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FORUM

Top-down control of herbivores varies with ecosystem types

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Summary

1. Björkman *et al*. comment on Adams and Zhang's finding of more leaf herbivory with increasing latitude, pointing out that top-down control by predators on insect herbivores might cause less herbivory in warmer regions.

2. Stronger top-down control with more plant diversity has been found mostly in systems that are less diverse overall, such as agricultural fields and grassland. Studies have also concentrated on small spatial scales. Whether top-down control is relatively more important at large spatial scales in the most highly diverse tropical or warm temperate forests is still in doubt.

3. *Synthesis*. The importance of top-down predator control of herbivores may vary with the system studied. Future work to understand the controls of herbivores needs to precisely monitor and compare the dynamics of individual herbivore species and their predators at a large spatial scale.

Key-words: herbivory, natural enemy, plant–herbivore interactions, predators, scale, system type, temperature, top-down control

In response to our recent study (Adams & Zhang 2009), Björkman, Berggren & Bylund (2010) point out that a negative relationship between herbivory and temperature may be due to greater 'top-down' control of insect herbivores by predators in warmer-climates. We are grateful to Björkman *et al*. for making this important point. We agree that there is a need for entomologists and plant ecologists to work together more closely and to include experimental systems to understand the controls of herbivores. We would also like to point out the considerable background of relevant work which should be considered in future studies.

One explanation why warmer climate ecosystems may have stronger biotic controls of herbivorous insect populations has been around for some time, in the form of the enemies hypothesis (Root 1973). Root suggested that in more diverse plant and insect communities, the greater number of links in food webs – and more refuges for shelter of insect predators and prey in a structurally more complex plant community – means more efficient and constant checks and balances, tighter control of insect herbivore populations and less herbivory overall (Root 1973; Russell 1989; Jactel, BrockerhoV & Duelli 2005). By implication, in a warmer-climate ecosystem we may expect more links in food webs within the taxonomically more diverse plant and animal community.

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The enemies hypothesis has been experimentally tested mainly in fairly low-diversity systems or at a small scale, such as in agricultural (Risch, Andow & Altieri 1983; Russell 1989; Andow 1991; Bommarco & Banks 2003; Jactel, BrockerhoV & Duelli 2005; Kaitaniemi *et al*. 2007; Sobek *et al*. 2009) and grassland systems (Siemann *et al*. 1998; Koricheva *et al*. 2000) or in laboratory experiments. The results from agricultural systems largely support the enemies hypothesis (Pimentel 1961; Risch, Andow & Altieri 1983; Russell 1989; Andow 1991; Coll & Bottrell 1994). In agricultural systems, predation and parasitism rates are generally higher in polycultures than in monocultures (Andow 1991). A review conducted by Russell (1989) found that in diverse agro-ecosystems, the populations of insect herbivores may indeed be reduced.

However, the applicability of the enemies hypothesis varies with ecosystem type (Vehvilainen, Koricheva & Ruohomäki 2007). Root (1973) predicted that control of insect herbivores would be more pronounced in perennial plant systems than in annual systems (Risch, Andow & Altieri 1983; Andow 1991). In contrast, Koricheva *et al*. (2000) found that abundance of herbivore predators (spiders and carabids) declined with increase in diversity in perennial grasslands, which is contradictory to the enemies hypothesis. A comprehensive review found that effects invoked in the enemies hypothesis vary with scale in agricultural experiments (Bommarco & Banks 2003). Predators were affected by plant diversity in intermediate-sized

(28–196 m^2) but not in large (> 256 m^2) plots, apparently because predators can more quickly redistribute themselves in experiments with smaller plot size, and be aggregated in more diverse plots that may harbour alternative prey and resources.

Studies investigating variation in predation control of plant – herbivore interactions have rarely been carried out at larger spatial scales, or for complex forest ecosystems (Riihimaki *et al.* 2005). In a study involving stands of different tree species diversity in forests in south-eastern China, it was found that herbivory even increases locally in stands with higher plant and herbivore diversity (Schuldt *et al.* 2010). Schuldt *et al.*'s study thus did not support the key prediction of the enemies hypothesis that predators should significantly suppress overall herbivory levels in diverse plant communities. Recent studies have reached the point of questioning the relevance of the enemies hypothesis to forest ecosystems and have revealed that the effects of plant diversity are in fact very much species-dependent (Jactel & BrockerhoV 2007; Vehvilainen, Koricheva & Ruohomäki 2007; Vehvilainen, Koricheva & Ruohomaki 2008). In one study testing the enemies hypothesis in a coniferous forest in western Finland, it was found that details of tree species composition, rather than species diversity or tree density, determines predators' survival and disappearance rates (Riihimaki *et al.* 2005). In a study conducted in northern Europe, it was found that staphylinid, carabid and opilionid predators concentrated on stands composed of particular tree species (Vehvilainen, Koricheva & Ruohomaki 2008). In a review analysis of 119 studies regarding the relationship between tree diversity and herbivory, it was found that tree species composition is a more critical determinant of the effects on herbivory than tree richness (Jactel & BrockerhoV 2007).

The likely reason for this variability relating to details of forest stand composition is that the interactions among plants, herbivores and predators are often highly specific (Heil 2008). Herbivory patterns seem to be determined primarily by the identity and abundance of particular tree species, rather than the overall tree diversity (Sobek *et al.* 2009). Predators normally have strong preferences towards hunting on plants, which can benefit the predator by providing a reliable food source, favourable microclimate, better shelter (Vehvilainen, Koricheva & Ruohomaki 2008) and benefit plants by saving energy spent in fulfilling the optimal defence requirement (Heil *et al.* 1997). Predators can improve predation efficiency by foraging on particular plants, because a diverse stand composed of species that predators are not adapted to might hamper their predation (Riihimaki *et al.* 2005). As a result, a predator's abundance may depend primarily on the presence of a particular tree species with its herbivores, rather than overall tree diversity (Riihimaki *et al.* 2005; Koricheva *et al.* 2006; Jactel & BrockerhoV 2007; Kaitaniemi *et al.* 2007; Vehvilainen, Koricheva & Ruohomäki 2007; Schuldt *et al.* 2008; Vehvilainen, Koricheva & Ruohomaki 2008). To put it another way, the effects exerted by tree species composition are more important than those exerted by tree species diversity on determining predator diversity (Stamps & Linit 1998; Finch 2005; Riihimaki *et al.* 2005; Koricheva *et al.* 2006; Kaitaniemi *et al.* 2007).

However, it is possible that certain mutualisms between plants and insect predators are more common in warmer climates, and this might lead to stronger predator pressure against herbivores. Reviews that compared the prevalence of extrafloral nectaries – which often attract ants that prey on insect herbivores (Novotny *et al.* 1999; Floren, Biun & Linsenmair 2002; Heil & McKey 2003; Heil 2008) – have suggested that they are more prevalent in the tropics (Oliveira & Leitão-filho 1987; Coley & Aide 1991; Pemberton 1998). A recent meta-analysis showed that the effects of experimentally excluding ants were generally stronger in tropical than in temperate regions (Rosumek *et al.* 2009). However, it is unclear whether the difference in ant-based plant defences and ant predation would be evident only between the tropical and temperate zones, or also between the cool and warm temperate zones which we compared in our latitudinal study. As with other insect predators, details of stand composition in forests and the types of insect prey have a major effect on the prevalence of ant predation (Ito & Higashi 1991; Yu & Davidson 1997; Bluthgen *et al.* 2000; Dejean *et al.* 2000; Apple & Feener 2001; Hossaert-McKey *et al.* 2001; Wirth & Leal 2001; Riihimaki *et al.* 2005; Heil 2008). The volatile organic compounds (VOC) and food bodies that enable direct or indirect defences can be produced by only a portion of specific plants to attract certain predators (Ibarra-Manriquez & Dirzo 1990; Fiala & Linsenmair 1995). Based on the VOC released, carnivores can discriminate among plants infested by different herbivore species and among different plants infested by the same herbivore (Powell *et al.* 1998; Dicke 1999).

In conclusion, while we support Björkman *et al.*'s suggestion that 'top-down' predation control of insect herbivores may be greater in warmer climates, we feel it necessary to emphasize the full range of work on this subject that has already been performed – and the need to design theoretical models and experiments that are complementary to this work. The enemies hypothesis is a starting point, even though the evidence for it operating in forest systems is not strong. Understanding why it does not seem to operate as predicted on a local scale may be useful for understanding observed geographical temperature-related gradients in herbivory. Further work needs to focus on the precise monitoring of the dynamics of individual herbivore species and their predators, in the tradition of forest entomologists dealing with selected pest species (Turchin 2003). However, whereas traditional forest entomology has focused only on certain pest species in areas where they are problems, a true understanding of geographical gradients in herbivory may depend on the study of selected examples of obscure insect species which have no status as pests through all or most of their range.

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