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Ecological Traits Fail to Consistently Predict Moth Species Persistence in Managed Forest Stands

Keith S. Summerville¹

Abstract

Species traits have been used as predictors of species extinction and colonization probabilities in fragmented landscapes. Thus far, trait-based analytical frameworks have been less commonly employed as predictive tools for species persistence following a disturbance. I tested whether life history traits, dietary traits, and functional traits were correlated with moth species persistence probabilities in forest stands subjected to varying levels of timber harvest. Three harvest treatments were used: control stands (unharvested since 1960), shelterwood cut stands (15% canopy removed), and patch cut stands (80% standing bole removed). Logistic regression models were built to assess whether species persistence probabilities were a function of species traits; separate models were constructed for each level of timber harvest treatment. Species persistence probabilities were mainly a function of pre-harvest abundances. Species traits had idiosyncratic effects on species persistence depending on the level of timber harvest employed. These results suggest that species traits may indirectly influence how moth species assemblages change as a result of forest management by determining pre-harvest abundance rather than persistence per se. The absence of significant trait effects on persistence probabilities may also reflect prior reduction in species trait space. That is, the range of species trait combinations sampled in this study was much lower than observed in historically unlogged eastern deciduous forest systems. Thus, the lack of significant trait-persistence correlations observed here might indicate historic extinctions of species from prior logging events that have not been offset by post-harvest recovery of original species assemblages.

Forest fragmentation is known to cause significant changes in lepidopteran community structure and diversity (Summerville and Crist 2004, Fox 2013, Slade et al. 2013). In general, loss of species richness and shifts in species composition are a function of the magnitude of disturbance to the forest landscape (Forkner et al. 2006). Recovery of species richness can be rapid, especially for forest stands with a limited disturbance footprint (Summerville 2013). Recovery of pre-disturbance species composition appears to require longer time-courses, and there is some question about how we develop baseline community targets with which we can assess species recovery (Usher and Keiller 1998, Merckx et al. 2009). How the recovery of species within ecological communities correlates to reestablishment or recovery of functional processes within forests is also a major unknown.

Explicitly linking shifts in species diversity and composition to persistent shifts in ecosystem function has been challenging (Boerschig et al. 2013). Ecologists, however, are increasingly recognizing that the effects of fragmentation need to be understood as a disturbance that may impair ecosystem function

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beyond merely reducing species diversity per se (Luck et al. 2012). Finding clear correlations between changes in lepidopteran diversity and forest ecosystem properties has revealed equivocal conclusions. For example, variation in herbivory by larval Lepidoptera is connected to litter quality in forest systems, but how specific species contribute to this phenomenon is less resolved (Chapman et al. 2003). A species' contribution to ecosystem function is determined, in part, by the evolved traits of that species (Pla et al. 2012). Thus, understanding whether variation in traits among species predicts response to forest disturbance is an important first step to linking how changes in species diversity correlate to alternation of ecosystem function (Öckinger et al. 2010).

Traits may influence how likely a species persists in the face of disturbance in a variety of ways. First, life history traits such as fecundity, body size, voltinism, and overwintering stage are connected to variation in population size in both space and time (Spitzer and Lepš 1988, Betzholtz and Franzén 2011, Boerschig et al. 2013). Body size in particular has proven a useful predictor of both fecundity and dispersal capacity (Spitzer et al. 1984, Sekar 2012). Analysis of dietary traits, such as host plant breadth, feeding mode (e.g., borer, chewer, miner), and host plant type suggests that greater levels of specialization render lepidopterans more vulnerable to disturbance (Summerville and Crist 2002, Koh et al. 2004, Mattila et al. 2006, Slade et al. 2013). Less well studied are functional traits, which explicitly identify the contribution of species to processes such as pollination, decomposition, nutrient cycling, or carbon sequestration (Schowalter 2000, Chapman et al. 2003). Pollinators and decomposers might be considered more vulnerable to forest disturbance given their seeming inability to move through heterogeneous land cover types and sensitivity to soil temperature and moisture, respectively (see Hohn and Wagner 2000, Bommarco et al. 2010).

The goal of this study was to determine whether specific traits or trait combinations of forest moths were related to species persistence probabilities in stands experimentally managed with differing levels of timber harvest. I obtained three types of trait data for each moth species sampled: life history traits, ecological traits, and functional traits. I hypothesized that species would be more likely to persist in managed forest stands if they were multivoltine, generalist herbivores that used a combination of herbaceous and woody larvae hosts. Furthermore, I predicted that pollinators and detritivores would be especially sensitive to harvest disturbance, and species performing these functions would be unable to persist in managed stands. Finally, I tested whether post-disturbance species' persistence probabilities were affected by pre-harvest abundance in conjunction with species traits.

Methods

Study System. This research was performed within Morgan-Monroe State Forest; a $\approx 9,725$ ha managed system in south central Indiana. Morgan-Monroe State Forest occurs within the North-Central Interior Dry-Mesic Oak Forest and Woodland ecological system (39°31'28"N, 86°44'13"W). In unfragmented landscapes, canopy cover tends to be dense, although historic fire regimes maintained open canopy (Homoya et al. 1985). *Quercus montana* Wilde. (chestnut oak) is a dominant species with *Q. alba* L. (white oak), *Q. rubra* L. (red oak), or *Q. velutina* L. (black oak) present depending on soil moisture regimes. *Carya cordiformis* Koch (bitternut hickory) and *C. ovata* (Mill.) Koch (shagbark hickory) are also common. Additionally, this ecoregion is among North America's richest for herbaceous plants and shrubs with over 2,000 species described (Homoya et al. 1985).

Experimental Design. This study is part of a long term research project designed to test for critical thresholds in levels of timber removal and biodiversity changes within eastern deciduous forests (Hardwood Ecosystems Experiment, HEE; see <http://www.heeforeststudy.org/>). In early 2007, I identified three large forested landscapes within Morgan-Monroe State Forest for

lepidopteran sampling (see Summerville 2011). These landscapes possessed a similar history of timber harvest, most were clearcut ≈ 60 y in the past, but the historical data regarding levels of timber removal were unavailable (D. Vadas, personal communication). A subset of forest stands in each of these landscapes was manipulated with timber harvest in 2008. One of two harvest methods were used to manipulate forest stands in 2008: patch-cut harvests, in which 80% of the standing forest canopy was removed in a 3–5 ha patch, and shelterwood logging, in which the first of three planned cuts removed 15% of the standing canopy. Furthermore, control treatments, in which 100% of the standing biomass was retained within the entire forest stand, were designated. To determine whether species persistence in managed stands was influenced by combinations of species traits, I established moth sampling points in patch-harvested stands, shelterwood cut stands, and controls. In total, I identified 4 stands that were patch-cuts, 4 stands that were unlogged controls, and 3 stands forest stands that were managed with shelterwood techniques. All forest stands were 3–5.8 ha in area.

Sampling Methodology. Lepidoptera were sampled from all 11 forest stands in 2007, one year prior to timber harvest. Then, in 2008, private timber concessionaires were contracted to remove trees from management concessions with specific harvest allocations corresponding to the experimental design. All stands were re-sampled in 2009. Moths were collected from forest stands using Universal blacklight traps (12-watt, BioQuip Products, Inc., Rancho Dominguez, CA) powered by 12 V, 26 Amp-hr batteries. Traps were located in the approximate center of each forest stand to reduce edge effects from the surrounding forest. On nights of operation, a single trap was placed at each site on a platform 2 m above the ground and remained lit from 2000–700 CDT. I sampled Lepidoptera every 9–14 days from 30 May–30 August in both 2007 and 2009, producing 55 total samples from the 11 sites (5 per site) per sampling year (110 samples across both years). Weather and moon intensity are known to affect sampling efficiency of blacklight traps, so trapping was restricted only to nights that had a minimum temperature $\geq 16^{\circ}\text{C}$, no precipitation, and low levels of ambient moonlight ($\frac{1}{2}$ to new moon phases) (Summerville et al. 2006). Species nomenclature and authorities follow Hodges et al. (1983), with revisions following Ferguson (2008) and Lafontaine and Schmidt (2010). Voucher specimens were deposited at in the insect collection at Drake University.

Trait Classification. Measurement of species traits followed the same general protocol as Summerville et al. (2006) with several important exceptions. First, I expanded the range of traits modeled based on the results of Koh et al. (2004) and Mattila et al. (2006). This involved determining two critical aspects of species natural history: the overwintering stage and species function in the ecosystem (e.g., pollinator, detritivore). Such data are readily obtained for a large number of Erebidae, Noctuidae, Geometridae, Notodontidae, Saturniidae, and Sphingidae but were lacking for other less well-known microlepidoptera taxa (see Covell 2002, Tuttle 2007, Ferguson 2008, Wagner et al. 2011). Thus, I was only able to obtain complete natural history data for 278 out of the 389 total species sampled. These were the only species retained in the trait-based analysis. In total, the following traits were assigned to species: voltinism, overwintering stage, diet breadth, host plant type, use of *Quercus* as a larval host, use of *Acer* as a larval host, role as a pollinator (after species descriptions in Wagner et al. 2011 and LeCroy et al. 2013), role as a detritivore, and body size (see Table 1 for a more complete breakdown for how these species traits were coded for each species). It is important to note that my assessment of species' role in pollination services is conservative; additional species of Noctuidae and Erebidae may provide pollination services without being formally documented as doing so in the primary literature.

Data Analyses. I used logistic regression models to determine if particular species traits were significant predictors of species persistence probabilities

Table 1. Species traits used as predictors of persistence probabilities in forests managed with different harvest regimes. Species traits fall into one of three categories: dietary traits, functional traits, and life history traits. Trait categories follow Summerville (2006) and Pla et al. (2012).

Species Trait	Trait category	Trait measurement
Diet Breadth	Dietary	Two levels: generalist or specialist following Summerville (2006)
Host plant type	Dietary	Four levels: woody plant feeder, herbaceous feeder, fungivore / lichivore, and generalist after Summerville and Crist (2002)
Use of <i>Quercus</i> spp.	Dietary	Two levels (0 = no; 1 = yes)
Use of <i>Acer</i> spp.	Dietary	Two levels (0 = no; 1 = yes)
Role in pollination	Functional	Two levels (0 = no; 1 = yes)
Role in detritivory	Functional	Two levels (0 = no; 1 = yes)
Voltinism	Life history	Number of adult generations per year (1-4)
Overwintering stage	Life history	Four levels (egg, larvae, pupae, adult)
Body size	Life history	Mean wingspan after Gaston and Reavey (1989)

within patch-cut, shelterwood, and control stands. To perform these analyses, I first screened the trait variables for significant intercorrelations using Pearson product-moment correlation coefficients (PROC CORR, SAS Institute, Cary, IN). Most trait variables were orthogonal (Pearson $r < 0.30$); however, host plant type was highly intercorrelated with a number of factors. It was subsequently excluded from analyses. In addition, overwintering stage was strongly intercorrelated with voltinism (multivoltine species tend to winter as larvae). Thus, I also removed overwintering stage from logistic regression models.

I used the SAS Enterprise system to create separate logistic regression models for each of the three harvest treatments. Species were considered to have 'persisted' if they had a post-harvest abundance > 5 (across all replicate stands within a harvest treatment) and occurred in at least one stand per treatment in both 2007 and 2009. These cut offs were chosen to be consistent with other recent studies that have examined persistence probabilities in lepidopteran communities (see Koh et al. 2004). To some extent, the specific values are arbitrary, but species with post-harvest abundance > 5 have detection probabilities > 0.80 . Higher detection probabilities suggest that species absences from ecological communities reflect the impact of timber harvest rather than sample bias (Summerville et al. 2006). Models that retained singleton and doubleton species (i.e., those that possessed only one or two sampled individuals) produced qualitatively identical results as models built using this more conservative definition of persistence. Model significance was assessed using likelihood ratios, which tested the global null hypotheses that included trait variables have no effect on persistence probabilities (Piegorch and Bailer 1997). In addition, I followed the recommendations of Nagelkerke (1991) and calculated the generalized R^2 parameter to further describe the fit of the model to the data. Voltinism and body size values were log-transformed prior to analyses to meet the assumptions of logistic regression. *Quercus* use, *Acer* use, pollinator status, and detritivore status were square root transformed prior to analyses (Sokal and Rohlf 1995).

In addition to trait variables, I also included each species' abundance in 2007 as a random covariate. That is, I tested whether species persistence probabilities were related to pre-harvest population size (as sampled using light traps) rather than species traits per se. Because I lacked a well resolved phylogeny to test for relationships among the species traits and moth taxa (families, sub-families) (see Felsenstein 1985), I followed the method of Koh et al. (2004) and created a second logistic regression model with a dummy variable used to code for lepidopteran families. The effect of moth family on persistence probability was non-significant in this model (Wald $\chi^2 = 1.34$; $df=1$; $P = 0.19$) despite there being a significant correlation between moth family and body size (Pearson correlation = 0.54; $P < 0.01$), voltinism (Pearson correlation = 0.28; $P < 0.05$), and role in detritivory (Pearson correlation = 0.75; $P < 0.001$). The significance of all model effects was assessed using Wald χ^2 statistics.

Results

Trait data were available for 278 of the moth species sampled from Morgan-Monroe State Forest in 2007. Of this total, 64 species persisted in the stands managed with patch cut harvests, 66 species persisted in the stands managed with a shelterwood cut, and 83 species persisted in the stands treated as controls. To place these data in context, in 2007 the richness of moth species in stands allocated for patch harvests was 177 and the richness of moths sampled in stands to be managed with shelterwood cuts was 159. The pre-harvest richness of moths in control stands was 150. Thus, richness was lower across all three treatments in 2009 compared to 2007. The decrease in species richness, however, was greater in managed stands. Finally, the five most abundant species that were sampled in 2007 were the same five most abundant species in 2009: *Halysidota tessellaris* (Smith) (Erebidae), *Hypoprepia fucosa* Hübner (Erebidae), *Nadata gibbosa* (Smith) (Notodontidae), *Lambdina feruidaria* Hübner (Geometridae), and *Heterocampa obliqua* Packard (Notodontidae).

Persistence probability for moth species in control stands was a function of *Quercus* use by larvae and pre-harvest abundance ($\chi^2 = 38.47$; $df = 7$; $P < 0.0001$). The model R^2 was calculated to be 0.30, indicating about one-third of the variance in species persistence was described by the model effects. Functional traits and life history traits, however, were not significant predictors of species persistence (Table 2). Species that persisted in control stands post-harvest in Morgan-Monroe State Forest were those that did not rely on *Quercus* as a host plant ($\chi^2 = 3.73$; $df = 1$; $P < 0.05$) and those that were sampled at high abundance in 2007 ($\chi^2 = 18.30$; $df = 1$; $P < 0.0001$).

In contrast to the persistence model for the control stands, the likelihood that a moth species sampled in 2007 persisted in shelterwood harvested stands in 2009 was a function of one functional trait and initial abundance (Table 3). The overall model was significant ($\chi^2 = 37.57$; $df = 7$; $P < 0.0001$), but the R^2 value was slightly lower than the model for the control stands ($R^2 = 0.28$). Persistence probabilities were lower for species that were considered detritivores ($\chi^2 = 3.99$; $df = 1$; $P = 0.045$) and those species that were sampled at low abundances in 2007 ($\chi^2 = 22.87$; $df = 1$; $P = 0.006$). Diet breadth, host plant type, voltinism, and body size were not significant predictors of persistence probabilities (Table 3).

Species traits were not significant predictors of persistence probabilities for moths sampled within patch cuts harvest stands (Table 4). The full model was significant ($\chi^2 = 53.73$; $df = 7$; $P < 0.0001$) but persistence appeared solely to be a function of initial sampling abundance ($\chi^2 = 33.92$; $df = 1$; $P = 0.0001$). The Nagelkerke R^2 value for this model was the highest of the three ($R^2 = 0.38$). Species that were abundant in 2007 tended to persist in stands managed with the patch cut harvest treatment. *Quercus* feeding might be considered a minor contributor to species persistence with a low but non-significant test statistic (Table 4). Species known to feed on *Quercus* leaves were less likely to persist

Table 2. Results of logistic regression model relating moth species traits to persistence probabilities in control forest stands. Replicate forest stands ($n = 4$) were sampled pre-harvest in 2007 and post-harvest in 2009. The full model was significant ($\chi^2 = 38.47$; $df = 7$; $P < 0.0001$).

Model parameter	df	Estimate	Wald χ^2	<i>P</i>
Use of <i>Quercus</i> species	1	-0.79	3.72	0.05
Diet breadth	1	0.56	0.05	0.82
Role in pollination	1	0.61	0.46	0.50
Role in detritivory	1	-14.87	0.01	0.97
Voltinism	1	0.06	0.04	0.83
Body size	1	2.65	0.89	0.67
Log initial (2007) abundance	1	-1.60	18.30	0.0001
Intercept	1	1.25	3.28	0.001

Table 3. Results of logistic regression model relating moth species traits to persistence probabilities in forest stands managed with a shelterwood cut. Stands ($n = 3$) were sampled pre-harvest in 2007 and post-harvest in 2009. The full model was significant ($\chi^2 = 37.57$; $df = 7$; $P < 0.0001$).

Model parameter	df	Estimate	Wald χ^2	<i>P</i>
Use of <i>Quercus</i> species	1	-0.23	0.34	0.56
Diet breadth	1	0.42	0.68	0.41
Role in pollination	1	0.56	0.71	0.40
Role in detritivory	1	-1.45	3.99	0.04
Voltinism	1	-0.15	0.34	0.56
Body size	1	3.29	1.89	0.23
Log initial (2007) abundance	1	-1.55	22.87	0.0001
Intercept	1	1.71	7.49	0.006

Table 4. Results of logistic regression model relating moth species traits to persistence probabilities in forest stands managed with a patch harvest. Stands ($n = 4$) were sampled pre-harvest in 2007 and post-harvest in 2009. The full model was significant ($\chi^2 = 53.73$; $df = 7$; $P < 0.0001$).

Model parameter	df	Estimate	Wald χ^2	<i>P</i>
Use of <i>Quercus</i> species	1	-0.63	2.38	0.10
Diet breadth	1	0.16	0.08	0.78
Role in pollination	1	-0.63	0.92	0.34
Role in detritivory	1	-0.96	1.59	0.21
Voltinism	1	0.03	0.01	0.92
Log body size	1	0.89	1.12	0.29
Log initial (2007) abundance	1	-2.09	33.93	0.0001
Intercept	1	2.47	13.84	0.0002

in the patch cut stands post-harvest compared to those moths known to feed on other host species ($\chi^2 = 2.38$; $df = 1$; $P = 0.10$). However, the power of this test is fairly low due to the limited replication of stands within management category ($\beta = 0.60$).

Discussion

The response of lepidopteran species to contrasting levels of timber harvest was only weakly predicted by species traits, and no single trait was consistently related to species persistence following logging. Previous studies in this system, however, have demonstrated that removal of standing timber biomass is correlated with significant loss of species richness (Forkner et al. 2006; Summerville 2011, 2013). The equivocal nature of species trait-species persistence relationships complicates efforts to link changes in lepidopteran assemblages to alteration of forest ecosystem function. Low levels of replication within harvest treatments and across the forested landscape of the Hardwood Ecosystem Experiment certainly contributed to lack of significant model effects (i.e., the power of some of my tests was ≈ 0.60). Accommodating lower statistical power by allowing significance to be assigned at a higher *P*-value (e.g., 0.10), however, only adds one significant species trait in the patch cut treatment (*Quercus* use, see Table 4). Variability between years due to environmental stochasticity may also dilute the effects of management treatment on lepidopteran persistence (Lepš et al. 1998), but I did not detect a clear pattern of significance in sampling year \times species trait interactions.

Within the context of background annual variation and lower than optimal statistical power, forests managed with timber harvest possess fewer species, but loss of species within lepidopteran communities does not confined to a single feeding guild, life history strategy, or functional group (e.g., pollinators). Instead, the single best predictor of a species' persistence probability post-harvest was its initial abundance. The abundance of moths in these forest stands is related to voltinism, body size, and feeding guild (Summerville et al. 2013). Multivoltine species with smaller body sizes and larvae that develop on a wide range of woody plant foliage were more abundant pre-harvest and thus more likely to persist following logging (see also Summerville and Crist 2002). In addition, inclusion of initial abundance as a co-variate accounts for potential 'noise' associated with species' detection probabilities. Some subset of those species that 'persist' are likely 'persistent' because they are readily sampled using light traps.

Studies of lepidopteran communities in grasslands suggest that functional homogenization results from landscape disturbance as species persisting in communities become more generalist (Lepš et al. 1998, Boerschig et al. 2013). Furthermore, extinction probabilities of forest butterflies and moths in fragmented forests are significantly predicted by species traits (e.g., Koh et al. 2004, Mattila et al. 2006, Beck et al. 2006, Slade et al. 2013). Species more likely to experience an extinction event post-fragmentation were specialists (as larvae), small-bodied, and univoltine. Species persisting in highly managed landscapes tended to be 'generalists' (e.g., see Summerville et al. 2006). One major difference between these studies and the results presented here is the spatial scale at which species persistence was assessed.

Spatial scale clearly influences how the effects of logging are measured (Hamer and Hill 2000). In this study, relatively small forest stands (3–5 ha) were disturbed and most of the intervening landscape was maintained as unmanaged forest > 60 years old. Studies that tend to document significant correlations between species traits and persistence probabilities occur at the other end of the landscape disturbance gradient (Slade et al. 2013). In these studies, forest stands that were sampled represented isolated patches in a more highly managed landscape (Koh et al. 2004). The matrix was more inhospitable and less likely to facilitate re-accumulation of species (Ricketts et al. 2001). Thus, persistence probabilities of moth species may be a function of the species composition of the undisturbed matrix when the disturbance footprint is small relative to the extent of the unmanaged forest. Indeed, species that were the most abundant in forest stands pre-harvest (and thus more likely to persist) were also more abundant in unmanaged forest matrix pre-harvest (Summerville et al. 2013). When the disturbance footprint of logging is larger, effectively fragmenting the landscape, species traits may become better predictors of which moths will contribute to the recovering forest community.

The lack of significant trait correlations observed in this study may also reflect the legacy of past timber harvest. There are few historic data that would allow a comparison of trait distributions for forest moth communities prior to the timber harvest that occurred in 1930s and 1940s and the trait distributions measured in this study. In contrast to old-growth and historically unlogged forests in states such as Ohio (USA), however, the moth communities sampled here contain a higher proportion of generalist feeders and many fewer *Quercus* specialists (Summerville et al. 2008). Perhaps when generalists dominate a community, only their pre-disturbance abundances will be consistent predictors of which species survive. How ecologists define the reference point by which we evaluate species persistence or changes in ecosystem function is therefore critical (e.g., Murphy and Romanuk 2014). Managing for recovery of the 2007 moth communities in Morgan-Monroe State Forest will miss important aspects of lepidopteran biodiversity that is present in stands lacking historic logging activities. Our current forest moth assemblages may be highly altered artefacts of historic lepidopteran communities, even if logging has not occurred for long time periods. Establishing a framework to understand how both historic and current forest management affects functional diversity of insects will be critical to understanding how to conserve eastern deciduous forests as they are additionally impacted by future climate and invasive species stressors.

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