Ecological traps in bees and butterflies

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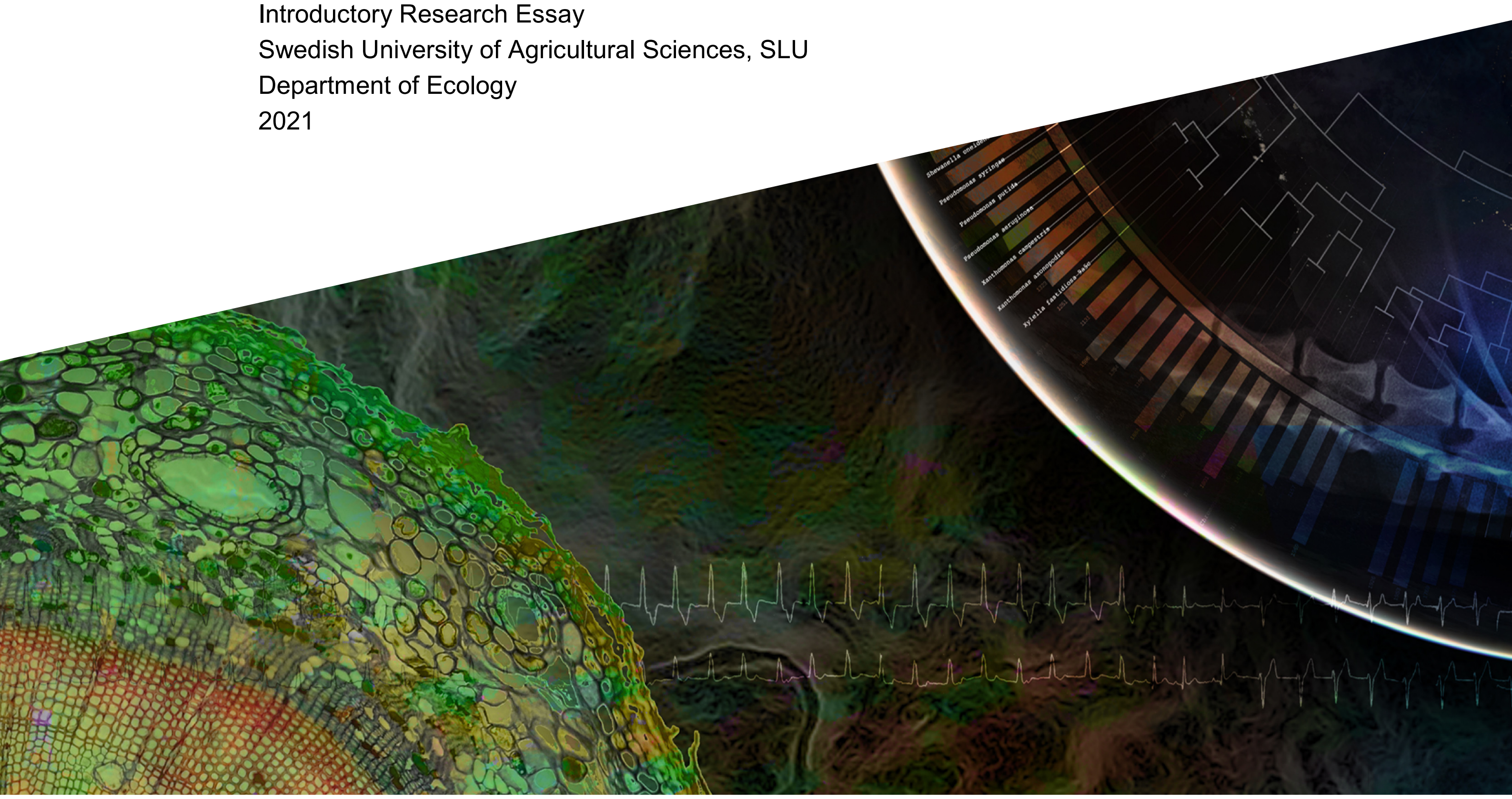

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Abstract

Among many other decisions in life, the selection of a suitable habitat is shaped by a set of cues. However, human induced rapid environmental changes can alter the relationship between cues and the environmental conditions they have been coupled to over the past. For example, cues that usually indicate habitat attractiveness can become decoupled from actual habitat suitability. As a result, there is a risk that an individual experiences an ecological trap if it inaccurately assesses the fitness value of a habitat, and responds with maladaptive behaviour by choosing a habitat that will negatively affect its fitness.

In this essay, I searched the literature for publications on ecological traps in bees and butterflies. The research output on this subject area is scarce, and most studies were unable to provide enough evidence to determine the existence of an ecological trap. Three criteria determine an ecological trap: (i) An individual (equally) prefers a poorer over a better habitat, (ii) the individual's fitness differs between both kinds of habitats, and (iii) the individuals' fitness outcome is lower in the preferred habitat. Literature indicates that the scarce research may not be the result from ecological traps being rare, but from being difficult to prove. This is reason for concern, as severe ecological traps may not only lead to population decline and local extinction, but possibly also have negative effects on metapopulations. Therefore it is necessary to promote research on this topic and to include ecological trap theory into conservation and management schemes.

Contents

Introduction

The concept of the ecological trap was first introduced almost 50 years ago by Dwernychuk & Boag (1972). They observed that ducks nesting on the same Canadian in-lake islands as gulls at first benefitted from the indirect protection of gulls fending off egg predators. But later on, the ducks lost a great deal of their successfully hatched offspring to preying gulls, which fed their chicks with the ducklings. With this study, the authors defined the fundamental definition of an ecological trap: An individual actively selects a habitat in which its fitness is compromised. Habitat selection is shaped by a set of cues, but in changing environments cues that usually indicate habitat attractiveness can become decoupled from actual habitat suitability (Robertson & Hutto, 2006). As a result, individuals may unwittingly make maladaptive habitat choices (Schlaepfer et al., 2002). For the ducks studied by Dwernychuk & Boag (1972), terns colonizing newly emerged islands may have been the original cue for habitat attractiveness, a species that is known to fend off egg predators without preying on ducklings. Although this benefit diminished as soon as gulls settled on the islands, the ducks continued to choose these islands for nesting, possibly being either positively imprinted with terns alone or maybe also not distinguishing between terns and gulls (Dwernychuk & Boag, 1972). While this study describes a natural cause creating the ecological trap, the concept further developed and is nowadays based on changing environmental cues due to sudden anthropogenic changes (Schlaepfer et al., 2002).

Human-induced rapid environmental changes (HIREC) include among other examples habitat loss and fragmentation, spread of exotic species, pollution, exploitation and climate change, and can alter the relationship between environmental cues and the conditions they have been coupled to over the past (Sih et al., 2011). Consequently, an individual is at risk of inaccurately assessing the fitness value of a resource and may respond to the change with maladaptive behaviour by unknowingly choosing a resource that is likely to negatively affect its fitness in time (Robertson et al., 2013; Sih et al., 2011). This phenomenon is called an evolutionary trap and includes any maladaptive decisions regarding any resources such as food, mating partner or habitat (Robertson et al., 2013; Schlaepfer et al., 2002). The ecological trap is classified as part of the evolutionary trap theory, but only focuses on the maladaptive choice of habitat (Robertson et al., 2013; Schlaepfer et al., 2002). Although habitat use is often seen as a species-specific trait, environmental cues are perceived individually and possibly with intra-specific variation (Van Dyck, 2012).

Three possible causes for an ecological trap to arise have been proposed. One possibility is that the original cue remains the same, but the habitat changes (Schlaepfer et al., 2002). The unaltered cue still triggers the same behavioural response from the individual as previously, but this cue is no longer a good indicator of habitat suitability; just like the ducks only accounted for the indirect protection of the terns but not the threat from the presence of gulls in the study mentioned above (Dwernychuk & Boag, 1972; Schlaepfer et al., 2002). Another possible cause can be that both the cue and the habitat change, but the cue still triggers the normal behaviour of the individual (Schlaepfer et al., 2002). For example, both ponds and asphalt roads polarize light horizontally, and mayflies using the light polarization as cue for habitat suitability were shown to mistakenly lay their eggs on roads, even though ponds were available in the vicinity (Kriska et al., 1998). A third possibility is that the cue but not the habitat changes, resulting in the unaltered habitat being more attractive (Robertson & Hutto, 2006). There are three specific criteria necessary to demonstrate the existence of an ecological trap (Robertson & Hutto, 2006). First, the individuals either prefer a poorer over a better habitat, which is called a ‘severe trap’, or individuals equally prefer both kinds of habitats, called an ‘equal-preference trap’. Second, the individuals’ fitness, or a surrogate for it such as reproduction or survival, differs between both kinds of habitats. And third, the individuals’ fitness outcome is lower in the preferred or equally preferred habitat. Others have argued that an not only needs the individual’s fitness outcome to be lower in the preferred habitat, but that the overall population growth rate needs to turn out net negative (Gilroy & Sutherland, 2007). This assumption highlights possible population level effects of ecological traps, which in turn can have implications for species conservation. An ecological trap can therefore result in population decline or local extinction (Schlaepfer et al., 2002) and thus even affect metapopulations by affecting fecundity and survival of local populations (Hale et al., 2015).

The most recent literature review covering ecological traps found only 29 studies that could prove ecological traps following the definition and criteria by Robertson & Hutto (2006) (Hale & Swearer, 2016). The majority studied birds, followed by arthropods, and fewest studies were found on fish, amphibians and reptiles. Looking at the studies on arthropods, eight covered insects, and seven of these showed traps for several aquatic species, which were attracted by different sources of light pollution and polarized light simulating the polarization of water bodies (Boda et al., 2014; Hale & Swearer, 2016; Horváth et al., 2007, 2010; Kriska et al., 1998, 2008; Robertson et al., 2010; Szaz et al., 2015). The review found only one study demonstrating an ecological trap for a non-aquatic insect, the butterfly *Lycaena xanthoides* (Hale & Swearer, 2016; Severns, 2011), described below. While the lack of research about ecological traps for terrestrial insects in general is alarming, the aim of this essay is to get an overview of the literature regarding ecological traps in bees and butterflies. Butterflies are important indicator species as they are sensitive to habitat structure and change (Erhardt, 1985) and they are commonly used as model organisms to investigate the effects of HIREC. Pollinators, including butterflies and bees, have next to their intrinsic value high ecosystem and economic values as they are important for food production, but suffer from HIREC (Potts et al., 2010). The few solid studies found on ecological traps in this group before indicated that the outcome of this search might be sparse.

Therefore, I also aim to find examples of publications that prove or indicate ecological traps, but where either not aware of this phenomenon or did not mention and discuss the terms in their study. I investigate if evidence suggests that the low attention from empirical research about ecological traps in bees and butterflies can be explained by ecological traps being either difficult to detect, hard to prove, or from being a rare phenomenon. Finally, I discuss possible implications for species conservation and management.

Current evidence for ecological traps in bees and butterflies and their causes

Robertson & Hutto (2006) reviewed 45 publications that purpoted to demonstrate ecological traps or which were cited by other authors as proving ecological traps. Of those, they determined only five studies that proved ecological traps based on their three criteria (Robertson & Hutto, 2006). Following their footsteps, Hale & Swearer (2016) reviewed 127 publications, and found that only 29 could prove an ecological trap. Only one study was found in any of the reviews that demonstrates an ecological trap in a butterfly (Severns, 2011), and no study was found about bees. Their work is the most recent literature review, and in order to get an overview of the literature about ecological traps in bees and butterflies after 2016, I searched the Web of Science Core Collection using the queries "ALL=("evolutionary trap*" OR "ecological trap*") AND ALL=("bees" OR "Apiformes" OR "Apoidea")" and "ALL=("evolutionary trap*" OR "ecological trap*") AND ALL=("butterfl*")". Although ultimately I was only interested in ecological traps, I included the search for 'evolutionary trap' because per definition the term can include ecological traps as well. In total, the search resulted in 35 publications, of which 31 came up including the term 'butterfly' or 'butterflies' and six including the term 'bees'. Assuming that all publications including the terms 'ecological trap' and or 'evolutionary trap' were assessed by Hale & Swearer (2016), I excluded publications published before 2016 not listed as a 'demonstrated trap' in their review.

My search resulted in twelve publications that cover ecological traps in bees and or butterflies, of which one publication is a review (Gardiner et al., 2018) and one is a meta-analysis (Yoon & Read, 2016). For the remaining ten studies, I evaluated whether the environmental change was of anthropogenic origin, i.e. whether it was a human-induced rapid environmental change (HIREC). Additionally, I evaluated whether the study met the three criteria for an ecological trap as by the definition of Robertson & Hutto (2006), i.e. (i) if an individual (equally) preferred a poorer to a better habitat, (ii) if the individuals' fitness differed between habitats, and (iii) if the individuals' fitness outcome was lower in the (equally) preferred habitat (see Table 1). If all three criteria were met, I

Title	Authors	Ecological trap	(Equally) prefer poorer to better habitat	Fitness differs between habitats	Fitness is lower in the (equally) preferred habitat	HIREC
Habitat restoration facilitates an ecological trap for a locally rare, wetland- restricted butterfly	(Severns, 2011)	Yes	Yes	Yes	Yes	Yes
Lethal trap created by adaptive evolutionary response to an exotic resource	(Singer & Parmesan, 2018)	'Eco-evolutionary trap'	Yes	Yes	Yes	Yes
Invasive paper wasp turns urban pollinator gardens into ecological traps for monarch butterfly larvae	(Baker & Potter, 2020)	Potentially		Yes		Yes
Comparing diversity to flower-bee interaction networks reveals unsuccessful foraging of native bees in disturbed habitats	(Carman & Jenkins, 2016)	Potentially	*			Yes
Roadside habitat impacts insect traffic mortality	(Keilsohn et al., 2018)	Potentially		Potentially		Yes
Experimental field evidence shows milkweed contaminated with a common neonicotinoid decreases larval survival of monarch butterflies	(Knight et al., 2021)	Potentially, experimental study		Yes		Yes
Butterflies do not alter oviposition or larval foraging in response to anthropogenic increases in sodium	(Mitchell et al., 2019)	Potentially	Potentially			Yes
Traffic influences nutritional quality of roadside plants for monarch caterpillars	(Mitchell et al., 2020)	Potentially		**		Yes
Biogeography and phenology of oviposition preference and larval performance of Pieris virginiensis butterflies on native and invasive host plants	(Augustine & Kingsolver, 2018)	Potential future scenario, theoretical experiment	Yes	Yes	Yes	Yes
Climate change and an invasive, tropical milkweed: an ecological trap for monarch butterflies	(Faldyn et al., 2018)	Potential future scenario, theoretical experiment	Yes	Yes	Yes	Yes
Rights-of-way: a potential conservation resource	(Gardiner et al., 2018)	Review that suggested that 'rights-of-way' can act as ecological trap				
Consequences of exotic host use: impacts on Lepidoptera and a test of the ecological trap hypothesis	(Yoon & Read, 2016)	Meta-analysis that showed that invasive plants can act as ecological trap				

Table 1 Publications studying ecological traps in bees and butterflies. Empty cells indicate insufficient or unavailable data. HIREC = Human Induced Rapid Environmental Change. * Density was used as a measure of habitat preference, which is debated to be no viable indicator for it (Robertson & Hutto, 2006). ** Only the amount of chemicals in caterpillars were assessed but not the actual fitness effects.

evaluated the study as proving an ecological trap. If only one or not all criteria were met, I evaluated if the study is showing evidence for possible ecological traps. Only one study met all necessary criteria and demonstrated an ecological trap (Severns, 2011), which is the study also evaluated as such by Hale & Swearer (2016). Six publications found indicators towards an ecological trap, but did not study or proof if all criteria were fulfilled (Baker & Potter, 2020; Carman & Jenkins, 2016; Keilsohn et al., 2018;

Knight et al., 2021; Mitchell et al., 2019, 2020), and one publication observed what they termed an 'eco- evolutionary trap' (Singer & Parmesan, 2018) (Table 1).

Two publications discuss potential ecological traps that might arise in the future (Augustine & Kingsolver, 2018; Faldyn et al., 2018) (Table 1), which will be discussed in a later chapter. The eight case studies which prove or indicate traps and their causes and effects will be discussed in the following subchapters, depending on the HIREC involved.

Restoration

When thinking of environmental changes driving populations into decline or extinctions, changes towards a more degraded habitat come to mind, like through fragmentation or pollution. This is also reflected by literature focussing on habitat degradation as cause for ecological traps (Battin, 2004; Delibes et al., 2001; Gilroy & Sutherland, 2007; Robertson & Hutto, 2006; Schlaepfer et al., 2002) However, also the opposite can be the case. The study of Severns (2011) is so far the only to provide sufficient evidence for an ecological trap involving butterflies, and alarmingly shows interventions aimed at improving habitat quality as the cause for the trap to arise. In western Oregon, USA, several seasonally flooded wetland prairies were restored, resulting in a mosaic of restored and degraded habitat. The restored wetlands were planted with *Rumex salicifolius*, the exclusive host plant of the local butterfly *Lycaena xanthoides*, and are otherwise dominated by a native grass which does not overgrow the host plant. *R. salicifolius* also grows naturally in the non-flooded areas, but in these areas is largely overgrown with exotic grasses. Because the flight period of *L. xanthoides* does not overlap with the seasonal flooding, the butterfly is unlikely to be able to distinguish inundated and non-inundated host plants. Instead, the physically more apparent host plant in the flooded habitat acted as misleading cue for habitat attractiveness, resulting in a more frequent oviposition combined with larger egg loads on inundated plants, although the egg survival was about seven-times lower than on the overgrown host plant in the non-flooded habitat, as shown in a previous study (Severns et al., 2006). All three criteria needed to demonstrate an ecological trap were met; habitat preference, lower fitness through impaired habitat-specific reproduction and preference for the lower quality habitat (Robertson & Hutto, 2006; Severns, 2011) (Table 1).

Management of semi-natural habitats

Habitat management can be conducted for different reasons, such as safety in infrastructure habitats or for aesthetic purposes in urban or recreational areas, but it can also have a habitat or species conservation centred approach. Mowing or grazing semi-natural grasslands is necessary to retain an open vegetation and the often typical high diversity of both plants and animals, but there is an ongoing debate about the best management, as both higher and lower frequencies of mowing or intensity of grazing can have both positive and negative effects on the local biodiversity (Tälle et al., 2018). Carman & Jenkins (2016) investigated whether differently managed habitats could act as ecological trap for bees. They compared one undisturbed scrub habitat with three managed habitats of different disturbance levels caused by management through roller-chopping once or twice and grazing, and measured flower and bee diversity and observed flower-visiting bees. The results of this study showed that although the abundance of bees did not decrease with increasing disturbance, the interaction of flowers and bees did decrease, also reflected by simpler interaction networks under disturbance. This indicates that bees still foraged in less rewarding habitats, which might result in higher costs of time and energy. However, the authors also point out that this is insufficient data to reflect if the fitness is actually impaired. Actually, the possibly lower fitness in human disturbed habitats is the only criterion for an ecological trap that was investigated in this study (Table 1). It was not sufficiently examined if the bees preferred one habitat over the other. Their abundance may only result from the inability to forage far enough to find better habitat, or from other community processes. The authors mention that the distance between the study sites ranged from 0.2 km to 8.5 km, which could mean that the bees can migrate between all or perhaps only some sites, and there is no information given on the size of each area, nor on the time since the same management is applied. Therefore, within this study design it cannot be investigated whether a bee prefers one site over another, and if the habitat of lower quality is deemed more attractive (Table 1).

The abandonment of previously managed grasslands and the concomitant vegetation succession can have negative effects on the number of butterfly species (Öckinger, Hammarstedt, et al., 2006). Although butterflies may at first benefit from the resulting taller and more heterogeneous vegetation (Kruess & Tscharntke, 2002; Öckinger, Eriksson, et al., 2006), the richness of grassland butterfly species is likely to decline with increasing shrub and tree cover (Öckinger, Hammarstedt, et al., 2006). Adult butterflies are very mobile and able to emigrate if the habitat is no longer suitable, which makes them a practical indicator species for habitat change (Erhardt, 1985). However, there can be severe consequences if individual butterflies do not realize that the previously suitable but now abandoned habitat has changed to their disadvantage and do not emigrate. The study by Singer & Parmesan (2018) shows how a butterfly population can go extinct when they are not able to adapt behaviour to habitat changes due to misleading cues for habitat attractiveness. On a meadow in western North America, the butterfly *Euphydras editha* experienced higher larval survival on the exotic *Plantago lanceolata* than on its original host, *Collinsia parviflora*, and was shown to first evolve a preference and later full dependence on the new host (Singer et al., 1993; Singer & Parmesan, 2018). However, the advantage through the new host only remained as long as the meadow was grazed by cattle (Singer & Parmesan, 2018). Once the grazing ceased a few decades later and grasses were overgrowing *P. lanceolata*, the local butterfly population went extinct. The authors hypothesize that a change in temperature on *P. lanceolata* and presumably higher larvae predation rates in the lush vegetation have been the causes (Singer & Parmesan, 2018; Wiklund & Friberg, 2008). *E. editha* likely misinterpreted *P. lanceolata* as cue for reproductive success, without knowing that the changed habitat, i.e. the higher vegetation surrounding the host plants, would diminish all benefits. Earlier observations by Singer et al. (1993) showed the butterfly's preference for the exotic *P. lanceolata*, and the advantages through the new host were so strong that the population developed full dependence on it. The local extinction of the butterfly decades later and after the withdrawal of management is a clear sign for lower fitness of the butterfly population (Singer & Parmesan, 2018) (Table 1). However, the individual butterflies did not actively prefer the habitat of lower quality, because it was the only option available. Over just several decades, the local population was imprinted on the new host, and the old host did not even represent another possibility anymore. Therefore, the criteria of preferring a habitat of lower quality was not exactly met and the studied events cannot be termed a true ecological trap by the definition of Robertson & Hutto (2006).

Agricultural intensification

Neonicotinoid insecticides have received great attention during the last years, due to increasing evidence of their lethal and sub-lethal effects not only on targeted but also non-targeted organisms. Neonicotinoids are mostly applied as seed coating, which allows the chemicals to be distributed within the whole plant during the plants' development and protects the plant already from the beginning from attacking insects (Jeschke et al., 2011). The treatments are primarily targeted at sucking and chewing insects damaging the plants (Jeschke et al., 2011) but were also shown to negatively affect bees and butterflies (e.g. see Basley & Goulson, 2018; Kessler et al., 2015; Knight et al., 2021; Rundlöf et al., 2015). The study from Knight et al. (2021) compared the effect of exposed and non-exposed milkweed to the neonicotinoid clothianidin on the reproductive success of the monarch butterfly, *Danaus plexippus*. While the authors found more eggs laid on the exposed milkweed, they acknowledge their data to be insufficient to prove habitat preference (Table 1). They could not show if the amount of eggs depended on the individual, i.e. the amount of eggs laid per female, or on the number of females laying eggs. Larval survival was lower on clothianidin exposed milkweed (Knight et al., 2021), indicating a reduced fitness through decreased reproductive success (Table 1). However, they could not study the adult survival between individuals from exposed and non-exposed milkweeds, and lacked knowledge on the possible influence of arthropod predators on larval survival. In the field experiment, all exposed milkweed plots were located adjacent to another agricultural field, while all non-exposed milkweed plots were located adjacent to a field margin with shrubs and trees, and the study was not able to investigate possible effects from this design (Knight et al., 2021). While it is hardly possible to study adult survival of a migrating butterfly in the wild, observing individual egg laying might enhance the understanding of clothianidin influence on the behaviour and possible environmental cues of *D. plexippus*, in combination with larval survival. Additionally, to verify that habitat preference does not result from adjacent land cover, future studies might consider using more study sites.

Road verge habitats

Land adjacent to roads is managed to maintain an open vegetation for traffic safety reasons and has been shown to possibly harbour as much or even higher biodiversity as natural or semi-natural grasslands (Gardiner et al., 2018). However, species in these habitats can also be exposed to multiple threats e.g. through traffic mortality and mowing (Muñoz et al., 2015). For example, increased pollen and nectar resources close to roads can risk the creation of an ecological trap, attracting species to a habitat associated with possibly decreased fitness or even increased mortality (Battin, 2004; Gardiner et al., 2018; Keilsohn et al., 2018).

Keilsohn et al. (2018) showed that the type of habitat bordering the road (lawn, meadow, or woods), as well as the presence of a vegetated median (or central reservation) had an impact on the mortality of bees and butterflies. For bees, mortality was positively related to flower abundance, and the highest mortality was found at roads with lawn verges and a median. The authors offer two explanations: First, that clover which was dominant in lawn transects could have acted as cue for habitat attractiveness for honeybees and bumblebees, bringing them dangerously close to the road, and second, that the lawn was not attractive enough, so the bees decided to continue foraging and crossed the road to explore the median, resulting in a higher mortality. Butterflies also showed highest mortality with a median present, but along meadow verges. The authors point out that road verges could act as ecological traps if they attract insects but at the same time put their survival at risk due to traffic mortality. Further research is needed regarding distance to the road, road barriers, the interaction of traffic volume and speed, and the turning point at which more insects are supported than killed (Keilsohn et al., 2018; but also see Gardiner et al., 2018; Phillips et al., 2020). However, in order to determine if road verges are ecological traps, other information is needed as well. The study showed higher mortality at certain types of road verge habitat, but not if the abundance of living insects also differed in the studied habitats. Therefore, it is not possible to say how the mortality of insects relates to their abundance in the verge, and if and how this changes between different verge types. Thus it is not possible to clearly state the difference of fitness between habitats (Table 1). Furthermore, habitat preference was not assessed (Table 1). To determine whether road verges can act as ecological traps, it must be studied if the insects choose the road verge habitat over another habitat within their range, and if mortality is aimed as a measure of fitness, the mortality rate of the local population would be more viable data than just the mortality itself.

The publication by Mitchell et al. (2019) studied if the monarch butterfly *D. plexippus* and the cabbage white butterfly *Pieris rapae* experiences an ecological trap through elevated sodium in their milkweed host plants along roads. Sodium can be beneficial but also toxic in too large amounts and can accumulate in road verges and road verge vegetation through the use of de-icing salt or adjacent crop irrigation (Mitchell et al., 2019; Snell-Rood et al., 2014). The study showed that female butterflies did not prefer host plants with increased sodium content, but equally preferred various concentrations of sodium. However, larvae of tended to avoid the highest concentrations of sodium used. This means that although ovipositing females equally preferred plants of different sodium concentrations, larvae might still be able to adjust their feeding behaviour and account for plants with potentially toxic sodium content. However, Mitchell et al. (2019) did not study if there is an actual fitness effect of the sodium on the butterflies. Nevertheless, in a publication that can partly be seen in connection to the previous study, Mitchell et al. (2020) studied the uptake of several chemicals in milkweeds along roads, including sodium, by larvae of *D. plexippus*. They found out that although the milkweeds showed signs of pollution through various chemicals, most of the plants were probably still suitable as host plants for the monarch larvae. Only very few plants that were located close to the road edge and along high traffic roads contained amounts of sodium that are likely to be toxic. However, Mitchell et al. (2020) only used the content of sodium in the larvae, and hypothesized that increased sodium content might be toxic without studying visible fitness effects on living specimen. A recent publication showed that although high levels of sodium can have stressful effects on larval development, for example through longer development time, even the highest levels of sodium that was found along roads did not impact larval survival (Shephard et al., 2021).

Private gardens

Urban gardens can constitute refuge habitat for pollinators suffering from unfavourable agricultural environments (Wenzel et al., 2020). Also negative effects of urbanization can be buffered by offering additional floral resources using wild seed mixes or by reducing lawn mowing (Wenzel et al., 2020). It is increasingly common that private persons aim to attract bees and butterflies to their gardens, and this is also encouraged e.g. by conservation organisations promoting seed mixes, or garden centres selling insect hotels. However, similar to attracting pollinators to road verges, attracting them to private gardens can expose them to unaccounted dangers. Baker & Potter (2020) argue that private gardens in Kentucky became ecological traps after citizens were encouraged to plant milkweeds to support the monarch butterfly *D. plexippus*. They observed that the invasive paper wasp *Polistes dominula* attacked larvae of *D. plexippus* in urban pollinator gardens. Using sentinel larvae, they found significantly higher predation on milkweeds in urban gardens than in rural meadows (Baker & Potter, 2020). *D. plexippus* might have recognized the milkweed as an attractive host plant, with no cue available for increased predation in urban gardens. Higher mortality through increased predation was proven, but there was no examination of fitness of living larvae between the habitats. The authors discuss that even if *P. dominula* does not successfully kill the larvae, also the interruption in feeding e.g. by causing the larvae to plunge from the plant could reduce the fitness, and it would be interesting to investigate this further. As with many of the previous examples, habitat preference was not assessed. The study design did not allow the investigation of whether the monarch butterfly (equally) preferred urban garden habitats to the also studied more rural habitats, and therefore it is not possible to draw conclusions whether milkweeds planted in gardens can act as ecological traps (Table 1).

Are we looking for ecological traps in the right way?

The case studies prove or indicate traps involving various HIREC, and do not only include changes towards a more degraded habitat such as agricultural intensification (Knight et al., 2021), but also positively intended changes, such as the restoration of natural land (Severns, 2011) or plantings of host plants in urban gardens (Baker & Potter, 2020). Only one out of ten studies was able to meet all necessary criteria to demonstrate an ecological trap (Severns, 2011), but the remaining studies show more or less strong evidence that individuals in diverse habitats affected by various HIREC may suffer from ecological traps (Table 1). This underlines the apparent difficulties in appropriate and feasible methods to detect and study ecological traps by providing sufficient information about habitat preference and fitness.

Habitat preference

Of the three criteria used to demonstrate an ecological trap, habitat preference seems to be the most difficult to examine. To investigate habitat preference in butterflies, all publications that studied this criterion used oviposition preference. This is not only a viable measurement for comparing host plants as cue for habitat attractiveness, but is also a feasible method to conduct in the field. The larvae are not as mobile as the adults and their survival and fitness depends on the chosen oviposition site (Doak et al., 2006). Butterflies are often specialized on one or a few host plant species, therefore it can be a good method to look for the species' respective host plant. However, when studying oviposition there is a difference in counting egg loads on individual plants and observing the egg-laying behaviour of individual butterflies. While the first approach gives more information on behaviour on a population level, only the latter provides viable information about if the amount of eggs laid depends on the individual butterfly, or on the number of females that laid eggs (Knight et al., 2021). In order to prove host plant preference only by accounting for the total number of eggs laid on each plant, all potential host plants should be located within the same habitat, i.e. the same plots. Accounting for the egg laying behaviour of every individual would also allow the comparison of different populations in separated habitats. Another possible method might be to assess butterfly abundance separately in each habitat, and analyse the relationship between observed butterflies and number of eggs. However, with increasing spatial scales these methods also get increasingly impractical to realise.

For the only study on bees addressing habitat preference, the comparison of the number of bees in different habitats was used as a measure. However, density, i.e. the abundance per unit area, is not a viable measurement for habitat preference (Robertson & Hutto, 2006). Furthermore, habitat preference is not interchangeable with habitat use or habitat selection (Robertson & Hutto, 2006). Preference is the active choice for one habitat when other habitats are available to choose as well, whereas habitat use or selection can be forced if e.g. no other habitat is available, like in source-sink dynamics (Battin, 2004). If there is constant migration e.g. from a source to an attractive sink habitat (i.e. an ecological trap), studying only the number of individuals present in the sink habitat might disguise the fact that the habitat is actually less attractive (Delibes et al., 2001). If more studies included a viable measure for habitat preference, it is likely that the number of detected ecological traps would increase (Yoon & Read, 2016). However, it can be time and resource demanding and might still be the most difficult criterion to prove.

Fitness

When no viable measure for habitat preference is provided or assessed, it is not possible to draw conclusions if the preferred or equally preferred habitat offers lower fitness. Therefore, for these studies, only the criteria about a difference in fitness between the studied habitats can be addressed. This can still point towards possible ecological traps, but might also be an indication for source-sink dynamics (Delibes et al., 2001). Therefore, only using fitness must be considered with caution when discussing an ecological trap scenario. To measure fitness in butterflies, the most commonly used variable in the described studies was larval survival, but also larval body mass and egg survival were used. These methods provide important data on fitness by means of reproductive success when two or more habitats are compared. Regarding bees, Carman & Jenkins (2016) argue that a decrease in foraging resources in bees might lead to an increase of time used for foraging and thus to lower fitness through a decrease in energy. However, it is difficult to prove the direct effect on individual solitary bee species. Studying the effects of resource availability on bees, one possibility could be to observe foraging time of individuals nesting in a trap nest (artificial nesting structure), and assess the amount of stored pollen for the offspring in relation to the time spent collecting it (e.g. Ganser et al., 2021). For social species, this method could be applied as well, e.g. by assessing the colony size of bumblebees in relation to foraging resources (e.g. Kämper et al., 2016). However, using artificial nesting structures interferes with the ability to draw conclusions on habitat preference, as it is impossible to know which nesting sites individuals perceive as inferior or superior (Robertson & Hutto, 2006). Another measurement for decreased fitness is mortality. Mortality of bees and butterflies through vehicle collisions was used in a study on roadside habitat (Keilsohn et al., 2018) and is feasible to assess in habitats including areas where dead bodies accumulate, such as roads. Direct mortality can be a clear measurement for decreased fitness in an individual but its effect may depend on the time of death, for example if a female dies before or after lying eggs.

Are we overlooking ecological traps?

Ecological traps are maybe not as rare as literature suggests

Literature reviews found only a few publications on ecological traps fulfilling all criteria (Hale & Swearer, 2016; Robertson & Hutto, 2006; this essay). Although there was an increase from five demonstrated traps in the review of 2006 to 29 in the review of 2016, only 10 years later, it still reflects a very low research output. To see if there are studies about bees or butterflies that might have missed an ecological trap, I conducted a literature search in the Web of Science Core Collection using keywords that can be associated with ecological traps, such as maladaptive and behavioural mismatch (Hale & Swearer, 2016; Robertson & Hutto, 2006), or sink (Battin, 2004; Delibes et al., 2001). Using the query “ALL=("maladaptive" OR "behavioral mismatch" OR "behavioural mismatch") AND ALL=("butterfl*" OR "Lepidoptera" OR "bees" OR "Apiformes" OR "Apoidea")”, I aimed to identify studies after 2015 (assuming that previous publications were covered by Hale & Swearer (2016)) that possibly came across ecological traps but either didn’t detect them or didn’t use the terminology. The search resulted in 25 publications, and by evaluating the abstracts, no study seemed to possibly have encountered ecological traps. Additionally, I searched the literature for studies about sinks, as ecological traps and human-caused attractive or equally attractive sinks to source habitats are similar in their theory (Battin, 2004; Delibes et al., 2001). In the Web of Science, I applied the query “ALL=("sink") AND ALL=("butterfl*" OR "Lepidoptera" OR "bees" OR "Apiformes" OR "Apoidea")”, which resulted in 178 publications. Therefore, I additionally filtered for the following research areas: Ecology OR Entomology OR Biodiversity Conservation OR Zoology OR Biology OR Evolutionary Biology OR Environmental

Sciences. This search resulted in 111 publications, and after reading the abstracts and in uncertain cases downloading the full paper, again no study seemed to possibly have encountered ecological traps under first impression, but failed to detect it.

There are three reasons for this outcome; ecological traps are either hard to expose, very rare, or the authors are not aware of the concept (Battin, 2004; Robertson & Hutto, 2006). Regarding the increase in studies demonstrating ecological traps, it is likely that there often is insufficient data on all necessary criteria and thus it is not possible to analyse whether the studies could actually indicate ecological traps in such a quick assessment. Less than 10% of the studies that Hale & Swearer (2016) determined to have failed to demonstrate an ecological trap even assessed habitat preference. Studies in ecology often compare abundance, number of species or various diversity indices between habitats, but do not assess habitat preference as this is often complicated to examine. In my initial literature review I found studies indicating possible ecological traps in various environments, which points towards the possibility of their existence under diverse circumstances. These findings, combined with the apparent difficulty in measuring habitat preference, suggest that rather than being extremely rare, ecological traps are instead somewhat difficult to detect.

Evidence for undetected ecological traps

To determine which habitats might have the potential to act as ecological traps, meta-analyses and reviews can also be helpful tools by compiling information of different studies that in the best case verify and complement each other. For example, the meta-analysis by (Yoon & Read, 2016) examined if invasive plant species can act as ecological traps for butterflies and moths by analysing data on oviposition preference and offspring survival and performance of several different studies. Invasive plants can have a negative effect on the abundance of butterflies and diurnal moths by decreasing native host plant diversity through competition (Valtonen, Jantunen, et al., 2006). They were able to demonstrate that while some species preferred native hosts for oviposition, the summary of all studied Lepidoptera showed that native hosts were not significantly selected over invasive hosts (Yoon & Read, 2016). This indicates that invasive host plants were equally preferred to their native counterparts. However, larval survival was lower on invasive hosts, and larvae on invasive hosts had decreased body mass compared to larvae on native hosts (Yoon & Read, 2016), proving a reduced fitness in the equally preferred habitat.

A review by Gardiner et al. (2018) discussed whether rights-of-way could act as ecological traps. Not only the land adjacent to roads (see earlier chapter), but also along railways and electric power lines is managed to maintain open vegetation, harbouring as much or even higher biodiversity as natural or semi-natural grasslands (Gardiner et al., 2018; Phillips et al., 2020). However, species in these habitats can also be exposed to possible threats e.g. through mowing (Valtonen, Saarinen, et al., 2006), pollution and traffic mortality (Muñoz et al., 2015) or by electrocutions on power lines (Gardiner et al., 2018). Managing rights-of-way can benefit biodiversity, but potential effects of attracting species to a habitat associated with possibly decreased fitness or even higher mortality need to be considered (Gardiner et al., 2018). Different mowing regimes of road verges were shown to influence butterfly abundance, as mowing at time of oviposition can reduce host plant availability and possibly lead to an increased mortality of already oviposited eggs or larvae (Valtonen, Saarinen, et al., 2006). Power-line corridors can facilitate the spread and establishment of invasive plants (Lampinen & Anttila, 2020), which can cause ecological traps for butterflies (Yoon & Read, 2016). Along roads, chemicals from e.g. exhaust, de-icing salt or run-off from adjacent agricultural land can accumulate in plants, which can make plants more attractive for insects even though the concentration of chemicals might be toxic for them (Mitchell et al., 2020). Although there are several studies providing information or indicating reduced fitness in habitats of rights-of-way, so far no study was able to investigate all three criteria needed to actually demonstrate an ecological trap.

Future environmental change risking ecological trap creations

Besides investigating possible undetected ecological traps in the present, it is also important to look for traps that might arise under future conditions. This also offers the possibility to study traps before and after they form, which can provide valuable information for management plans, allowing to predict the effects of habitat changes and to monitor populations before and after the change occurs (Hale & Swearer, 2016).

Ongoing climate change is changing and shifting habitats and phenology of bees and butterflies (e.g. Kammerer et al., 2021; Van Dyck et al., 2015), which can possibly result in future ecological traps. One such possible future scenario was demonstrated by Faldyn et al. (2018); they showed that under increasing temperatures, the concentrations of cardenolides in an exotic milkweed species may increase and change from beneficial to detrimental, which could affect the fitness of the monarch butterfly *D. plexippus* in south-eastern USA. Under current temperature conditions, *D. plexippus* experienced higher larval survival on the exotic compared to the studied native milkweed species. However, under increasing temperatures, there was a strong decline in butterfly performance (using larval survival, adult body mass and forewing length as variables), but only for the exotic milkweed. Under future climate conditions, the monarch butterfly might misinterpret the exotic host plant as cue for habitat attractiveness, although its changed concentration of cardenolides possibly leads to a decreased fitness (Faldyn et al., 2018).

Next to increasing temperatures in the future, it is also possible to look at the potential spread of exotic plants and their impact on the habitats they may invade. Augustine & Kingsolver (2018) found that in south-eastern USA the invasive *Alliaria petiolata* is utilized as host plant by *Pieris viriginiensis*, as it is related to their native host plant, although larval survival was much lower on the invasive host. They found that *P. viriginiensis* individuals originating from a region where *A. petiolata* had not yet invaded, but is expected to do in the future, also utilized it as host plant. Although individuals from both populations did not show oviposition preference between the native and invasive host in the early season, late season females clearly preferred the invasive host, possibly due to the early senescence of the native host (Faldyn et al., 2018). First, this indicates that individuals in the already invaded regions might already experience an ecological trap, as they (equally) prefer the invasive plant as host, although it subjects them to lower fitness through decreased larval survival. Second, this study shows that other *P. viriginiensis* populations might suffer the same fate in the future, if *A. petiolata* will spread to their habitat. However, this study was purely experimental, and in order to gain clearer insights and knowledge on population level effects, it is necessary to observe oviposition and survival in the field.

These examples show that studying potential future ecological traps can give valuable information about their possibility to arise in space and time, and help to find measurements that can be taken to counteract their formation or population effects. Also studying already existing traps can help to understand conditions of formation and population effects under various circumstances. Overall, as the scientific knowledge about ecological traps grows, it is likely that the increased understanding of the underlying processes facilitates the detection not only of more but also of more concealed trap scenarios, including those that stretch over long periods of time such as the example of the eco-evolutionary trap from Singer & Parmesan (2018).

What are the implications of ecological traps for conservation and management?

If the behavioural response of an individual to an environmental change is maladaptive and leads to a decreased fitness, the result could be a population decline or even a population extinction (Schlaepfer et al., 2002). The inferior habitat can thus act as a population sink. In source-sink dynamics, organisms preferably settle in the source habitat, which supports population growth, and only settle the sink habitat with a negative population growth rate when the source habitat is occupied (Battin, 2004). However, this only holds when the sink is actually avoided, but when an organism is deceived and changes to a preference of the inferior habitat, then a sink becomes attractive (Delibes et al., 2001). If the environmental cue that deceived the organism is caused by sudden anthropogenic changes, then the attractive sink is equivalent to an ecological trap (Battin, 2004). Unfortunately, even habitat changes intended to support biodiversity seem to be a possible cause risking potential ecological traps to arise, e.g. through habitat restoration (Severns, 2011), establishing host plants in new environments (Baker & Potter, 2020), or managing rights-of-way to increase floral resources (Keilsohn et al., 2018).

By attracting organisms to a harmful environment, ecological traps evidently have implications for conservation management. They can appear in a large variety of habitats and affect many species (e.g. Hale & Swearer, 2016; Robertson & Hutto, 2006). Still, ecological traps have mainly been studied on a local scale by comparing two or a few habitat patches, or by modelling potential landscape effects comparing only between inferior and superior habitat types (Hale et al., 2015). However, landscapes are much more complex and can comprise habitats of various qualities, especially when they are under the influence of anthropogenic change. Therefore, ecological traps are likely to also affect metapopulations (Hale et al., 2015). How strong the negative effects of a trap are depends on various factors. First, it is important to look at the attractiveness of a trap. If the trap is equally preferred to other available habitats, the probability of organisms to settle in the equally preferred trap is likely to be lower than the probability of settlement in a more attractive trap (Hale et al., 2015). This highly attractive trap is also termed 'severe' trap (Robertson & Hutto, 2006) and it was shown that more attractive traps also have higher fitness costs (Hale & Swearer, 2016). On a population level, extinction is more likely to happen when the respective population size is small, and when the inferior habitat leads to very high fitness costs (Schlaepfer et al., 2002). Even metapopulations were shown to suffer from ecological traps that affect fecundity and survival of a local population, with survival having stronger effects (Hale et al., 2015). Furthermore, the proportion of the sink habitat within a landscape is of importance, for both local populations and metapopulations (Delibes et al., 2001; Hale et al., 2015). In a theoretical model, the proportion of an equally preferred ecological trap could be higher and still have the same impact on population changes than an attractive trap constituting a lower proportion (Delibes et al., 2001). Population extinction can be possible even when the ecological trap only makes up a small proportion of the landscape (Schlaepfer et al., 2002). This indicates that conservation of high quality habitat alone might not be sufficient to support a population, as long as only a small fragment constitutes an ecological trap (Battin, 2004; Schlaepfer et al., 2002). Gilroy & Sutherland (2007) describe three possible methods to reduce the effect of an ecological trap: (i) Improve the actual habitat quality and therefore increase the individuals' fitness to at least the point at which the net population growth rate is not negative anymore, (ii) decrease the likelihood of selection of the trap habitat by removing the misinterpreted cue, or (iii) increase the likelihood of selection another, better habitat. In the future, management needs to include considerations of landscape-scale effects of traps, i.e. how managed habitats fit into the mosaic of other occurring habitats of different qualities (Hale & Swearer, 2016). Additionally, it must be taken into consideration that the structural habitat we perceive might not actually correspond to the functional habitat that individuals of other animal species experience (Van Dyck, 2012).

Conclusion

Existing studies about ecological traps in bees and butterflies prove or indicate that different human-induced rapid environmental changes (HIREC) can be the underlying cause for maladaptive behaviour in habitat selection. Worryingly, not only changes towards a more degraded habitat such as agricultural intensification risk ecological traps to arise, but also positively intended changes, such as the restoration of natural land. While almost all studies were able to provide sufficient information about fitness outcomes in the respective habitats, most studies identified in the literature search were unable to entirely prove or investigate habitat preference. Therefore, the findings of this essay suggest that the low but increasing research output about ecological traps can be attributed to traps being rather difficult to detect than extremely rare. Meta-analyses and literature reviews might be a helpful tool in revealing potential circumstances causing ecological traps.

Nevertheless, there is evidence that ecological traps can not only drive local populations into decline or even extinction, but also have landscape-scale effects. There is a need to incorporate the theory and possible (meta)population effects of ecological traps further into ecosystem research, and study the anthropogenic impact in changing habitats in light of these findings. It is important not only to focus on the well-being of populations in scenarios in which a negative change is expected, e.g. through pollution or habitat fragmentation, but also on the actual effects of positively intended management of habitats, such as restoration.

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