landscapes have reached a point in which all remaining fragments matter, meaning that losing any further areas may vanish unique interactions with unknown consequences for ecosystem functioning.

KEYWORDS
calcareous grasslands, landscape ecology, mutualism, network theory, plant–pollinator interactions

INTRODUCTION

To understand the impacts of global change on species survival and community composition, we need to look beyond the species richness level and incorporate the fact that all species are connected by ecological interactions (Valiente-Banuet et al., 2015). Ecosystem functions and services, many of which are essential to human well-being, are underpinned by species interactions (Galetti et al., 2013; Traill et al., 2010). Plant–pollinator interactions, for example, are mutualistic associations fundamental to the reproductive success of 88% of all flowering plants and consequently to the functioning of natural and agricultural systems (Ollerton et al., 2011). Plant–pollinator interactions organise themselves in intricate networks based on the local plant and pollinator pools (Biella et al., 2019; Delmas et al., 2019; Memmott, 1999). Studying the properties of these networks gives information about their functionality and stability, which ultimately determines species persistence (Burkle et al., 2013; González et al., 2018; Landi et al., 2018). Understanding changes in ecological networks following

habitat fragmentation, from local community to broader metacommunity levels, would greatly advance basic knowledge needed for successful species conservation (Emer et al., 2018; Tylianakis et al., 2010; Tylianakis & Morris, 2017).

The effects of habitat fragmentation on plant–pollinator networks have been studied to some extent (Ferreira et al., 2013; Pellissier et al., 2018). Most studies have used bipartite approaches at local scales that have helped to understand network changes in terms of structure and stability (Grass et al., 2018; Spiesman & Inouye, 2013). However, local approaches cannot capture the properties of plant–pollinator interactions emerging at broader scales, where multiple communities engage in metacommunities (Hagen et al., 2012). To overcome this limitation, plant–pollinator interactions can be studied in a metanetwork framework in which local communities are connected by the interactions they share (Emer et al., 2018). From a conservation perspective, it is fundamental to identify and protect the most important nodes within a metanetwork (i.e. central interactions or habitats, Emer et al., 2018), which importance can be quantified through the concept of node 'centrality' (Jordán, 2009). Central nodes are those that maintain network cohesiveness and stability and, when lost, have the strongest detrimental effects for the whole system (Estrada, 2007; Freeman, 1978; González et al., 2010). The loss of central nodes can lead to the breakdown of a spatial metanetwork resulting in isolated communities and the extirpation of ecological functions at the landscape level (Emer et al., 2018).

Species traits determine their centrality in local networks (Morán-López et al., 2020). Likewise, trait combinations of interacting partners may determine the centrality of an interaction within a metanetwork perspective. Among the different species traits that can be related to centrality, body size and habitat specialisation are of particular ecological importance (Grass et al., 2018). For instance, wing and body size are correlated with flying capacity in bees and butterflies (Gathmann & Tscharntke, 2002; Stevens et al., 2013; Westphal et al., 2006). In a scenario of habitat fragmentation and low-risk matrix (Fahrig, 2007), large species would be expected to be able to cross the matrix and use habitat patches that are out of reach for smaller species (Thomas et al., 1992). High habitat specialisation entails that a given species is mostly restricted to a certain habitat (Segura et al., 2007). Therefore, at the landscape level, habitat specialists cannot establish viable populations in the matrix, being restricted to available habitat fragments. Habitat specialisation and body size can thus be used to identify key interactions of metanetworks, as well as to identify changes in plant–pollinator interactions caused by habitat fragmentation at the landscape scale.

In addition, the metanetwork approach can be used to identify key traits of habitat fragments that are fundamental to maintain metacommunity functionality.

Fragment size and fragment spatial connectivity (i.e. measure of proximity to other sites) could predict fragment centrality, as these characteristics are related to the number of individuals that a certain fragment can support and to the frequency of immigration events, respectively (Hanski & Ovaskainen, 2000; Steffan-Dewenter & Tscharntke, 2002). Furthermore, the characteristics of the matrix in the surroundings of a fragment can also influence fragment centrality, given that the matrix composition affects available food resources and is known to affect the capacity of organisms to cross it (Boesing et al., 2018; Nowicki et al., 2014; van Halder et al., 2017).

Here we aim to understand the structural properties of a plant–pollinator metanetwork from a temperate hotspot of biodiversity and test which interacting species traits and habitat features are the most important to determine centrality in fragmented landscapes. We studied plant–pollinator interactions along a habitat fragmentation gradient in calcareous grasslands, which are threatened centres of plant and pollinator diversity in Europe (Habel et al., 2013). Specifically, we asked the following questions: (1) What is the structure of the metanetwork? (2) Which are the traits of the species involved in the most central plant–pollinator interactions? And (3) which are the traits of the most central habitat fragments that maintain functional cohesiveness of the metanetwork?

We hypothesised that: (1) the overall metanetwork structure is poorly connected and highly modular because of the presence of many interactions performed by small-bodied species, not able to cross the matrix, and therefore, forming distinct modules composed by a single or a few fragments and the unique interactions they hold (Emer et al., 2018). (2) Interactions involving habitat specialist plants and large-bodied pollinators show higher centrality, as habitat specialist plants are better adapted to exploit the resources of calcareous grasslands and depend exclusively on them across the fragmented landscape (Büchi & Vuilleumier, 2014), while large-bodied pollinators can exploit resources at greater distances and potentially cross the matrix due to their higher flying capacity (Bergman et al., 2018; Westphal et al., 2006), therefore possessing the combined traits needed to occur in a larger number of fragments. (3) Large and well-connected habitat fragments with high diversity of cover types in the surrounding landscape show high centrality as they provide more floral and habitat resources for both plant and pollinators than isolated fragments in low-diversity landscapes (Loos et al., 2021; Steffan-Dewenter et al., 2002); thus, they harbour higher numbers of plant–pollinator interactions.

We predicted that: (1) Metanetwork modularity is larger and metanetwork connectance smaller than expected by null models. (2) Interactions involving habitat specialist plants and large-bodied pollinators show higher degree and weighted degree than those involving habitat generalist plants and small-bodied pollinators.

(3) Large and well-connected fragments with high diversity of cover types in the surrounding landscape show higher degree and weighted degree than small and poorly connected fragments with low diversity of cover types in the surroundings.

MATERIALS AND METHODS

Study system

Calcareous grasslands are the most species-rich habitats in central Europe and are therefore considered biodiversity hotspots (Habel et al., 2013; van Swaay, 2002). Once widely spread, they have been greatly reduced due to agricultural intensification and the abandonment of the historically common extensive grazing, essential to avoid bush encroachment (Cremene et al., 2005; WallisDeVries et al., 2002). Although highly fragmented, they still harbour many rare and specialised plant and invertebrate species (Steffan-Dewenter & Tscharntke, 2002) and are therefore protected by law in Germany and other European countries (Filz et al., 2013).

Study area

Our study region around the city of Göttingen (Germany) comprises 285 sharply delimited semi-natural calcareous grasslands that differ in size, spatial connectivity, management and successional stage (Krauss et al., 2003b). These grasslands are embedded in an agricultural matrix mainly composed of arable land (42%) and managed European beech (*Fagus sylvatica*) forests (37%) (Krauss et al., 2003a). We conducted our study on 29 calcareous grassland fragments (Figure S1) during the spring and summer of 2017 and 2018 (April–September). These fragments were selected in a previous study (Krauss et al., 2003a) along independent (i.e. non-correlated) gradients of habitat area and spatial connectivity.

Landscape metrics

We characterised the calcareous grasslands at the local (fragment area and fragment spatial connectivity) and landscape levels (percentage of cover types and Shannon diversity of cover types) using the 'landscapemetrics' package (Hesselbarth et al., 2019). Fragment size ranged from 82 m² to 52,557 m², excluding zones dominated by shrubs. The distance between study fragments with respect to the closest neighbouring grassland ranged from 55 m to 1894 m (Krauss et al., 2003a). Fragments' spatial connectivity was quantified with a connectivity index developed by Hanski et al. (1994) and considered all calcareous grasslands in a radius of 2 km around the study grasslands (see SM for details). Larger values of this index indicate higher spatial connectivity (Table S1). We calculated percentages of land cover types at multiple radii from our focal fragments (i.e. fragment centroids) from 100 m until 500 m radius in 50 m intervals, based on reported spatial scales at which bees and butterflies perceive their environment (Gathmann & Tscharntke, 2002; Steffan-Dewenter & Tscharntke, 2002; Stevens et al., 2013; Westphal et al., 2006). The mapped land cover types were: oilseed rape, grainfield, maize, other crops, forest open, forest closed, field margin, hedgerow, pasture, calcareous grassland, orchard, settlements, water bodies, streets, grassroads and bare soil. We tested the effect of arable land (mainly composed of oil-seed-rape, wheat and maize plantations), semi-natural habitat (including calcareous grasslands, orchards, hedgerows, field margins and flower strips) and the Shannon diversity of cover types, on site centrality (see section Statistical analyses). To choose the optimal scales at which these variables had the strongest effects on fragment centrality, we compared linear models at different spatial scales, and chose the scale with the highest predictive value, using the corrected Akaike information criterion for small samples (AICc). Shapefiles of land use were constructed using ArcGis 10.5.1 and all statistics were performed in R (R Development Core Team 2019).

Field data collection

Each calcareous grassland was visited three times per year in order to capture the succession of flower visitors (hereafter pollinators) and wildflower species throughout the season. We established seven observation plots in each site, totalling 1218 observations of 10 min each. Surveys were carried out from 9:00 to 17:00 on days with a minimum temperature of 15 °C and at least 50% clear sky, or with a minimum temperature of 18 °C in any sky condition (van Swaay et al., 2012). Sites were surveyed at different times of the day to avoid any potential confounding effect of daytime.

Observation plots were circular (3 m radius, 28.3 m²) and were established in flower-rich areas. Within these, all interactions between pollinators (butterflies, Lepidoptera: Papilionoidea; burnet moths, Lepidoptera: Zygaenidae; and bees, Hymenoptera: Apiformes) and flowering plants that occurred in a 10-min period were registered. We focused on these three functional groups as they are the most common and frequent flower visitors in natural grasslands (Sexton & Emery, 2020). A wider sampling of biological groups, such as flower-visiting Coleoptera and Diptera, that can play a role in plant pollination (Orford et al., 2015; Sjödin et al., 2008), could potentially influence some features of the metanetwork. Yet sampling interactions are a time-consuming and logistically demanding task (Jordano, 2016), thus we decided to focus on the most likely and frequent interactions in our study system to ensure a robust characterisation of

these groups. A visit by a pollinator was considered to be an interaction as soon as the insect touched the plant reproductive organs. Pollinators not easily recognisable at a distance were captured with a sweep net and photographed or collected for later identification by taxonomists. The timer was paused while handling insects. We excluded interactions involving *Apis mellifera* as the presence of this species in the region is solely related to the existence of bee keepers in the surroundings. *A. mellifera* interactions accounted for 1181 from a total of 8114 interactions registered and were present in all sites (range 1–166 *A. mellifera* interactions per site).

Plant–pollinator traits

Plants and pollinators were classified according to their life-history traits. Habitat specialisation followed Brückmann et al. (2010) and Poschlod et al. (1998) for plants, Jauker et al. (2013) and Hopfenmüller et al. (2014) for bees and van Swaay (2002) and Brückmann et al. (2010) for butterflies. Body length values for bees were taken from Westrich (2018) and wing length values for butterflies were taken from Sterry and Mackay (2004). All values were standardised to make them comparable by subtracting the mean and dividing by the standard deviation of each group. Butterflies were considered large whenever their wing length was equal or larger than 16 mm (median wing length of butterflies), otherwise they were classified as small. On the other hand, bees were considered large when having a body length of 10 mm or more (median body length of bees) and were otherwise considered small (Figure S2).

Metanetwork structure

A metanetwork was built by pooling the 29 calcareous grasslands into an Aij adjacency matrix, in which i are the studied sites and j is the pairwise plant–pollinator interactions. The aij elements correspond to the frequency of interactions j found in site i. First, we characterised the overall structure by calculating: (1) pollinator richness, plant richness and plant–pollinator interaction richness; (2) connectance: here defined as the realised proportion of plant–pollinator interactions per fragment regarding all possible interactions at the metanetwork level (Dunne et al., 2002); (3) modularity: here, the organisation in subgroups of fragments and interactions that are highly connected among themselves but less with other subgroups; estimated using the DIRTLPAwb+algorithm (Beckett, 2016).

Second, we estimated the centrality (Freeman, 1978; González et al., 2010) of the metanetwork nodes by calculating: (4) interaction degree, as the number of fragments in which a given interaction occurs; (5) interaction weighted degree, as the frequency of an interaction across all fragments; (6) fragment degree, as the number of unique pairwise combinations of each pollinator and plant species recorded interacting in a given fragment (sensu Emer et al., 2018, i.e. interaction richness per site); (7) fragment weighted degree, as the frequency of interactions that a given fragment holds (i.e. interaction frequency per site).

All network metrics were calculated using the 'bipartite' package in R (Dormann et al., 2008).

Statistical analyses

(1) To examine the structure of the metanetwork, we assessed the significance of the metanetwork connectance and modularity against independent null models that constrain network size while randomising the distribution of links among rows and columns, but holding the marginal totals constant (Dormann et al., 2009). That is, fragments maintain the same number of interactions in the null models, and interactions maintain the same number of fragments in which they occur. We obtained the mean and standard deviation of 100 iterations of each null model to test against the observed values of each corresponding metric (i.e. obtaining their z-scores). In a post hoc analysis, we used linear and generalised linear models to explore local (fragment area and connectivity) and landscape (diversity of cover types) level effects on the number and proportion of single-fragment interactions.

(2) To test whether species traits affected the centrality of plant–pollinator interactions (i.e. interaction degree and interaction weighted degree), we used generalised linear mixed models. Specifically, we tested for the effects of the plant and pollinator habitat specialisation, as well as pollinator size and guild (i.e. bumblebee, solitary bee or butterfly), on the centrality of the interactions they perform. Our full models included the mentioned explanatory variables, all their two-way interactions, the plants' and animals' active period regarding season (categorical with three levels: spring, summer or spring and summer) and number of months active. Furthermore, we included plant's and animal's identity as crossed random intercepts.

(3) To test whether fragment and landscape traits affected fragment centrality, we tested the effects of (log) fragment area, (log) connectivity index and the Shannon index of cover types (hereafter, landscape diversity) against fragment degree and weighted degree. Percentage of semi-natural habitat was excluded from the analyses as it was correlated with fragment area (Pearson's corr = 0.66, $p < 0.001$) and with landscape diversity (Pearson's corr = 0.51, $p = 0.004$). We tested for spatial autocorrelation (Dormann et al., 2007) performing Moran's I tests with the 'DHARMa' package and observed no evidence of spatial autocorrelation in our models.

We used a truncated negative binomial distribution and the 'glmmTMB' package in all centrality models (Magnusson et al., 2017). We selected the minimum adequate models using backwards model selection with likelihood ratio tests. All non-significant explanatory variables ($p > 0.05$) were sequentially removed. Post hoc tests were performed with the 'lsmeans' package (Lenth, 2017). All network and statistical analyses were performed in R (R Development Core Team 2019).

RESULTS

Metanetwork structure

The metanetwork had a total of 6936 plant–pollinator interaction events from a pool of 842 unique pairwise plant–pollinator combinations among 131 plant species and 118 pollinator species throughout the 29 calcareous grassland fragments (Figure 1). From those, 4722 (68.1%) plant–pollinator interactions occurred among 46 butterfly species and 99 plant species, comprising a total of 474 unique pairwise plant–butterfly interactions (56.3%). On the bees' side, we found 12 bumblebee species interacting 1891 (27.3%) times with 89 plant species, totalling 214 unique pairwise plant–bumblebee interactions (25.4%). In addition, we found 320 (4.6%) interactions among 60 solitary bee species and 50 plant species, involving 154 unique pairwise plant–bee interactions

(18.3%). On average, each fragment comprised 28.2 ± 6.7 (mean $\pm$ SD) pollinator species, 22.3 ± 5.2 plant species and 71.5 ± 21.7 unique pairwise interactions.

Overall, the metanetwork was significantly less connected ($C = 0.08$, $p < 0.001$) and more modular ($M = 0.39$, $p < 0.001$) than expected from null models (Figure S3). The modular structure was organised around 17 modules, with an average of 1.7 fragments and 49.5 unique interactions per module (Figure 1).

Single-fragment interactions

Only 305 (36.2%) unique pairwise plant–pollinator interactions occurred in at least two fragments, but these made up for the majority of observed plant–pollinator interaction events (6171, or 89%). This means that more than half of the unique plant–pollinator combinations were rare and local (i.e. occurred in a single fragment). Landscape diversity at 100 m scale had a positive effect on the number of single-fragment plant–pollinator interactions ($X^2 = 12.25$, $p < 0.001$, Figure 2a) and at 500 m scale a negative effect on the proportion of single-fragment interactions with respect to all unique interactions in a certain fragment ($F = 8.08$, $p = 0.008$, Figure 2b). Fragment area and fragment connectivity did not have significant effects on the number of single-fragment interactions or their proportion with respect to all interactions (Table S3).
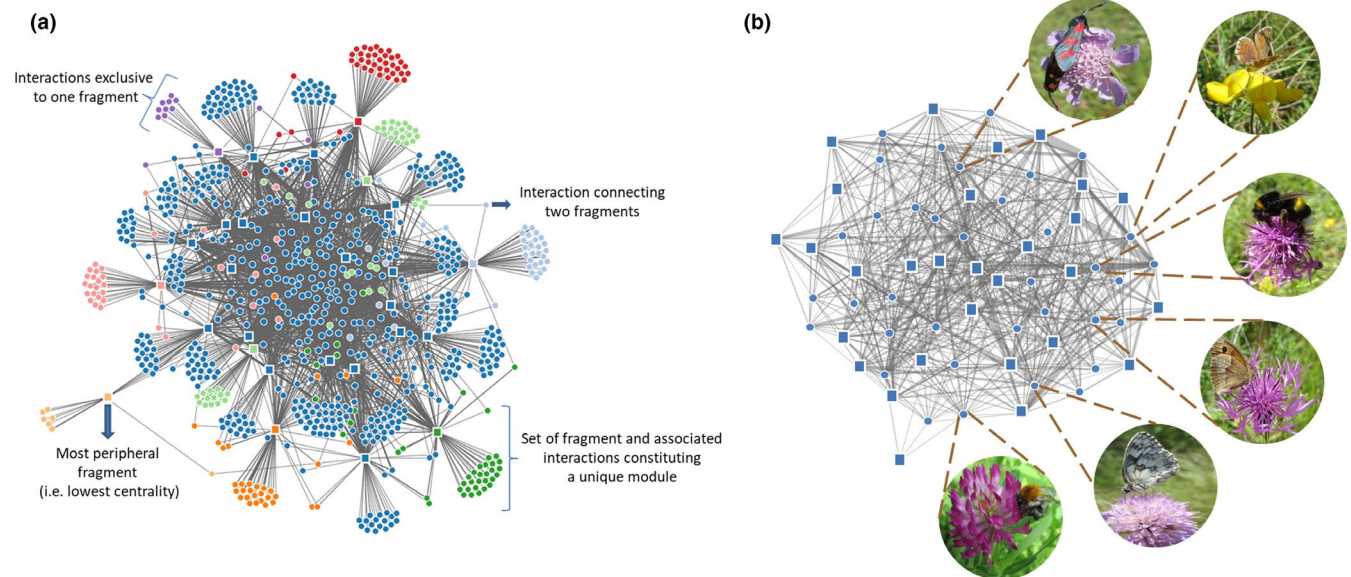

FIGURE 1 (a) The plant–pollinator metanetwork structure of the calcareous grassland fragments. Circles indicate unique pairwise combinations of plant and pollinator species that perform pollination interactions ($n = 842$) and squares represent the studied sites ($n = 29$). Interactions occurring in at least two sites form links connecting them. The thickness of links (grey lines) is proportional to interaction frequency (range 1–254). Colours represent metanetwork modules based on the Walktrap community-finding algorithm (igraph package). This algorithm indicates the presence of sub-graphs that constitute a distinctive community. Nodes with greater centrality occur in the central positions of the graph (Bannister et al., 2013). (b) Sub-graph of the metanetwork, zooming into the core plant–pollinator interactions (here those present in more than 10 sites)
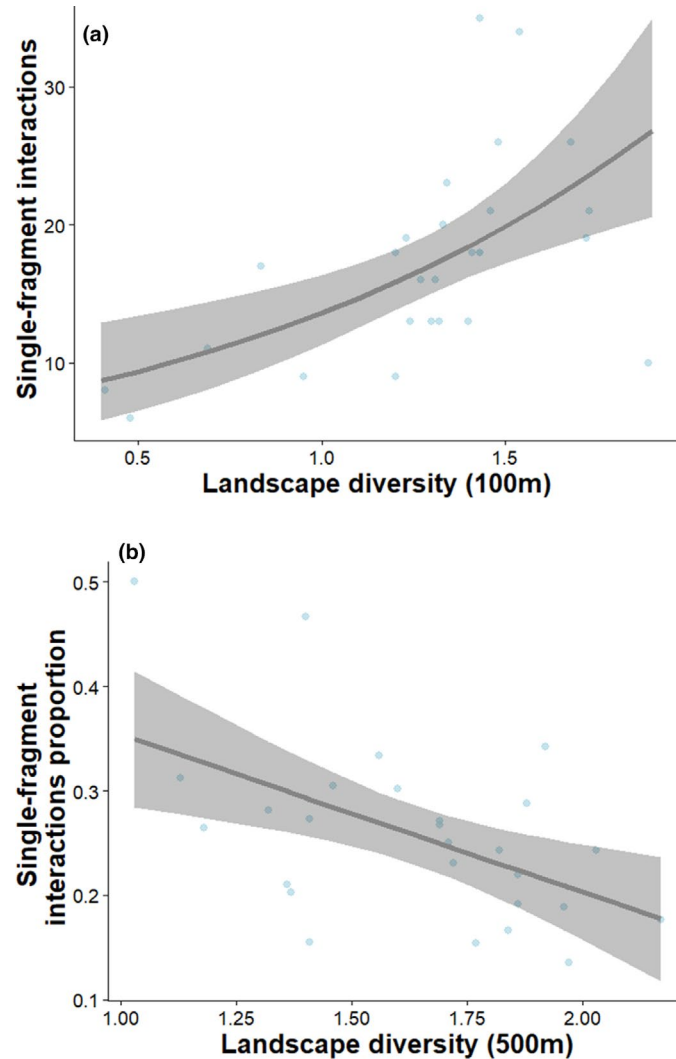
FIGURE 2 Relationship between (a) the number of single-fragment interactions (i.e. those that occur in only one fragment from the 29 fragments studied) and (b) the proportion of single-fragment interactions, with landscape diversity. The proportion is the number of single-fragment interactions divided by interaction richness in a specific fragment. Light-blue circles represent raw data points and the grey area is the 95% confidence interval

Interaction centrality and biological traits

Plant habitat specialisation was a significant predictor of interaction degree ($X^2 = 12.78$, $p < 0.001$, Table S2). Specifically, interactions involving habitat specialist plants had significantly higher degree than those involving habitat generalist plants (Figure 3a). Additionally, pollinator identity and the interaction between plant habitat specialisation and pollinator size were found to be significant predictors of interaction weighted degree (Table S2). Specifically, interactions involving habitat specialist plants and large-bodied pollinators had higher weighted degree than those involving habitat generalist plants and small-bodied pollinators ($X^2 = 5.28$, $p = 0.021$, Figure 3b). Moreover, interactions performed by butterflies ($t = -2.50$, $p = 0.034$) and bumblebees ($t = -2.75$, $p = 0.016$) had higher weighted degree than those performed by solitary bees (Figure 3b).

Fragment centrality and landscape features

Larger calcareous grassland fragments were more central in the metanetwork, as indicated by the positive effect of fragment area on fragment degree ($X^2 = 4.24$, $p = 0.04$) and fragment weighted degree ($X^2 = 11.40$, $p < 0.001$, Figure 4). In addition, landscape diversity also had a positive effect on fragment centrality as evidenced by increased fragment degree ($X^2 = 4.67$, $p < 0.001$) and weighted degree ($X^2 = 12.54$, $p < 0.001$). Conversely, fragment connectivity and arable land had no significant effects on fragment degree ($X^2 = 0.95$, $p = 0.33$; $X^2 = 1.27$, $p = 0.26$) nor on fragment weighted degree ($X^2 = 0.013$, $p = 0.91$; $X^2 = 2.37$, $p = 0.12$).

DISCUSSION

Here we analysed a plant–pollinator metanetwork along a habitat fragmentation gradient over a 2-year period.
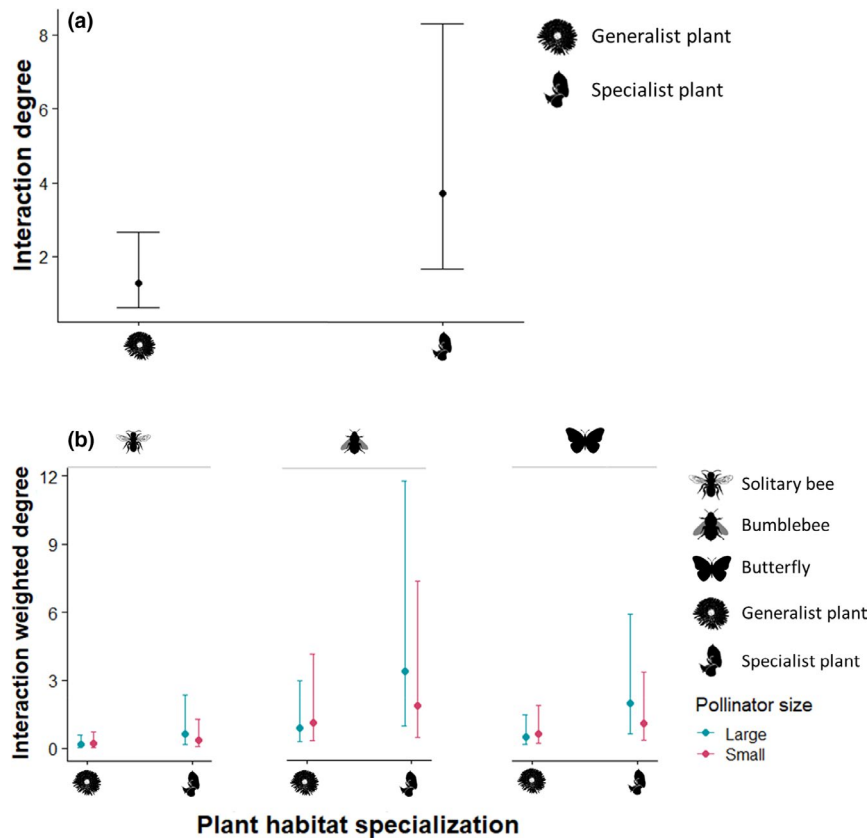
FIGURE 3 Relationship between (a) interaction degree (i.e. number of fragments on which a specific pairwise plant–pollinator interaction occurs) with plant habitat specialisation and (b) interaction weighted degree (i.e. interaction frequency across all fragments) with plant habitat specialisation, pollinator size and pollinator identity. Bars represent 95% confidence intervals

We found that plant–pollinator interactions involving habitat specialist plants and large-bodied pollinators were the most central in our system. Bumblebees and butterflies established more central interactions than solitary bees. Moreover, large fragments embedded in landscapes with high land cover diversity exhibited the highest centrality, while small fragments harboured a high share of unique interactions not found on larger fragments.

Plant–pollinator metanetwork structure

The plant–pollinator metanetwork was more modular and less connected than expected by chance. The different modules within the metanetwork reflect the presence of unique pools of interacting species in different fragments of calcareous grassland where local species tend to establish specific associations among each other. Network theory predicts that modularity can reduce the sensitivity of interconnected systems to perturbations as these will not easily spread to the whole network (Olesen et al., 2007). However, modularity has also been associated with reduced stability in mutualistic networks (Thébault & Fontaine, 2010). A highly modular network depends on the presence of connector species (i.e. species

establishing interactions across modules) to maintain its integrity and prevent it from breaking apart into separate modules. Once modules are disconnected, they become smaller independent networks on their own and consequently become more prone to collapse given their smaller size and higher sensitivity to stochastic events (Lever et al., 2014).

As established by Olesen et al. (2007), only a small proportion of species are structurally important to a network, however, when these are lost, cascades of extinctions might occur, leading to a general collapse of the system. In our case, the species involved in the interactions shown in Figure 1b are the most important to the metanetwork, as they are the key connections among otherwise segregated modules. Interestingly, all pollinator species involved in the most central interactions were habitat generalists (except for *Polyommatus coridon*), but most plant species were habitat specialists, that is, characteristic species of calcareous grasslands. This means that in addition to protecting habitat specialist species of calcareous grasslands by targeted management strategies (Filz et al., 2013), biodiversity-friendly measures in the matrix, such as flower strips, hedgerows and crop diversification, could help to protect central pollinators acting as mobile links (Kleijn et al., 2006; Sirami et al., 2019). Protecting habitat generalist pollinators, in turn,
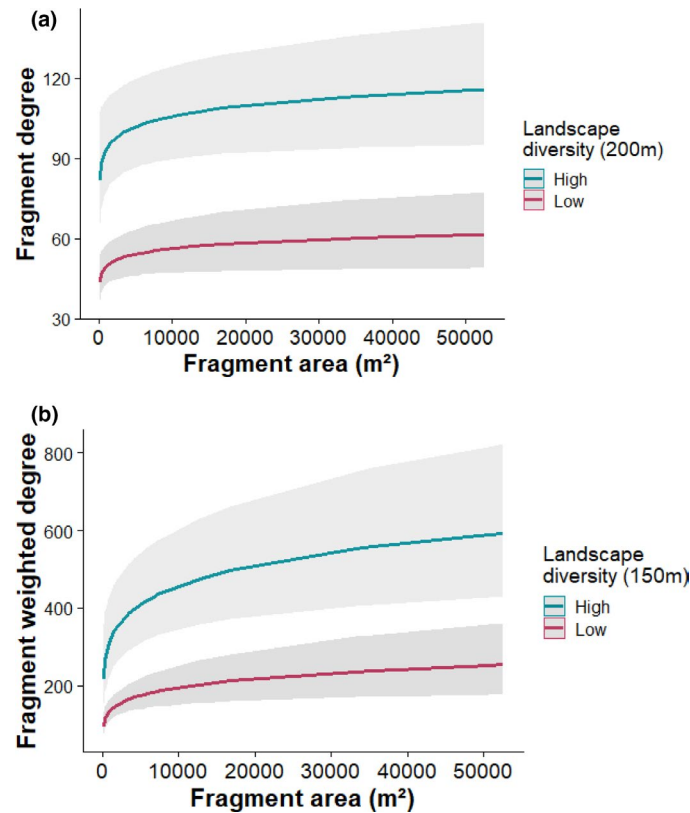
FIGURE 4 Effects of calcareous grassland fragment size and landscape diversity (here calculated as the Shannon diversity index of cover types) on (a) fragment degree and (b) fragment weighted degree. Grey areas represent 95% confidence intervals

maintains the cohesiveness of the metanetwork, thereby also protecting habitat specialist plant species (directly) and habitat specialist pollinator species (indirectly). In other words, conservation measures aiming at this core group of generalist species may indirectly help to conserve also specialist species.

Single-fragment plant–pollinator interactions

All unique pairwise interactions, including single-fragment interactions, increased with landscape diversity, but the proportion of single-fragment interactions decreased with it, that is, the rate at which all unique pairwise interactions increase with landscape diversity is higher than that of single-fragment interactions. An increase of single-fragment interactions with landscape diversity at a small spatial scale (100 m) could be related to a positive effect on the occurrence of small-bodied pollinators. These pollinators may be favoured by the augmented variety of resources offered by a diversified landscape (e.g. nesting and flower resources), but as they are usually restricted to their natal patch due to sedentary behaviour and a small flying capacity, they would establish interactions that occur only locally and are therefore mostly restricted to a single fragment (Gathmann & Tscharntke, 2002; Wilson & Thomas, 2002). On the other hand, highly mobile large-bodied pollinators,

such as large-bodied butterflies and bumblebees, are affected by the landscape structure at larger spatial scales (Bergman et al., 2018; Westphal et al., 2006). As central place foragers, bees are attached to the nest position to which they need to come back regularly, independent of their sociality level, but butterflies are not attached to a nest and therefore can potentially move longer distances than bees throughout their lives. As a consequence of their high mobility, large-bodied butterflies are expected to connect the metanetwork by reaching multiple calcareous grassland fragments. Hence, differently from bees, the majority of the interactions established by large-bodied butterflies may not be restricted to a single fragment. Therefore, we suggest that the negative effect of landscape diversity on the proportion of single-fragment interactions at 500 m scale may be mostly driven by large-bodied butterflies.

Interaction centrality and species traits

Our results show that interactions between habitat specialist plants and pollinators are fundamental to the calcareous grassland metanetwork. Despite representing only 17.6% of the plant species found and despite being involved in only 38.9% of all unique pairwise interactions, interactions conformed by habitat specialist plants and pollinators were more central than those involving

habitat generalist plants. Hence, habitat specialist plants in calcareous grasslands establish interactions that provide cohesiveness and stability to the metanetwork, highlighting the importance of their conservation. Contrastingly, although habitat generalist plants establish numerous interactions, those interactions do not belong to the core interactions of the plant–pollinator metacommunity in calcareous grasslands. A notable exception is the habitat generalist plant *Knautia arvensis*, which established many central interactions particularly with large-bodied butterflies. Whether this is a consequence of interaction rewiring due to the absence of the related habitat specialist *Scabiosa columbaria* remains to be studied.

As expected, large-bodied pollinators established more central interactions than small-bodied ones. Movement capacity is positively correlated to body size (Stevens et al., 2014). Large pollinators have larger foraging ranges (Greenleaf et al., 2007), which may allow them to reach a higher amount of calcareous grassland fragments, increasing the number of plant species available with which they can potentially interact. From the plant species perspective, it is reasonable to expect that habitat specialist plants benefit from interacting with large-bodied pollinators that are not constrained to the local fragment and can eventually disperse their pollen at greater distances, therefore ensuring gene flow among populations. This assumption is supported by our finding that the core of the most central interactions is in fact formed by habitat specialist plants and large-bodied pollinators. Whether this pattern is a consequence of habitat fragmentation or a characteristic feature of calcareous grasslands needs to be further explored, for example, by analysing plant–pollinator interactions exclusively in large continuous calcareous grasslands.

Solitary bees were found to be involved in interactions of lower centrality than those of butterflies and bumblebees. In comparison to social bees, such as bumblebees, solitary bees typically have much more restricted foraging ranges (Gathmann & Tscharntke, 2002; Westphal et al., 2006). This may be partially explained by a smaller body size in several species compared to bumblebees (with a few exceptions in the *Anthophora* and *Andrena* genera) and by their solitary life strategy, given the positive association between colony sizes and foraging ranges (Westphal et al., 2006). Also, bumblebees establish numerous interactions with both specialist and generalist plants, given their high abundance favoured by their social life in colonies (Biella et al., 2019; Leidenfrost et al., 2020). Regarding the lower centrality of solitary bee interactions in comparison with butterfly interactions, this effect is probably driven by large-bodied butterflies, as small-bodied butterflies have a much smaller capacity and probability to cross the matrix and reach other fragments (Habel et al., 2020).

Fragment centrality and landscape traits

As expected, habitat fragment size had a positive effect on fragment degree and on fragment weighted degree. This result is not surprising given that larger fragments tend to harbour larger species populations and consequently have a higher probability of interaction establishment. Although larger fragments might favour the presence of area-sensitive, monophagous and rare specialist species (Rösch et al., 2015; Steffan-Dewenter & Tscharntke, 2002), it has been demonstrated that in a fragmented landscape many small fragments harbour a larger amount of habitat specialist species than a single large fragment of the same area (Rösch et al., 2015; Tscharntke et al., 2002). Given the high amount of unique pairwise interactions involving habitat specialist species that were restricted to small fragments, a similar importance of small fragments seems to hold for species interactions. Therefore, it needs to be highlighted that although large fragments are fundamental for the metanetwork stability and cohesiveness, small fragments contribute many unique pairwise interactions that cannot be conserved by only focusing on large fragments. Similar findings have been reported for seed-dispersal interactions from a highly fragmented tropical forest in which many unique plant–animal mutualistic associations were found exclusively in small areas (Emer et al., 2018). Thus, mounting evidence is showing that distinct fragmented landscapes have reached a point in which all remaining fragments matter, meaning that losing any further areas, even the small ones, may vanish unique interactions with unknown consequences for ecosystem functioning.

Interestingly, fragments embedded in landscapes with high land cover diversity exhibited higher fragment centrality, meaning that these fragments had higher numbers of unique and total plant–pollinator interactions. This finding has important implications for conservation as it highlights the essential role of not only protected habitats, but also the surrounding landscape to protect plant–pollinator interactions. A diverse landscape multiplies the number of resources available for pollinators, such as nectar, pollen and nesting opportunities, and therefore contributes to their persistence in the landscape (Landis et al., 2005). Furthermore, the presence of linear elements such as flower strips and hedgerows can facilitate animal movement through the landscape and between fragments (Davies & Pullin, 2007; van Geert et al., 2010; Holzschuh et al., 2009; Klaus et al., 2015). In addition, cropland diversification can play an important role. For example, promoting field borders and reversing current trends towards larger field sizes can enhance the connectivity of the agricultural landscape for bees, and substantially promote their abundance and pollination services (Hass et al., 2018). The ability of large-bodied specialist butterflies, such as *Polyommatus coridon*, to cross the matrix and reach surrounding calcareous

grasslands needs to be further explored. However, some studies have found that a small proportion of individuals of this species can cross matrix gaps of a few hundred metres and exceptionally a few kilometres (Schmitt, 2015; Schmitt et al., 2006). The protection of this particular butterfly species and the interactions it establishes appears fundamental for the integrity of the metanetwork system.

Limitations and generalities

Ecological studies involving metacommunity processes at large spatial and temporal scales cannot deal with all possible levels of complexity associated to the interactions that affect an individual fitness. Therefore, we focused on two major taxonomic groups (i.e. bees and butterflies with burnet moths included) to capture most of the complexity involving plant–pollinator interactions across the studied calcareous grasslands. Although bees and butterflies are regarded as the most abundant, most important and diverse flower visitors in calcareous grasslands, other flower-visiting taxa such as Diptera and Coleoptera are also present in this habitat (Boetzl et al., 2021; Lack, 1982; Steffan-Dewenter & Tscharntke, 2002) and may play an additional role in the pollination of certain plant species.

Syrphidae (i.e. hoverflies) and non-syrphid Diptera (particularly Bombyliidae) are considered important pollinators in some cases (Orford et al., 2015) and are mostly very mobile, similar to large bees (Meyer et al., 2009). In our region and in the same habitat type, a study analysing wild bee and hoverfly contributions to plant–pollinator network structure in calcareous grasslands found that network properties were mostly attributed to wild bees, not syrphid flies (Jauker et al., 2019). Yet whether the apparently non-significant presence of syrphids at the local network level would scale-up to affect the metanetwork structure is difficult to predict and beyond the scope of this study. Furthermore, the inclusion of low-mobility flower-visiting Coleoptera organised in distinctive assemblages at local scales could lead to more single-fragment interactions, which may increase modularity of the network.

A. mellifera can interfere with native bee flower visitation and can reduce the fruit set and fitness of plants (Gross, 2001; Gross & Mackay, 1998). Additionally, *A. mellifera* can affect the structure and functionality of plant–pollinator networks (Lázaro et al., 2021; Valido et al., 2019) through mechanisms such as exploitative competition (Magrach et al., 2017). However, no interference between honeybees and wild bees was found in a former study conducted in the same calcareous grasslands we sampled (Steffan-Dewenter & Tscharntke, 2000). Although native to Europe, honeybees in Germany are nowadays mostly managed and feral colonies are restricted to few unmanaged forests as a consequence of

habitat loss, domestication and spread of pathogens and parasites (Kohl & Rutschmann, 2018; Requier et al., 2020). In our study region, honeybees show little competitive effects because of two reasons. First, because our study region is placed in the honeybee native range and second, because of the high resource availability in calcareous grasslands (Mallinger et al., 2017). Furthermore, the presence of *A. mellifera* in our study areas was limited to few bee hives placed in the surroundings of some study sites for only a short period of time, not constantly throughout all three rounds of sampling, this is in contrast to studies analysing honeybee effects on networks, where honeybee hives were dominant. *A. mellifera* occurred sparsely in space and time without monopolising flower resources and was not related to any landscape variable.

CONCLUSION

We identified the most central plant–pollinator interactions and habitat fragments in a plant–pollinator metanetwork and the traits associated with their centrality. We found that plant–pollinator interactions involving habitat specialist plants and large-bodied pollinators were the most central and thus structurally important in our system. Furthermore, bumblebees and butterflies established more central interactions than solitary bees, highlighting the importance of social bees and mobile butterflies for maintaining plant–pollinator interactions in fragmented landscapes. Importantly, large fragments embedded in landscapes with high land cover diversity exhibited the highest centrality. Conserving large grasslands fragments and diversifying the agricultural matrix is thus fundamental for the cohesiveness and stability of plant–pollinator metanetworks. In particular, crop diversification and conservation schemes such as agri-environmental schemes may promote metanetwork stability. However, although large fragments were the most central in our system, small fragments also need protection as they harbour a high proportion of unique interactions not found in large fragments.

AUTHORSHIP
FLE, TT and IG designed the study methods and rationale; FLE and CG collected data; CE did major

contributions to analyses; FLE analysed data and wrote the first draft of the manuscript. All authors contributed substantially to revisions.

PEER REVIEW

DATA ACCESSIBILITY STATEMENT

The authors state that, should the manuscript be accepted, the data supporting the results will be archived in an appropriate public repository, and the data DOI will be included at the end of the article.

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