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Habitat isolation affects plant–herbivore–enemy interactions on cherry trees

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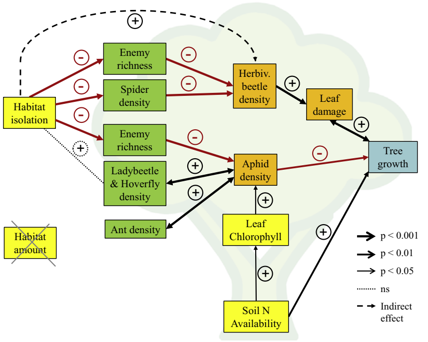
HIGHLIGHTS

- Habitat isolation, not landscape composition, affected herbivores and their enemies.
- Herbivorous beetles were released from natural enemies at isolated sites.
- Leaf damage by beetles did not translate into lower growth of trees.
- Some aphid enemies responded to aphid density rather than reducing it.
- Aphid density (top-down) and nutrient availability (bottom-up) affected tree growth.

GRAPHICAL ABSTRACT



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ABSTRACT

Understanding the interactions between herbivores and natural enemies in fragmented landscapes is essential for conservation biological control. Studies including multiple enemies affecting multiple herbivores, plant damage and growth are needed. Here, we separated independent effects of (1) isolation of cherry trees from woody habitat and (2) the amount of woody habitat in the surrounding landscape (500 m buffers) on interactions between different groups of herbivores with their natural enemies and resulting changes in the growth of young cherry trees. Most predatory arthropods declined with habitat isolation, except some aphid predators (ladybeetles and hoverflies). Herbivores either increased with isolation (herbivorous beetles) or showed no significant response (aphids). In contrast, the amount of woody habitat in the landscape was not relevant for herbivore–enemy interactions at the investigated scale. Plant growth was affected by bottom-up (nutrient availability) and top-down (aphid density) forces but did not change significantly with habitat amount or isolation. We conclude that herbivores can be released from natural enemies at isolated sites, in accordance with the hypothesis that habitat connectivity improves pest control. However, each herbivore group responded differently to the landscape context and had contrasting effects on the same host plant, demonstrating the difficulty to predict landscape effects on plant growth.

1. Introduction

1.1. Natural pest control and plant growth

Natural enemies are expected to promote plant growth by reducing herbivores, but the presence of natural enemies does

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not necessarily translate into suppression of herbivores and increased plant performance (Chaplin-Kramer et al., 2011). In other words, the delivery of an ecosystem service like pest control depends not only on the density of service providers but also on their effectiveness (Kremen, 2005): First, predation of herbivores is positively correlated with herbivore densities in some systems (Thies et al., 2005), suggesting that herbivore density affects enemy populations more strongly than *vice versa* (Chaplin-Kramer et al., 2011). Second, herbivore densities may be reduced by the availability and distribution of their resources rather than by enemy suppression (Bengtsson, 2010; Chaplin-Kramer et al., 2011). Third, multiple predators may negatively interact with each other (Martin et al., 2013; Snyder et al., 2006). And fourth, the effectiveness of herbivore control may depend much more on the presence of specific, highly effective species rather than on total density of predator groups (Philpott et al., 2009; Straub and Snyder, 2006). Therefore, the ecosystem service of pest control is more adequately measured as plant damage and growth rather than only as density of enemies, but studies measuring plant damage and growth are still rare (Chaplin-Kramer et al., 2011; Veres et al., 2013). Further, it is necessary to include multiple predators in one study to understand additive or synergistic effects emerging in the presence of multiple predators (Losey and Denno, 1998; Sih et al., 1998). In addition to negative effects by herbivores, plant growth is largely dependent on the availability of nutrients (Throop, 2005; Zehnder and Hunter, 2008). Therefore, integrating both bottom-up and top-down forces is necessary to understand the relative importance of each factor for plant growth (Hooper et al., 2005; Hunter and Price, 1992; Müller et al., 2005).

1.2. Landscape effects

Herbivores and their enemies are often mobile organisms influenced by the distribution of resources in the landscape (Kremen et al., 2007; Tscharntke et al., 2012). Therefore, plant growth may not only depend on local but also on landscape factors. Densities of herbivores on crops can be affected by the landscape either indirectly by a spillover of natural enemies from adjacent (semi-) natural habitat into agricultural fields (Bianchi et al., 2006; Chaplin-Kramer and Kremen, 2012; Eilers and Klein, 2009; Tscharntke et al., 2005, 2007), or directly because herbivores themselves develop in these habitats and disperse from there (Martin et al., 2013; Thies et al., 2005). Therefore, positive effects of landscape complexity on enemies may be counteracted by positive effects on herbivores (Roschewitz et al., 2005). Numerous metrics have been used to evaluate the effect of landscape complexity on pest control (Chaplin-Kramer et al., 2011). Most widely used, straightforward and hence preferable is the percentage of (semi-) natural habitat surrounding focal crops (Chaplin-Kramer et al., 2011). However, the amount of habitat at the landscape scale is often correlated with measures of habitat fragmentation such as isolation (Fahrig, 2003). Experimental evidence for the effects of both habitat isolation and amount is needed to design agricultural landscapes that support biodiversity and ecosystem services (Hadley and Betts, 2012; Tscharntke et al., 2007, 2012). The amount of suitable habitat determines the pool of available species and individuals in a given landscape, whereas habitat isolation constrains access to this species pool (Tscharntke et al., 2012).

1.3. Importance of woody habitat

Semi-natural habitat including woody elements such as hedgerows, tree lines, traditional orchards, forest edges and forests promote biodiversity in agricultural landscapes (Attwood et al., 2008; Billeter et al., 2008; Diekötter and Crist, 2013; Dix et al., 1995). They provide suitable conditions for breeding and hibernation or continuous supply of hosts, prey, pollen or nectar for the majority of species (Bianchi et al., 2006; Corbett and Rosenheim, 1996; Duelli and Obrist, 2003; Kells and Goulson, 2003; Landis et al., 2000; Pywell et al., 2005) or serve as connectivity elements (Wamser et al., 2012). Heterogeneous landscapes have more crop to non-crop interfaces and allow colonization of crops by natural enemies (Bianchi and Van der Werf, 2003). Ladybeetles colonise aphid-infested plants from their hibernation sites in non-crop habitat such as hedgerows and forests (Bianchi and Van der Werf, 2003; Thomson and Hoffmann, 2013). Woodlots are a source of spiders and parasitic wasps controlling leafhopper pests in vineyards (Corbett and Rosenheim, 1996; Hogg and Daane, 2010; Isaia et al., 2006b). Cavity-nesting predatory wasps are negatively affected by the isolation from woody habitat and the loss of woody habitat at the landscape scale (Schüepp et al., 2011). Hedgerows provide high quality overwintering habitat for spiders and predatory beetles (Pywell et al., 2005). And arthropods and birds on fruit trees depend particularly on woody semi-natural habitat such as forest, hedgerows or traditional orchards (Bailey et al., 2010).

1.4. Hypotheses

Here, we study effects of resource availability and the surrounding landscape on a tri-trophic system of cherry trees, multiple herbivores and their natural enemies. We hypothesised that:

1. Density and richness of natural enemies decrease with increasing isolation from woody habitat and with decreasing amounts of woody habitat in the landscape.
2. Density of herbivores increase with habitat isolation and with decreasing amounts of woody habitat because of lower enemy suppression.
3. Plant growth decreases with increasing habitat isolation and with decreasing amounts of woody habitat because of higher herbivory.
4. Further, nutrient availability in the soil enhances and fungal leaf infections reduce plant growth.

2. Materials and methods

2.1. Study sites

The study was conducted in 2012 in the Swiss plateau between the cities of Bern, Solothurn, and Fribourg, where agricultural areas are interspersed with forest. The 30 experimental sites were spread over an area of 23 by 32 km and each site consisted of an 18-m-long row of seven 8-years-old wild cherry trees (*Prunus avium* L.). Trees were planted in 2008 on permanent grassland for the experiment and since then managed in a standardised manner (Stutz and Entling, 2011). The sites varied in altitude between 465 and 705 m above sea level.

2.2. Habitat amount and isolation

The study sites were selected systematically to cover a gradient in the percentage of woody habitat in a 500 m buffer (from 4 to 74%) and to differ in their level of local isolation from woody habitat independently of the percentage of woody habitat ($F_{2,27} = 0.004$, $p > 0.9$). We chose the landscape scale of 500 m radius because many studies find enemy and pest responses at scales of 300–1000 m (Chaplin-Kramer et al., 2011; Martin et al., 2013). Woody habitat comprised hedgerows, orchards, single-standing trees, tree lines, and forest. Isolation had three levels: ten of the sites were located at the edge of forest (adjacent), ten in a distance of 100–200 m from the next forest edge but directly beside small-sized woody habitat such as hedgerows or trees (connected), and