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Patch occupancy of grassland specialists: Habitat quality matters more than habitat connectivity

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ABSTRACT

Land-use change has caused degradation, loss and fragmentation of semi-natural habitats, especially in grassland ecosystems. Today, the remaining habitats are often situated in a matrix of intensively used agricultural land and are therefore more or less isolated from each other. Connectivity, area and quality of habitat patches have been identified as the most important drivers for the persistence of grassland specialists living in metapopulations. However, the relative importance of these factors is still under debate. We used a large-scale, multi-taxon approach to obtain a general pattern which would facilitate conservationists to promote many, instead of one, species. We studied the patch occupancy of 13 grassland specialists belonging to three different insect orders within a Central European landscape with 89 fragments of calcareous grasslands. To disentangle the relative importance of the three metapopulation parameters, generalized linear models (GLM) and variation-partitioning techniques were used. Our study revealed that habitat quality was the most important factor determining the occurrence of specialized species, followed by habitat area. In comparison to habitat connectivity, the variance explained by habitat quality was significantly higher across the studied species. Nevertheless, the persistence of at least six model organisms depended on the degree of habitat connectivity. We conclude that maintaining a high habitat quality on large patches should be the first choice for the conservation of habitat specialist insects in fragmented landscapes. As a secondary measure, conservationists should concentrate on the restoration of relict sites. This increases not only the habitat area, but also contributes to better habitat connectivity.

1. Introduction

The global decline of biodiversity has reached an alarming dimension. According to Pimm et al. (2014), the rate of species extinction is currently at least 1000 times higher than the natural background extinction rate. Land-use change is assumed to be the major driver of this development (Sala et al., 2000; Foley et al., 2005). The intensification of agricultural land-use, abandonment, afforestation and urbanization have caused degradation, loss and fragmentation of semi-natural habitats, especially in grassland ecosystems (WallisDeVries et al., 2002; Baur et al., 2006).

Among grassland ecosystems, calcareous grasslands have an outstanding value for nature conservation due to their very diverse flora and fauna (Poschlod and WallisDeVries, 2002). As a result of the above-mentioned processes, species-rich grasslands have lost much of their original extent and have become increasingly fragmented. Today, they are often situated in a matrix of intensively used agricultural land (Brückmann et al., 2010; Poniatowski et al., 2016) which makes them refuges for several specialized insect species (Krämer et al., 2012b; Poniatowski et al., 2018). The spatial distribution of such species in cultivated landscapes is determined by several environmental factors operating at two different spatial scales: (i) the landscape level and (ii) the habitat level. Based on metapopulation theory, habitat area and habitat connectivity have been identified as the most important factors determining the persistence of mobile habitat specialists at the landscape level (Hanski, 1999), i.e. these species depend for long-term survival on networks of spatially inter-connected subpopulations (Thomas et al., 1992; Anthes et al., 2003; Stuhldreher and Fartmann, 2014). Due to local extinction and recolonization events, metapopulations are characterized by a dynamic population structure (Leisnham and Jamieson, 2002; Baguette, 2003). The lower the connectivity of a subpopulation, the more prone to extinction it becomes and the less likely it is to be re-established (Carlsson and Kindvall, 2001; Fernández-Chacón et al., 2014). In the long-term, this can lead to extinction of the whole metapopulation (van Strien et al., 2011).

At the habitat level, there is consensus that habitat quality is a

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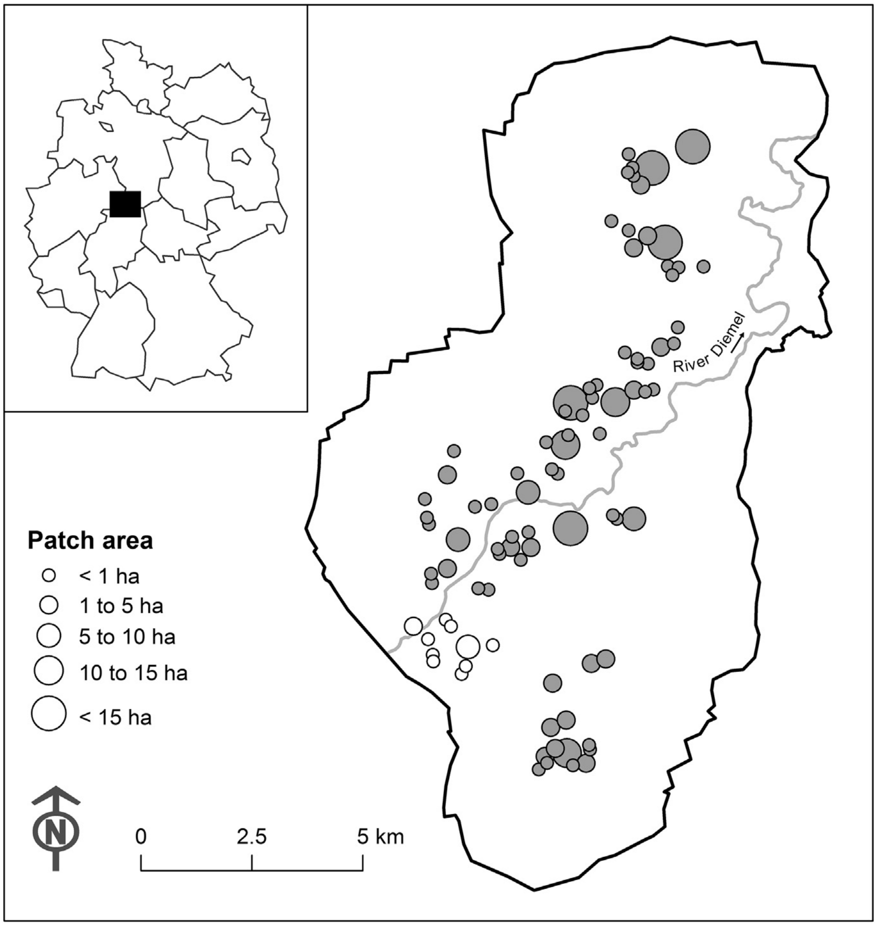

Fig. 1. Study area, the Lower Diemel Valley in central Germany (inlay), and the 89 study patches. Ten patches in the southwestern part of the study area were situated within a 2-km range of adjacent calcareous grasslands in the Middle Diemel Valley. These patches, indicated by white circles, were only used for calculating the functional connectivity of some of the remaining patches (grey circles), and were not used as focal patches. Concerning the 79 focal patches represented by grey circles, all existing calcareous grasslands within a radius of at least 2 km were incorporated in the calculation of the connectivity index.

further important driver of patch occupancy in many insect species (reviewed by Thomas et al., 2011). Habitat quality comprises a multifactorial complex, which is often dominated by the ecological requirements of the immature stages (eggs, larvae or nymphs, and pupae). This is because the immature stages are often much more sensitive to environmental changes than the adults (García-Barros and Fartmann, 2009). Temperature and humidity at oviposition sites, for instance, are crucial factors for successful egg development (Krämer et al., 2012a; Eilers et al., 2013). Oligo- or monophagous species, additionally, depend on the availability of their host plants (Biedermann, 2004; Eichel and Fartmann, 2008). Moreover, the occurrence of species living in the herb layer is determined by the spatial structure of the vegetation (Poniatowski and Fartmann, 2008; Helbing et al., 2017). In this context, the land-use intensity of the habitat is of particular importance due to its impact on vegetation structure and plant-community composition (cf. Marini et al., 2009; Littlewood et al., 2012). Furthermore, direct effects, such as mowing or trampling, may be crucial for the persistence of a species (Marini et al., 2008; van Klink et al., 2015).

In the early stages of insect conservation, emphasis was placed on reducing rates of local extinctions by maintaining habitat quality (e.g. Thomas, 1984). Somewhat later, in the context of Hanski's metapopulation theory, there was growing evidence that the landscape structure (habitat area and habitat connectivity) has a strong impact on species persistence as well (Hanski, 1994). Finally, both levels were linked to each other (Dennis and Eales, 1997; Thomas et al., 2001; Anthes et al., 2003; Bauerfeind et al., 2009). Even though these studies revealed an impact of habitat area or habitat connectivity, in combination with habitat quality, on patch occupancy, most of them considered only a single species. Large-scale metapopulation studies that take into account several species of different taxonomic orders within the same habitat network are almost completely absent (the only exception being Maes and Bonte, 2006).

Successful habitat management, in general, considers the ecological requirements of different groups of species (Samways, 2005). For conservationists it is therefore important to know which measure should be the first choice: improving habitat quality, increasing patch area or connecting isolated patches. Survival strategies vary from species to species and may differ regionally. Consequently, Zulka et al. (2014) proposed analysis of the responses of individual species with finely-tuned habitat and matrix variables, followed by aggregation of the results to obtain a general picture. This would help conservation managers to promote many instead of one species (cf. Maes and Bonte, 2006).

In this study, we applied the approach proposed by Zulka et al. (2014). We choose 13 habitat specialists of three different insect orders (Auchenorrhyncha, Lepidoptera and Orthoptera) as model organisms. In the study area, all of them are restricted to calcareous grasslands and exhibit very specific habitat requirements (Poniatowski et al., 2016). They are consequently well-suited to metapopulation and fragmentation studies.

The aim of this study was to quantify the relative importance of the three most important factors determining species persistence in fragmented landscapes. On the basis of our findings, we derive priorities for the conservation of highly specialized insect species.

2. Materials and methods

2.1. Model organisms

As model organisms we chose four Auchenorrhyncha (*Batracomorphus irroratus*, *Goniagnathus brevis*, *Kosswigianella exigua* and *Neophilaenus albipennis*), six butterfly (*Argynnis aglaja*, *Cupido minimus*,