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Perspective

Vanishing of the common species: Empty habitats and the role of genetic diversity

Jan Christian Habel[a,*], Thomas Schmitt[b,c]

[a] Terrestrial Ecology Research Group, Department of Ecology and Ecosystem Management, School of Life Sciences Weihenstephan, Technische Universität München, D-85354 Freising, Germany
[b] Senckenberg German Entomological Institute, D-15374 Müncheberg, Germany
[c] Zoology, Institute of Biology, Faculty of Natural Sciences I, Martin Luther University Halle-Wittenberg, D-06099 Halle an der Saale, Germany

A B S T R A C T

Biodiversity is declining, with major causes identified as habitat loss and a reduction of habitat quality. Recent studies have shown that particularly species with specific habitat demands are suffering in this way. Accordingly, habitat specialists have been nominated as umbrella species, which because they represent a much larger number of species, are thought best to fulfil the requirements of nature conservation. However, species which are ecologically intermediate between habitat specialists and generalists, and typically form networks of populations on adjoining habitats, might suffer even more severely under rapid habitat fragmentation than those specialists which had for a long time already occurred as discrete populations. Today, most of these formerly more widely distributed intermediate species also exist only as small and isolated populations which, because of their increasing geographic isolation, cannot counterbalance local extinctions by recolonisation. Furthermore, these species are mostly equipped with relatively high genetic diversity that is maintained by continual exchange of individuals between local populations. However, this high level of genetic variability frequently decreases after the collapse of population networks – with negative effects on the viability of these species. Thus, factors at the population and molecular levels may lead that formerly common species vanish in the near future.

1. Introduction

The loss of biodiversity is of major concern for conservation biologists (Primack, 2004; Meffe and Groom, 2006). However, a large array of reasons for these losses has already been detected. One major driver leading to biodiversity losses is the destruction of pristine habitats, which is particularly significant in the tropics and subtropics (Sala et al., 2000). While the negative effects caused by loss of pristine habitats are comprehensively discussed in many recent publications, we focus here on another important conservation problem: the loss of semi-natural habitats which owe their existence to traditional land-use systems. These species-rich habitats which often surpass the diversity of the original habitats (Habel et al., 2013a, 2013b) are of special concern to conservationists across Europe.

The comparatively species-poor European forest ecosystems have frequently been converted into heterogeneous agricultural landscapes. As a result of their long existence, and the immigration of species from adjoining regions, particularly species-rich habitats have developed, such as traditionally used flower-rich meadows and pastures (Uematsu et al., 2010). Consequently, the conservation problems of Europe are in many aspects diametrically different from most other parts in the world. In particular, it is not so much the expansion of agriculture into previously undisturbed pristine nature, but rather the transformation of the formerly extensively used agricultural landscapes into modern highly productive (i.e. industrial) agroindustry (and industrial forestry) that is one of the greatest threats to biodiversity across Europe (Tscharntke et al., 2012).

In a recently published contribution, Thomas (2016) summarised the history of species losses of butterflies during more than the last one hundred years, and explained these as caused by the transformation process from traditional land use systems to industrial land use. He emphasised that butterfly decline already started before the beginning of the 20th century, but that the rates of regional species losses have accelerated dramatically during the past few decades. This fact is strongly underlined by a study on butterfly community shifts conducted in southern Germany covering the period since 1840. This study revealed relatively moderate losses of species before the 1970's, but much higher rates during the following decades (Habel et al., 2016). This and

* Corresponding author at: Terrestrial Ecology Research Group, Department of Ecology and Ecosystem Management, School of Life Sciences Weihenstephan, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, D-85354 Freising, Germany.
E-mail address: Janchristianhabel@gmx.de (J.C. Habel).

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other studies particularly highlight the decline of specialist species. In another very recent contribution, Hallmann et al. (2017) communicated a 75% decline of biomass of flying insects over the past 27 years, based on data from Malaise traps operated at different sites and regions in Germany. All these traps were located in nature reserves, but mainly surrounded by intensively cultivated fields. This study presents the first evidence that the majority of arthropods, regardless of whether they are specialist or generalist species, are negatively affected by habitat loss and the deterioration of habitat quality, most probably due to agricultural intensification.

According to Thomas (2016), the observed pattern of biodiversity loss since the end of the 19th century was triggered by two distinguishable steps in the transformation process of landscapes and habitat quality across Europe: First, a severe loss of breeding habitats and the subsequently increased isolation of the remaining habitats in the wake of agricultural intensification (in most parts of Europe post 1950, but even before this in some regions with very intensive agriculture); and second, subsequent habitat degradation resulting in decreasing habitat quality of the remnant patches caused by atmospheric nitrogen loads (Stevens et al., 2004), drifting pesticides (Geiger et al., 2010) and the homogenisation of landscapes (Batáry et al., 2017). All these factors have tremendous effects on the viability of local populations and make them more vulnerable to stochastic processes and subsequent extinctions (cf. Melbourne and Hastings, 2008). This leads to declining abundances of taxa, and thus a reduction of biomass (Hallmann et al., 2017).

The magnitude of effects arising from these multiple factors varies strongly among taxonomic groups and single species, depending on their sensitivity, ecological requirements and dispersal behaviour. Species with specific habitat demands are assumed to particularly suffer under habitat degradation while habitat generalists are thought to be equipped with a higher ecological plasticity. The latter are therefore thought to be able to survive in a broader spectrum of habitat conditions, and thus to be more resilient to rapid environmental changes, such as fragmentation and the deterioration of habitat quality (Flohre et al., 2011). Furthermore, dispersal behaviour of species plays a central role, especially with respect to their resilience to habitat fragmentation (Thomas, 2000). However, most specialist species are sedentary (cf. Bink, 1992), which even aggravates the trend of species decline across Europe (cf. Thomas, 2016). While most sedentary specialists are seriously affected by degradation of their habitats, and not that much by fragmentation, the sedentary generalists are most seriously affected by fragmentation, but much less by habitat degradation. Mobile generalists, as a consequence, are the least affected group. This fact was already recognised by Thomas (2000), who observed that it is the species with intermediate mobility, and not the highly sedentary species, which are most seriously affected by population decline and subsequent extinction. However, more generally, this should account for species with an intermediate position between species with specialised habitat requirements and generalists. These intermediate species in the majority of cases rely much more on intact metapopulations than pure habitat specialists (Habel and Schmitt, 2012). In consequence, these intermediate species might react more sensitively to environmental changes, particularly increasing habitat fragmentation. Accordingly, various extrinsic and intrinsic factors are driving the current losses of species, not only in butterflies, but also in most other taxonomic groups (see Flohre et al., 2011).

2. Multifaceted factors driving biodiversity decline

The currently observed rapid loss of species can be interpreted as a two-step decline: First, specialist species vanish in particular due to losses of high quality habitat patches caused by habitat degradation. Second, less specialised but sedentary species are vanishing due to long-term isolation and the lack of recolonisations from adjoining populations (i.e. the collapse of metapopulations, see Thomas, 2000). This affects populations' (and species') persistence at the regional level. If this reasoning is accepted, the degree of specialisation per se (e.g. larval food plant specialisation; need for specific nectar sources; need for specific resting and mating structures; microhabitat structures required by the larvae; sensitivity to disturbance such as mowing or pasturing, and pesticides) should determine the prioritisation of selection of species for conservation management (Thomas, 1991, 2016). Thus, specialised species are frequently employed as umbrellas in nature conservation, and this was the intention underlying the selection of species listed on the annex 2 of the Natura 2000 directive. This approach is thought by its advocates to preserve high quality habitats for these particular species, while simultaneously allowing the survival of the vast majority of less specialised species in these high quality habitats, although the habitats were selected exclusively on the basis of the umbrella species' demands.

However, as a facet of the recently demonstrated massive loss of biomass across landscapes during the past decades (Hallmann et al., 2017), species other than habitat specialists obviously suffer from the ongoing habitat loss, landscape homogenisation and the deterioration of habitat quality. Thus, processes driving species loss and extinction are more complex (Fig. 1a). In the following, we point out why the current biodiversity crisis cannot be reversed by confining conservation management exclusively to specialised species, and the conservation of isolated nature reserves. Here, we incorporate the molecular dimension, and will subsequently draw a picture of `empty patches´ resulting from a gradual loss of species across landscapes. Hereby, we focus mainly on open land ecosystems of the temperate regions and on scientific results obtained from studies on butterfly species.

3. The genetic dimension

An important aspect, completely neglected in most contributions on species losses at the community and population level, is the genetic dimension of species conservation (Reed et al., 2003). Molecular analyses have demonstrated that the ecology and behaviour of species strongly influences their genetic structure (Habel et al., 2013a, 2013b). In general, habitat specialist species have a simple genetic make-up. As a result of purging of deleterious alleles due to increased selection against homozygotes (cf. Reed et al., 2003), they are equipped with low genetic variability within single populations when compared with generalist taxa. Therefore, genetic diversity within populations in general increases as the degree of specialisation decreases.

This pattern was, for example, demonstrated in a meta-analysis of population genetic structures of grassland butterfly species studied in western Germany (Habel et al., 2013a, 2013b). Consequently, conservation management has to consider the coherences between ecology, behaviour and population genetics of single taxa (Maes et al., 2004; Holderegger et al., 2016; Vanden Broeck et al., 2017), and not exclusively their ecological traits as often done in practice (Erhardt and Thomas, 1991; Thomas et al., 2001, 2004). In this context, we have to emphasise that high genetic diversity does not per se enhance the viability of populations. Although high genetic diversity often endows populations with a higher potential for adaptation (Reed and Frankham, 2004), the risk of inbreeding when passing through periods of population bottleneck is strongly increased with higher genetic diversity (Saccheri et al., 1998; Buza et al., 2000; Hedrick and Kalinowski, 2000; van Oosterhout et al., 2000; Nieminen et al., 2001; Reed et al., 2003). Therefore, the higher the genetic diversity within a species is, the less likely is its permanent preservation within isolated and small habitat fragments without gene flow among them (Habel and Schmitt, 2012).

Scientific studies have indicated that specialised species with sedentary behaviour suffer most from the ongoing habitat loss and deterioration of habitat quality (Thomas et al., 2001). Therefore, these species are often considered to be of key conservation concern, and are employed as umbrellas for nature conservation. Against the background