Effects of habitat isolation and predation pressure on an arboreal food-web

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Abstract: Habitat isolation is expected to reduce population densities of animals via reduced immigration. However, altered trophic interactions in isolated habitats may modify these effects, especially since the strength of isolation effects is expected to increase with trophic rank. Here, we studied effects of habitat isolation on a food-web module consisting of herbivorous beetles, predatory spiders, spider-preying wasps and arthropod-feeding birds. We compare two systems that were studied in subsequent years: a study on 29 mature apple orchards that varied in the degree of isolation from forest, and a study on 20 groups of newly planted cherry trees that showed similar variation in their degree of habitat isolation. No birds were observed on the young fruit trees. Wasps and spiders showed the expected lower abundances in isolated habitats. On mature trees, birds were present and showed lower abundances in isolated habitats. Wasps were reduced to a similar degree by habitat isolation as on the young trees. Surprisingly, spider densities on the mature trees were higher in isolated than in connected habitat. This contrasting response of spiders to habitat isolation is likely to be due to release from bird predation in isolated mature orchards. In both study systems, beetles showed no significant effect of habitat isolation. Our results confirm that the sensitivity to fragmentation increases with trophic rank, and suggest that trophic interactions should receive more attention in fragmentation studies.

Introduction

Fragmentation of natural and semi-natural terrestrial habitats is a major threat to biodiversity (Saunders et al. 1991). Habitat fragmentation leads to increasing isolation of remaining habitat patches. Habitat isolation disrupts species distribution patterns and forces dispersing individuals to traverse a matrix habitat that separates suitable habitat fragments from each other. This can lead to reduced immigration and consequently lower species richness and abundances in isolated habitat patches (Ewers and Didham 2006). There is an increasing concern that these effects on animal assemblages lead to modifications and disruptions of species interactions (Holt et al. 1999, Holt and Hoopes 2005). Hence, important ecosystem services such as biological pest control can be at risk (Tscharntke et al. 2005).

Although numerous studies have examined effects of habitat fragmentation, the results are often not consistent with the assumptions of decreasing species richness and abundances with increasing isolation. Instead, the relationship between invertebrate abundance or richness and isolation can be positive (Littlewood et al. 2009), negative (Steffan-Dewenter 2003) or absent (Krauss et al. 2003).

Counterintuitive positive effects of habitat isolation on abundance and species richness have been attributed to spill-over of generalist species from the landscape matrix into habitat patches (Cook et al. 2002), crowding effects caused by habitat loss (Littlewood et al. 2009), or varying susceptibility to isolation depending on different species traits (Ewers and Didham 2006).

However, not only direct effects of isolation, but also indirect effects may affect animal abundances in isolated habitats. Genetic inbreeding caused by habitat isolation for example reduces vital parameters and may therefore lead to a decrease in population size (Saccheri et al. 1998). Additionally, demographic stochasticity in terms of random demographic events may affect the population size in habitat patches (Melbourne and Hastings 2008). A relatively new explanation for isolation effects is the change of trophic interactions (Holt and Hoopes 2005). Such indirect effects could be caused by either altered prey availability or enemy pressure. Nevertheless, any of these indirect interactions are next to unexplored in a spatial context (Gripenberg and Roslin 2007). Positive effects of habitat isolation through release from predators may be widespread, because negative impacts of habitat fragmentation are predicted to become

stronger with increasing trophic rank (Kruess and Tscharntke 1994, Ewers and Didham 2006, Schüepp et al. 2011). Predators may be more vulnerable to habitat isolation because they can only colonise patches already occupied by their prey (Holt 2002) or since they might not disperse as well as their prey (Roland 1993). Both should reduce top-predators and subsequently increase abundances of the second highest trophic level in isolated habitats. Such isolation-induced effects have been shown in tri-trophic study systems including plants, herbivores and enemies, where increasing habitat isolation reduced the top-down effect on herbivores (Elzinga et al. 2005, Stutz and Entling 2011). As a consequence, the abundance of herbivores increased in isolated fragments resulting in higher plant damage. In a system involving mosquito larvae and their predators, reduced predation pressure in isolated ponds lead to higher mosquito densities (Chase and Shulman 2009).

Here, we investigated the impact of habitat isolation on abundances of weevils, spiders, wasps, and birds in an arboreal food-web. One study system consisted of mature orchards in which birds were present in addition to the arthropods. In the second system, we studied arthropod colonization on young trees that were too small to be utilized as foraging habitat by birds (Fernandez-Juricic 2000). We were interested in changes in animal abundance in response to habitat isolation, and if isolation effects varied between the two study systems. We hypothesized that (i) direct effects of habitat isolation are negative for weevils, spiders, wasps and birds, (ii) higher trophic ranks are more vulnerable to habitat isolation than lower trophic ranks, and (iii) the negative effect of isolation on top predators leads to positive isolation-effects on their prey.

Material and methods

Study sites

In 2007, 29 traditional orchards in north-eastern Switzerland were examined. The sites were distributed over an area of 20 km by 22 km in the cantons Thurgau and St. Gallen. The selected orchards were on average 61 years old, had an average size of 0.96 ha and were dominated by tall-growing mature apple trees (*Malus domesticus*) at an average density of 53 trees/ha. All orchards were under reduced insecticide management (for details, see Bailey et al. 2010).

In 2008, we selected 20 sites, each with seven four-year old cherry trees (*Prunus avium*) that were planted in rows of 18 m length between March and early April of the study year. As we only wanted to sample arthropods colonizing the trees from the landscape, all cherry trees were defaunated using winteroil (Maag Sanoplant Winteröl) prior to planting. The sites were distributed over an area of 23 km by 32 km in the cantons Bern and Solothurn.

None of the sites were treated with pesticides (for details see Bucher et al. 2010 and Schüepp et al. 2011). All 49 sites were located at altitudes between 420 and 700 m above sea level. Landscapes around the study sites mainly consisted of permanent grassland, arable fields, mixed deciduous forest, and other traditional orchards.

In both systems, half of the study sites (15 with mature trees; 10 with young trees) were directly adjoining to forest, the other half (14 with mature trees; 10 with young trees) were isolated by 100 to 250 m from the nearest forest. As habitat isolation normally correlates with habitat amount in fragmented landscapes (Fahrig 2003), both variables were kept as independent as possible through a GIS-based pre-selection of study sites (Farwig et al. 2009, Bailey et al. 2010, Bucher et al. 2010). In our calculations, scrub and hedgerows, other extensively used orchards, single trees, tree lines, and forest edge represented suitable habitats for the species.

Study organisms and sampling

We studied a food-web consisting of foliage-gleaning birds (*Parus ater, P. caeruleus, P. major, P. palustris*), spider-preying wasps (*Trypoxylon clavicerum, T. figulus, T. minus*), a weevil-preying spider species (*Araniella opisthographa*) and canopy-dwelling herbivorous weevils (mainly *Orchestes fagi* and *Phylobius* spp.). In addition to the mentioned prey species, the predators prey on additional groups such as caterpillars (*Parus* sp.), other web-building spiders (*Trypoxylon* sp.), and dipterans (*A. opistographa*). The selected species are not representative for all the species that occurred in our landscape. In fact, we biased our selection of species toward those that we thought were likely to respond to woody habitat isolation based on their habitat preferences.

Between April and October 2007, we conducted four beating tray samplings to collect *Araniella* spiders and weevils from the trees of the 29 mature orchards. We sampled four trees per orchard, two of which were located at the edge and two in the second row from the edge, respectively. All sampled trees were of similar height (4-6 m) and had trunk circumferences between 80 and 100 cm. The same trees were used for all four sampling events. We used a 0.25 m^2 textile funnel with a jar attached to its lower end. The funnel was held beneath a branch, which was struck sharply three times with a foam wrapped stick (IOBC 1978). The collected spiders were transferred to 70% ethanol. Four similar sized branches at heights of 1.5-2.5 m were sampled at each of the four trees, giving a total sample area of 4 m^2 per orchard per date. To avoid monitoring effects on the young fruit trees in 2008, we conducted four visual surveys between May and October. If two or more arthropods of the same species were present at one site, one individual was collected for identification.

The wasps, which naturally breed in deadwood, were sampled using trap nests (Steffan-Dewenter 2003). In April 2007 and 2008 four trap nests were installed at each of the sites. In each case, the trap nests were collected in October and stored in a climate chamber at 5 °C for at least 4 months. Afterwards, the nests were treated at 22-25 °C for at least 2 months and the emerging adults of four (2007) and two (2008) trap nests per site were identified. For a better compa-

rability between the two samplings, two trap nests per site were chosen randomly for the 2007 sampling period.

In 2007, territories of breeding birds were mapped for each site during three visits between April and June, following the breeding bird mapping scheme of the Swiss Ornithological Institute (www.vogelwarte.ch). For each site, the maps of the three visits were combined and territories determined based on clustered observations and known species-specific territory size. The young cherry trees studied in 2008 were too small to represent a foraging habitat of canopy-dwelling birds. During 15 visits of all 20 sites in 2008 and 2009, not a single individual of *Parus* spp. was observed.

Data analysis

In both years, densities of birds, wasps, spiders and weevils were compared between isolated and connected sites using a two-sample t-test in the PAST software (version 1.65, Hammer et al. 2001). If variances differed significantly between groups, a Welch's t-test was used. To analyze the effects of sampled animal groups on spider densities, linear models followed by ANOVA's were calculated in R software (version 2.10.1, R development core team 2009). Thereby, spiders were used as response variable and abundances of birds, wasps, weevils, and habitat isolation as explanatory variables.

Results

Densities of all three predator groups showed significant effects of habitat isolation (Fig. 1). However, habitat isolation had a highly significant negative effect on the abundance of observed *Parus* species in mature orchards (Fig. 1.A; $t = 4.4$; $p < 0.001$). In 2008, no *Parus* individuals were observed on the young fruit trees irrespective of their isolation (Fig. 1.B). *Trypoxylon* showed strong negative responses to habitat isolation in both mature orchards (Fig. 1.C; $t = 3.2$; $p < 0.01$) and young fruit trees (Fig. 1.D; $t = 3.2$; $p < 0.01$). In contrast, densities of *Araniella* increased with isolation of the mature orchards (Fig. 1.E; $t = 2.3$; $p = 0.02$), but decreased with isolation on the young fruit trees (Fig. 1.F; $t = 2.5$; $p = 0.02$). While *Parus* abundance was the most effective predictor for spider densities in mature orchards ($F_{1,23} = 9.96$; $p < 0.01$), spider densities on young trees were best explained by the distance of habitat isolation of the sampled patches ($F_{1,16} = 8.6$, $p < 0.01$). However, distance of habitat isolation also played a significant role in mature orchards ($F_{1,23} = 7.0$, $p < 0.05$). Herbivorous weevils showed no significant response to habitat isolation in either of the study systems (Fig. 1.G: $t = 1.1$; $p = 0.29$ Fig. 1.H: $t = 1.6$; $p = 0.15$).

Discussion

Our study demonstrated that habitat isolation can greatly reduce animal abundance at different trophic levels. These negative effects of habitat isolation became more significant towards higher trophic ranks. However, for the investigated spider species, this negative relation was only true for sites where the top predator was absent. In the presence of the top predator, the isolation effect was reversed. Thereby, we conclude that the higher presence of top predators in connected habitats leads to higher predation pressure on the spiders.

Representing the highest trophic rank in 2007, densities of *Parus* showed the most significant negative response to habitat isolation. The strong reduction of bird abundance by habitat isolation is in accordance with the trophic level hypothesis, assuming that the importance of regional versus local processes increases with trophic level (Holt et al. 1999, Holt and Hoopes 2005). The reduced densities of birds in fragmented orchards further confirm that many forest birds in temperate and boreal forests are gap-shy and sedentary, and thus sensitive to habitat fragmentation (Haddad et al. 2003). But it is not simply that isolation is just too large for the bird species to move but rather that they do not find the isolated patches. Opdam et al. (1984) concluded that distances of open ground in agricultural landscapes restricted immigration rates of woodland birds far below the distance they are able to cover by flight. Furthermore, an additional negative effect of reduced vital parameters due to inbreeding in isolated sites is possible (Saccheri et al. 1998). Nevertheless, this seems unlikely in our case, as the distance seems to lower immigration success in isolated sites but the distance of up to 200 m is still within the tits range of territory change (Andreu and Barba 2006). The fact that no *Parus* species were observed in 2008 is almost certainly due to the young age of the cherry trees. Especially *Parus* species as foliage foragers and tree hole nesters show decreasing abundances with decreasing fragment age (Fernandez-Juricic 2000).

Representing the second highest trophic level in our system, *Trypoxylon* wasps showed significant negative responses to woody habitat isolation in 2007 and 2008. As for the birds, such negative effects could have been induced by an insufficient dispersal ability to colonize our isolated patches. However, a recently published study showed that *Trypoxylon* wasps are able to colonize new habitats within distances up to 750 m (Krewenka et al. 2011). Although they are able to cover these distances, it is possible that these wasps were just unable to locate the isolated patches and therefore failed to colonize these habitats. In addition to their dependency on woody habitats to spot nesting sites, they may also use these areas as foraging habitats. While the wasps themselves use pollen and nectar as food source and may therefore utilize the surrounding open land as foraging area, they provide their brood cells with paralyzed spiders. These spiders comprise some tree-inhabiting species including *Araniella* sp. (Schüepp et al. 2011), but the vast majority of prey items are generalist spiders that are abundant in open habitats (Valérie Coudrain, unpublished data). Even though we used the same number of trap nests in both study years, there was a clearly higher abundance of *Trypoxylon* nests in young than in old orchards. This may be attributed to the structure and size of the older trees: as species of the genus *Trypoxylon* nest in pre-existing cavities such as holes in wood, and interior of galleries abandoned by Coleoptera larvae (Amarante 1999),

these older trees may offer alternative nesting cavities in addition to the established trap nests.

Just like the birds and wasps, the observed weevils tended to have lower abundances in isolated than in connected sites in both study years. In accordance with the trophic level hypothesis (Holt et al. 1999, Holt and Hoopes 2005), the influence of isolation on weevils was much lower than on the investigated predators. Being herbivores and therefore residing at the lowest trophic level in our study system, the weevils are only restricted by their own dispersal ability, in contrast to predators, which can colonize new patches only if their prey is already available (Holt 2002).

Unlike the other three investigated animal groups, the spider *Araniella opisthographa* showed contrasting, significant responses to habitat isolation in 2007 and 2008. On the young trees, *Araniella* showed a negative response to habitat isolation. This strong negative influence of habitat isolation was supported by the results of our linear model and a study by Bucher and Entling (2011), which showed that *Araniella* spiders in isolated habitats have a significantly lower body condition than spiders in connected habitats. In contrast, *Araniella* densities were apparently positively influenced by habitat isolation in mature orchards. However, results of the linear model showed that the abundance of the top predator was more important for spider densities in mature orchards than the distance to the next woody habitat. As *Parus* is able to reduce its prey populations (Mols and Visser 2002), the strong reduction of birds in isolated habitats could lead to enhanced population densities of their prey. The studied *Parus* species feed predominantly on caterpillars and spiders (Blotzheim 1997). Thus, the enhanced *Araniella* densities in isolated mature orchards are probably due to the release from predation by *Parus*. This way, habitat isolation had an indirect positive effect on the abundance of *Araniella*.

However, *Parus* species were strongly influenced by isolation and an inter-correlation between birds and habitat isolation can be assumed. Nonetheless, direct effects of the landscape which can explain higher spider densities in isolated sites seem to be unlikely. Crowding effects can be excluded as explanation for the counterintuitive results of *Ara-*
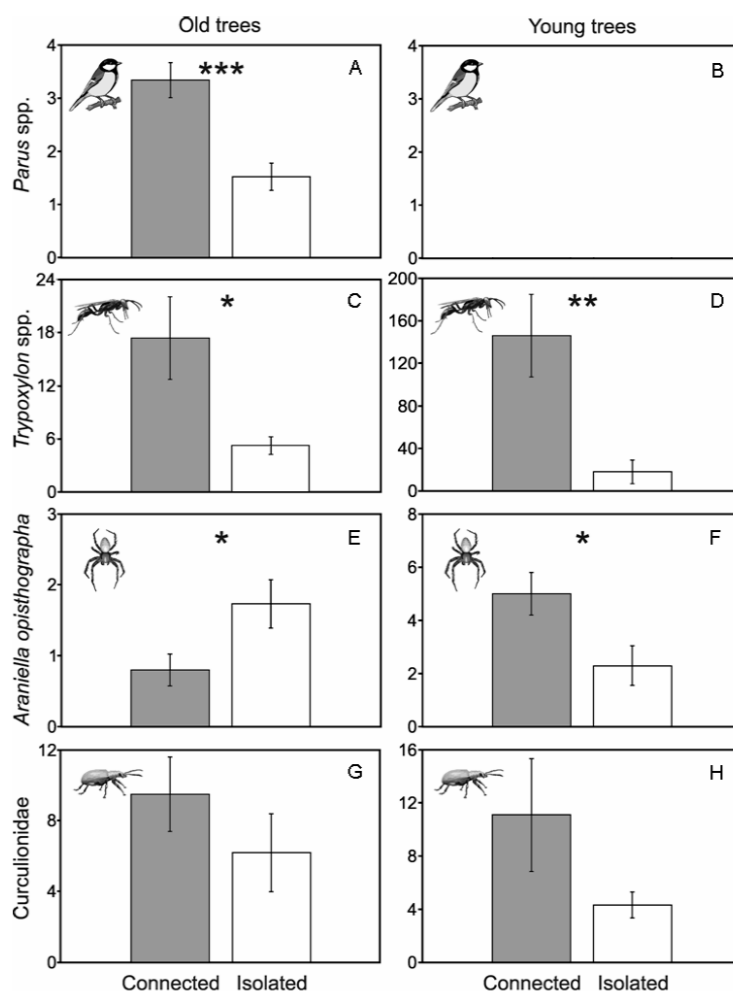

Figure 1. Influence of habitat isolation on densities of tits (*Parus* spp.), spider-eating wasps (*Trypoxylon* spp.), spiders (*Araniella opisthographa*), and weevils (*Phyllobius* spp. and *Orchestes fagi*; t-test; *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$). Y-axes indicate average individual numbers per site (respectively territories per site in the case of *Parus*). Error bars are ± SE around the mean.

niella in the mature orchards. None of the 29 study sites showed large changes in forest amount within eight years before our study (Felix Herzog, unpublished data). Additionally, spider abundance did not correlate with changes in the amount of fruit trees in the surrounding landscape (r = 0.0; p = 0.97). Furthermore, it is unlikely that spider immigration from the matrix played a strong role, because *Araniella opistographa* lives almost exclusively in tree canopies (Hänggi et al. 1995).

In addition to the presence or absence of birds, other differences existed between our two study systems that could have potentially influenced the different reactions of *Araniella* to habitat isolation. The study systems differed in tree species, tree size, and age; they were situated in different cantons and were studied in subsequent years. Even though sampling results of visual surveys are comparable to beating tray sampling (Deutscher et al. 2003), differences in the efficiency of arthropod sampling could not be excluded. All these differences are likely to lead to different species composition and abundance of animals on the trees (e.g. Boege and Marquis 2006). However, we are not aware of a plausible mechanism by which they could have led to the contrasting responses of *Araniella* to habitat isolation in the two systems. It is also conceivable that other indirect effects like demographic stochasticity and genetic inbreeding could have caused the differences in abundance between the connected and isolated sites. These effects could have enhanced the negative effects of isolation, but cannot explain the observed positive influence of isolation on mature trees. Thus, we conclude that enhanced densities of *Araniella* in isolated mature orchards were likely due to release from bird predation, although we cannot rule out non-significant bottom-up effects by weevils and prey groups such as dipterans that were not sampled.

Our study supports the hypothesis that habitat connectivity increases local population densities and thereby possibly reduces extinction risks for animals belonging to different trophic levels. However, counterintuitive, positive effects of habitat isolation can appear due to underlying trophic effects. As numerous studies on habitat fragmentation deal with only one trophic level, such trophic effects may often remain undetected and positive isolation effects may wrongly be attributed to spill-over and crowding effects. According to our results, trophic interactions should be more widely considered in studies of habitat fragmentation.

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