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Review

Synthesizing habitat fragmentation effects on plant–antagonist interactions in a phylogenetic context

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ABSTRACT

Plant–antagonist interactions shape the structure, composition and dynamics of plant communities and ecosystems. Due to their key importance, much research has been advocated to evaluate anthropogenic habitat loss and fragmentation effects on plant–antagonist interactions but no clear response patterns have arisen. Even recent quantitative reviews have failed to provide consistent generalizations. Here we conduct the first phylogenetically independent meta-analysis along with a traditional meta-analytical approach. We examined whether characteristics of the interaction, the fragmented landscape, and methodological approaches modulate the magnitude of effects. Traditional meta-analysis showed that plants within habitat fragments suffer on average less damage from antagonists. However, when incorporating the phylogenetic relationships among plants, the overall effect and the particular effects of moderators became non-significant. Interestingly, we found a strong and consistent trend between both meta-analytical approaches in the overall effect of habitat fragmentation on folivory elicited by insects. This implies the first genuine fragmentation effect that transcends the phylogeny of plants and is not undermined by statistical problems of pseudoreplication. Decreased insect folivory will favor certain plant species, especially those with acquisitive resource use traits such as pioneer and exotic invasive, thereby affecting plant community composition in fragmented habitats. Here, we highlight the importance of incorporating the phylogeny in meta-analytical contexts. Our results imply that current studies worldwide represent a phylogenetically-conserved sample of fragmentation effects on plant-antagonist interactions. Thus, more studies on distantly phylogenetically-related plants are needed to have a broader, more representative, sample of responses across angiosperms.

Contents

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1. Introduction

Antagonistic plant–animal interactions, the most common and ancient interactions in nature (Scott, 1983; Labandeira, 1998), involve the direct and indirect damages of plants by animals (or viruses and pathogens) for food or housing (Southwood, 1973; García and Chacoff, 2007). Antagonistic interactions include principally folivores (leaf consumers), florivores (flower consumers), and seed predators (seed consumers), and some frugivores (fruit consumers that damage seeds), which collectively are called herbivores. The interaction between plants and their natural enemies influences the dynamics and structure of ecosystems and vice versa. Emerging causal effects from the individual level to the population-level processes can potentially affect forest regeneration and maintenance of plant diversity (Faveri et al., 2008). For instance, plant demography can be altered if the impact of herbivory changes due to plant ontogenetic stage or to the type of tissue that is consumed (Crawley, 1997; Simonetti et al., 2006). This may also impact the community level if herbivores modify seedling recruitment altering the number or composition of plant species in the seed rain and seed bank (Hoffmesiter et al., 2005; Del Val, 2012). Also, being a fundamental part of the food webs, antagonists are of relevant importance on the ecosystems' energy flow, both in the effects of superior trophic levels, as well as in the reincorporation process of nutrients (McNaughton et al. 1997). Therefore, plant-antagonist interactions represent primary conservation targets because of their pivotal role in plant regeneration processes, plant community structure, ecosystem functioning, and biodiversity evolution (García and Chacoff, 2007). Interestingly, such antagonistic interactions are also affected by modifications at community and ecosystem levels in a feedback fashion.

The current rates of defaunation and habitat fragmentation are dramatically affecting the interactions between plants and their natural enemies (Galetti et al., 2003; Galetti and Dirzo, 2013; Dirzo et al., 2014). The transformation of continuous habitats into mosaics of isolated forest fragments exposes organisms surviving in the fragments to a modified surrounding environment, where decreasing population size and connectivity often disrupts biotic interactions (Murcia, 1995; Tscharntke and Brandl, 2004). Only 10% of recent publications referring to ecology of fragmented habitats evaluate interactions and focus mostly on mutualistic interactions, such as pollination and seed dispersal (Ghazoul, 2005; Aguilar et al., 2006, 2009; Markl et al., 2012). Much less attention is given to antagonistic interactions. Existent literature from the last decades show no clear response patterns on whether damage by antagonists decrease, increase or remain unaltered in fragmented landscapes. Some studies support the hypothesis of lower levels of damage in fragments, (Bersciano et al., 1999; Benítez-Malvido, 2001; Arnold and Asquith, 2002; Ledergerber et al., 2002; Vásquez et al., 2007; Simonetti et al., 2007; Faveri et al., 2008; Ruiz-Guerra et al., 2010), while others suggest increased damage in fragmented habitats (Kruess and Tscharntke, 1994; Lienert et al., 2002; Elzinga et al., 2005; Stoll et al., 2006; Christie and Hochuli, 2005; Galetti et al., 2015). Moreover, the amount and quality of food resources for antagonists may also change with habitat fragmentation negatively affecting plant productivity and leaf chemistry (Yamasaki and Kikuzawa, 2003).

Interestingly, three recent reviews have addressed the effects of habitat fragmentation on plant-animal interactions, including the antagonistic relations between plants and herbivores using different scopes, and they have also shown contrasting outcomes (De Carvalho Guimaraes et al., 2014; Magrach et al., 2014; Martinson and Fagan, 2014). While Martinson and Fagan (2014) found lower herbivory in habitat fragments than in continuous habitats, De Carvalho Guimaraes et al. (2014) found the inverse pattern: plants in habitat edges suffered more damage than plants inside habitats. Finally, Magrach et al. (2014) suggested that antagonistic interactions are more robust to habitat fragmentation since they did not find any effect of habitat fragmentation. Such disparity of general response patterns in the three reviews is quite surprising. Systematic quantitative reviews such as meta-analysis are powerful objective statistical tools that allow estimating an overall effect size of a common factor by combining the results of independent studies addressing similar research questions (Gurevitch and Hedges, 2001). Such contradictory overall effects among reviews may be ascribed to different approaches of effect size calculations, criteria of study inclusion, as well as the scopes and databases used by the different reviewers. Despite the reasons, these important attempts to summarize the existent empirical evidence have failed to find a consistent clear response pattern of habitat fragmentation effects on plant-antagonistic interactions.

Moreover, none of these three reviews accounted for phylogenetic non-independence in their overall effect size estimations. Meta-analytic data in ecology and evolutionary biology can seriously violate statistical assumptions of independence, especially when effect sizes are calculated from individual species, as is the case in these reviews. Common shared ancestry of taxonomically related species introduces a correlated error structure that needs to be accounted for in order to avoid misleading conclusions in meta-analyses (Lajeunesse, 2009; Chamberlain et al., 2012). Additionally, phylogenetically independent meta-analyses can also allow us to unravel the relative importance of evolutionary phylogenetic relationships over the ecological effects of habitat fragmentation.

The effects of habitat fragmentation on antagonistic interactions can be influenced by sources of variability related to the interaction and/or to external landscape features. Yet, these factors have not been thoroughly analyzed for multiple species. For instance, responses to habitat fragmentation may differ depending on the type of interaction and degree of specialization, where more specialized plant–antagonist interactions may be more susceptible to be lost in fragmented habitats compared to more generalist interactions. On the other hand, the identity of the interacting partner may also show differential response. For example, if we only consider the mobility of natural enemies we could expect that the higher mobility of birds and mammals may render less susceptibility to fragmentation effects compared to insects, which have comparatively lower mobility. Also, certain types of antagonist interactions may be more susceptible than others. If seed predation is mostly performed by birds and mammals (as in the tropics), then it may be less negatively affected by habitat loss compared to folivory, which is mainly accomplished by insects. Moreover, external landscape features of the fragmented habitats can also influence the magnitude of fragmentation effects on plant–antagonist interactions. The matrix surrounding the fragments may affect plant's susceptibility to antagonist animals by conditioning their dispersion and mobility capacity throughout the landscape (Driscoll et al., 2013; Mendes et al., 2015). Also, the time elapsed since the onset of fragmentation can determine when biotic interactions would show a change promoted by habitat fragmentation. Because local extinction of species can occur with a considerable delay after the event of habitat loss (i.e., undergo extinction debts; sensu Tilman et al., 1994), recently fragmented habitats may not show significant changes in biotic interactions relative to continuous, undisturbed original habitats. Finally, methodological approaches of published research may also influence the sensibility to find habitat fragmentation effects; experimental studies that deliberately create fragmented environments or place individuals within certain arrangements may have different ability to detect effects compared to observational studies. Despite the fact that experimental approaches are a key tool for disentangling causation, they may have a cost in terms of loosing external validity when facing complex and dynamic processes such as habitat fragmentation (Sagarin and Pauchard, 2009). In fact, the multiple approaches and definitions used by experimental studies may be introducing an important amount of artificial variance that dilutes important effects when studying habitat fragmentation. For instance, experimental approaches could mask the effect of factors such as number of generations since fragmentation, the spatial arrangement of fragments, and the degree of isolation of habitat fragments, among others.