

FUNCTIONAL GROUPS AND SPECIES REPLACEMENT: TESTING FOR THE EFFECTS OF HABITAT LOSS ON MOTH COMMUNITIES

KEITH S. SUMMERVILLE

Department of Environmental Science and Policy, Drake University, Des Moines, Iowa, 50311, email:keith.summerville@drake.edu

ABSTRACT. Species replacement, or the process whereby species from the surrounding landscape colonize a habitat remnant and potentially offset species loss, is gaining attention as an alternative mechanism to species impoverishment following habitat destruction. The challenge for butterfly and moth ecologists, however, is to devise analytical approaches that will identify species replacement and predict lepidopteran community structure following habitat alteration. The traditional approach to defining functional groups of Lepidoptera based on resource specialization is limited in these two regards. Here I propose a new approach to defining functional groups for moth communities in temperate deciduous forests that more explicitly incorporates information regarding host-plant type rather than resource specialization per se. In studies of moth diversity in temperate forest fragments, use of the proposed functional groups detected significant species replacement across a range of habitat area for moths in some forest regions but not others. The traditional approach to assigning lepidopterans to functional groups lacked sufficient power to detect species replacement regardless of region. I suggest that our ability to predict the effects of habitat loss on butterfly and moth communities will be greatly improved by adopting a functional group classification based on host-plant types rather than niche or diet breadth.

Additional key words: community composition, diversity, fragmentation.

Habitat loss is widely regarded as the single greatest threat to the diversity of terrestrial plant and animal communities worldwide (Fahrig 2001). Some field studies, however, have suggested that if only species richness is measured, the effects of habitat loss on forest lepidopteran communities may appear rather innocuous. For example, a number of studies have revealed that small patches of forest habitat are capable of supporting nearly as many butterfly and moth species as larger patches, and that this pattern appears in both temperate and tropical ecosystems (Brown & Hutchings 1997, Ricketts et al. 2001, Summerville & Crist 2003). It would be false, however, to conclude that large and small forests contain similar communities. Rather, in these butterfly and moth communities, habitat loss seems to be correlated with both (i) a reduction in the number of species dependent on forest interior habitat and (ii) and the occurrence of a greater number of edge-tolerant species in smaller habitat remnants. Thus, habitat loss may contribute to species replacement; species identity within communities changes in response to variation in habitat size while species richness remains constant.

Species replacement is a relatively new explanation for describing patterns in lepidopteran communities following forest disturbance or habitat loss (Summerville & Crist 2002a). Historically, the dominant theoretical approach for predicting the numbers of species found in woodlots of different size invoked expectations from the theory of island biogeography (Usher & Keiller 1998). The development of landscape ecology theory, however, emphasized that species from the matrix surrounding patches of forest habitat could contribute species to the focal community (Magurran 1985, Holt 1993). For example, when moth species from the matrix habitat surrounding

smaller forest patches colonize forest edges, the subsequent gain in species may offset any loss of species dependent on forest interior habitat (Summerville & Crist 2003). Thus, moth communities in smaller woodlots appear disproportionately comprised of species with larvae known to feed on herbaceous vegetation, while larger forests are dominated by woody-plant feeders. This is an example of an extreme case of species replacement compared to others which document species turnover along a seral gradient (e.g., Steffan-Dewenter & Tschardt 1997). In our study, species from different functional groups replaced one another along a gradient of increasing habitat loss. Thus, herbivory by lepidopterans shifted from the canopy to the understory layers in smaller woodlots.

In practice, documenting species replacement in butterfly or moth communities following habitat loss is not as simple as merely determining that large and small patches contain the same number of species; species replacement also requires that community composition differ in systematic ways. Measuring or describing changes in community composition following disturbance are not new for studies of Lepidoptera (e.g., Hill et al. 1995, Intachat et al. 1997, Usher & Keiller 1998, Horner-Devine et al. 2002). What is needed now are techniques that allow ecologists to tease apart how and why compositional shifts occur (Bierregaard et al. 2001). This last piece of information will allow ecologists to predict how much lepidopteran community structure will change in response to varying levels of disturbance or habitat loss (Summerville & Crist 2002a). Meeting this goal will be facilitated if lepidopterists expand their understanding of functional groups. Specifically, I argue that we must move away from defining lepidopteran guilds or functional groups solely using degree of resource specialization.

Instead, we should adopt a functional group classification created from our understanding for how different species utilize resources within different habitats.

LEPIDOPTERAN FUNCTIONAL GROUPS: TRADITIONAL APPROACHES

Traditionally, functional groups for butterflies and moths have been defined using a co-evolutionary approach based on the degree of specialization of the caterpillar to particular host-plant resources (Hunter 1991). The most commonly employed functional group classification acknowledges three primary assemblages: specialists, oligophages, and generalists. Specialists are usually defined as those Lepidoptera with caterpillars that utilize host plants of a single species or genus, oligophages use multiple plant species within a single family, and generalists are more cosmopolitan feeders (e.g., Steffan-Dewenter & Tscharnke 1997, Lepš et al. 1998). Of all three functional groups, the assignment of species to the level of oligophage tends to be the most variable, rendering comparisons among studies by different authors problematic (Hawkins & MacMahon 1989). Research adopting a traditional approach to functional group classification generally predicts that changes in habitat will be correlated with a reduction in the number of specialists within the community (see Summerville et al. 2002 and citations within). Thus, the traditional format for constructing functional groups is useful for predicting species' vulnerability to habitat change relative to their niche breadth.

Restricting functional group ranks to specialists and generalists, however, has proven problematic when interest lies in detecting species replacement or in predicting how changes in lepidopteran communities affect ecosystem function. Specialist Lepidoptera do not always show the most adverse effects of changes in forest habitat due to differences in plant composition or disturbance regimes (Lepš et al. 1998, Summerville & Crist 2002a, b). For example, even when specialists and oligophages are disproportionately lost from a forest patch following habitat loss, matrix-dwelling species with similar diet-breadth may be equally likely to occur in small woodlots from the surrounding landscape (Summerville & Crist 2003, in press). Species replacement will be obscured at the level of the functional group when an equal number of specialists are present in large and small forests. Detection of replacement will require an examination of changes in the occurrence of individual species, an inefficient process for hyper-diverse communities. This is not meant to imply that defining lepidopteran functional groups based on diet-breadth has no place in ecologi-

cal research, just that it may not be the most powerful approach to detecting species replacement or predicting post-disturbance community structure in Lepidoptera (Summerville & Crist 2002b).

LEPIDOPTERAN FUNCTIONAL GROUPS: A NOVEL APPROACH

Detecting the occurrence of species replacement for lepidopteran communities requires a novel approach to functional group classification. One method employed in studies of tropical forest Lepidoptera is to use a single functional group as an indicator of entire community diversity. For example, a number of studies have quantified the effects of habitat loss on frugivorous butterfly species as a surrogate for overall butterfly diversity (Beccaloni & Gaston 1995, DeVries et al. 1997). While discovering surrogate taxa is a useful technique for simplifying the species diversity of tropical forest lepidopteran communities, it offers less promise as a method for detecting species replacement because surrogates are often selected to mimic the response of an entire community. Thus, ecologists identify surrogate taxa by demonstrating that a significant correlation exists between changes in diversity of the species within a particular functional group and the total species richness within a community (i.e., both should respond negatively to habitat loss). Under conditions of species replacement, however, total species richness remains unchanged following a disturbance such as habitat loss.

Horner-Devine et al. (2003) come close to demonstrating species replacement in Costa Rican butterfly communities. The authors reach the conclusion that butterfly communities within coffee habitats and within Las Cruces Reserve differ in species composition but not species richness. Species replacement is suggested in Table 1 of Horner-Devine et al.; coffee habitats support a greater number of frugivorous Charaxinae and Nymphalinae than Las Cruces Reserve. Yet, both the reserve and coffee habitats contain roughly the same total number of frugivorous and non-frugivorous butterfly species. Species turnover occurs within each guild between coffee plantations and reserve forests, but non-frugivores do not replace frugivorous butterflies in more disturbed habitats. Therefore, this guild classification does not appear to be very amenable to identifying species replacement. Some form of species replacement is likely to occur in Neotropical forests following habitat disturbance or loss (Bieregaard et al. 2001), yet identification of the process might be expedited by using a different approach to classification of functional groups.

Recent research in temperate forest ecosystems

suggests that classifying moth species into functional groups based upon the life form of the host resource is a promising way to test whether species replacement occurs in fragmented landscapes (Summerville & Crist 2002a, 2003, in press). This classification produces roughly 5 guilds of forest moths: woody-plant feeders (e.g., many Noctuidae: *Catocala* spp.), herbaceous feeders (e.g., Noctuidae: *Papaipema* spp.), dead/de-caying vegetation feeders (e.g., Noctuidae: *Zanclog-natha* spp.), encrusting flora feeders (e.g., fungi, lichens, mosses; e.g., many Arctiidae: Lithosiinae), and generalized feeders that use ≥ 2 functional categories (e.g., Noctuidae: *Agrotis ipsilon* Hufn.). Functional groups based on life forms should provide lepidopterists with novel insights into how moth communities change during succession, in response to disturbance, and following habitat loss. In addition, this method of defining functional groups will allow ecologists to make explicit connections between changes in lepidopteran communities and forest architecture after habitat loss. Similar approaches to defining functional groups were developed long ago by plant ecologists (e.g., Raunkiaer 1937) and several have proven useful when describing species replacement in floras such as described for Amazonian forest fragments (e.g., Bierregaard et al. 2001).

FUNCTIONAL GROUPS, HABITAT LOSS, AND SPECIES REPLACEMENT

Indeed, the proposed functional group classification was recently used both to detect species replacement in temperate forest moth communities and to elucidate the moth assemblages among which functional species replacement occurs (Lepš et al. 1998, Summerville & Crist 2002a, 2003). For example, in forests of the unglaciated Western Allegheny Plateau ecoregion of Ohio, species replacement was observed across a gradient of forest stand sizes (Fig. 1a). Using linear regression, I determined that the number of moth species with woody host-plants dwindles as forest habitat size decreases ($df = 1$, $R^2 = 0.58$; $p \leq 0.05$). The overall reduction in moth species richness is partially offset because smaller forests gained additional species of herbaceous-plant feeders ($df = 1$; $R^2 = 0.73$; $p \leq 0.01$). Species replacement, however, is not a ubiquitous process structuring forest lepidopteran communities. In historically glaciated forests of the North Central Tillplain ecoregion in Ohio, reduction in forest area is not correlated with an increase in herbaceous-feeding moth species (Fig. 1b). In these forests, habitat loss significantly reduces only woody-feeding species ($df = 1$, $R^2 = 0.80$, $p \leq 0.01$).

It is important to emphasize that these trends would not have been observed if I had relied on an analysis

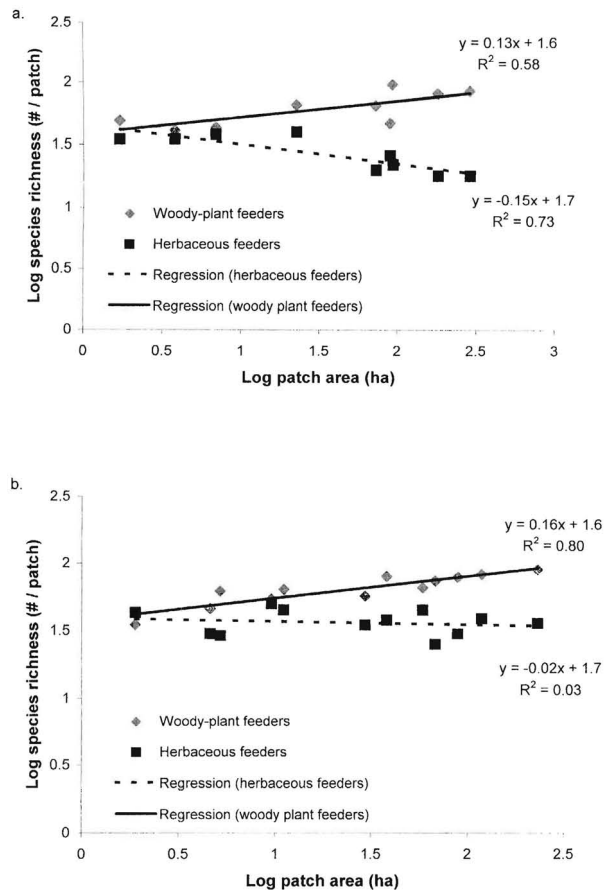


FIG. 1. Responses of species richness of moths that feed on either woody plant or herbaceous vegetation as caterpillars to variation in forest habitat area (ha). **a**, species replacement is observed in forests of the unglaciated Western Allegheny Plateau, but **b** in the historically glaciated North Central Tillplain, loss of forest habitat is only correlated with a decrease in species richness of woody plant feeders. Figure is modified from Summerville and Crist (in press).

framework grounded in testing hypotheses using the more traditional approach to guild classification. Out of the 344 moth species classified as either woody-plant feeders or herbaceous feeders, only 47 would have been considered specialists (i.e., species feeding only on host plants within a single genera), with the numbers of specialists split nearly evenly between woody plant feeders found in large forests and herbaceous feeders restricted to smaller woodlots (21 and 26 species respectively). Greater than 67% of the remaining species would have been considered generalists; thus the distribution of feeding strategies is strongly skewed to the generalist life history. In a different study designed to test for the effects of timber extraction on moths classified as either specialist or generalist, Summerville and Crist (2002) demonstrated that both functional groups responded negatively to timber harvest. Again, specialists were outnumbered by generalist species by nearly 4 to 1, render-

ing the power of the statistical test for a disproportionate response by specialists very low (KSS unpublished data). Therefore, for temperate moth communities, the traditional method of assigning species to functional groups appears to have limited potential to detect species replacement or differential responses of specialists to habitat disturbance. The question of why replacement occurs in some forest moth communities and not others remains to be explored, but the answer may be related to land use history or matrix vegetation type. Summerville and Crist (2003, in press) offer additional explanations for the factors contributing to species replacement in temperate deciduous forests.

CONCLUSIONS

In conclusion, lepidopterists need not feel confined to testing ecological hypotheses within the framework of traditionally defined functional groups. Rather, I suggest that alternative classification schemes for lepidopteran functional groups will allow lepidopterists to test more powerfully hypotheses regarding species replacement and the post-fragmentation responses of moth communities to habitat loss. Currently, Lepidopterists may be confined in extending the concepts outlined in this paper to tropical ecosystems, as host plant data is lacking for the immature stages of many species, including butterflies. As a general rule, the definition of ecologically-relevant functional groups should be tailored to the ecosystem in question and should be created with regard to the natural history of focal taxa (Hawkins & MacMahon 1989, Summerville & Crist 2002b). In temperate deciduous forests, I believe adopting a classification scheme based on the life form of the host-plant holds considerable promise, and has been used successfully in plant ecology. That habitat loss affects communities of butterflies and moths worldwide is not a new observation for lepidopterists. What are required now are predictive models that will allow ecologists to forecast how lepidopteran communities are likely to change in the face of anthropogenic disturbances. Developing an improved understanding of the mechanisms of species replacement will move conservation biology one step closer toward such a goal.

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