Moth Diversity in a Fragmented Habitat: Importance of Functional Groups and Landscape Scale in the Boreal Forest

B. C. SCHMIDT[1] AND J. ROLAND

Department of Biological Sciences, CW-405 Biological Sciences Building, University of Alberta, Edmonton, Alberta, Canada T6G 2E9

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ABSTRACT One of the leading concerns for both conservation biology and forestry has been how forest fragmentation affects biodiversity, and how forestry practices can be altered to mitigate diversity losses. However, the effects of habitat fragmentation on ecological functional groups within diverse taxa such as Lepidoptera are poorly known, particularly in boreal forests. We assessed landscape-level changes in moth species richness and abundance in relation to forest fragmentation, measured at multiple scales. We assessed fragmentation effects on three functional groups: tree- and shrub-feeding species, grass- and forb-feeding species, and species that act as hosts for parasitoids of an important forest defoliator, *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae). Total species richness showed a significant decline as a function of fragmentation at all measured spatial scales; both polynomial and threshold models tended to explain more variation than linear models, suggesting that there is little to no change in overall moth diversity between low and moderately fragmented stands. However, changes in diversity patterns within functional groups showed that total diversity measures may mask changes in community structure. Changes in overall diversity were driven largely by a decrease in species richness of tree- and shrub-feeding moths, although forb- and grass-feeding moths also showed marginally lower species richness at high fragmentation levels. Most species of the parasitoid host group decreased in abundance with increasing fragmentation. These findings show that overall diversity measures can mask important community changes, and that the optimal landscape scale at which these changes are measured is taxon dependent. Finally, the decrease in host availability to *M. disstria* parasitoids in fragmented forests may exacerbate population outbreaks of *M. disstria*.

KEY WORDS boreal forest, community composition, *Malacosoma disstria*, parasitoid, landscape structure

Studies of the effects of forest fragmentation on the function and diversity of insect communities have focused largely on tropical forests (Didham 1997), because the tropical realm contains the largest proportion of the earth's biodiversity. In contrast, knowledge of forest fragmentation effects on insect communities in the boreal forests of the northern hemisphere remains relatively limited (Norton 1996; but see Niemela 1997, and references therein). Several recent studies have examined lepidopteran community structure in North American temperate deciduous and mixed wood forest (Summerville et al. 2001, 2003; Summerville and Crist 2002, 2003; Thomas 2002) and boreal forest (Pohl et al. 2004). Although biological diversity of the boreal forest does not rival that of tropical forests or even eastern deciduous forests, one-third of the world's forests are classified as boreal, comprising ≈14% of the world forest biomass (Kauppi and Posch 1985), harboring an estimated 22,000 species of insects in North America (Danks and Footit 1989). The Lepidoptera are one of the most prevalent terrestrial insect groups and perform essential ecosystem services such as pollination, decomposition, and nutrient cycling and provide prey for passerine birds. In deciduous forests of eastern North America, it has been shown that increased forest fragmentation changes moth community composition as a result of both species impoverishment and replacement, but that diversity measures may not reflect community changes as well as changes in species composition (Summerville and Crist 2003). These community changes seem to be largely mediated by an influx of species associated with agricultural landscapes and a decrease in forest-associated species (Summerville 2004a, Summerville and Crist 2004).

To determine whether and how habitat fragmentation affects moth communities in a boreal forest, we examined responses of three lepidopteran functional groups, two based on larval host plant requirements and one based on host suitability for parasitoids of a forest pest, the forest tent caterpillar, *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae). Func-

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[1] Corresponding author, e-mail: bjorn@ualberta.ca.

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tional group classification based on larval host plant is more sensitive to changes in lepidopteran community structure than groupings based on niche or diet breadth (Summerville 2004b).

The parasitoid–host functional group is a subset of the larval host groups but provides an assessment of the role that landscape structure plays in parasitoid–host population dynamics as mediated by alternate hosts. The forest tent caterpillar is a widespread defoliator of deciduous trees throughout North America and is one of the most dramatic examples of a cyclic pest species, with outbreak periodicity varying according to geographic location (Fitzgerald 1995). Defoliation by this insect is a major natural disturbance factor. Natural enemies, such as predators, pathogens, and parasitoids are the major mortality factors in the dynamics of forest tent caterpillar populations and are often thought responsible for causing outbreak collapse (Witter and Kulman 1972, Roland and Taylor 1995). A forest tent caterpillar outbreak can vary in duration from 1 to 8 yr, some of this variation in duration being attributable to parasitoid efficacy mediated by forest structure (Roland and Taylor 1995). Population outbreaks of forest tent caterpillar can last several years longer in forests that have been fragmented by agriculture and forestry, compared with shorter outbreaks in large, continuous forests (Roland 1993). At high forest tent caterpillar density, forest fragmentation reduces the impact of most mortality agents, such as parasitoids (Roland et al. 1997, Roland and Taylor 1997) and viral pathogens (Rothman and Roland 1998).

The objectives of this study were to determine the effect of forest fragmentation on the diversity and community structure of moths in a boreal forest. Specifically, we addressed how loss of forest habitat in an agricultural landscape matrix affected overall diversity patterns compared with changes in diversity of three functional groups. Two functional groups were based on larval host plant requirements. We defined a third functional group based on larval suitability as a host to a specific parasitoid guild, i.e., parasitoids known to be important in the population dynamics of the forest tent caterpillar.

Materials and Methods

Sampling Sites. Sampling was carried out in the southern boreal forest of central Alberta, Canada, during 1999 and 2000. The sampling grid covered a 20- by 20-km area, centered on the Ministik Hills (113° 00′ W, 53° 25′ N) ≈35 km southeast of the city of Edmonton. The Ministik Hills are within the dry boreal mixed wood ecoregion (Strong and Leggat 1992), and the natural vegetation is dominated by trembling aspen, *Populus tremuloides* Michx., forest. Balsam poplar, *Populus balsamifera* L., occurs as a dominant or codominant species in more mesic sites. Paper birch (*Betula papyrifera* Marsh.), white spruce [*Picea glauca* (Moench) Voss], and black spruce [*Picea mariana* (Mill.) B.S.P.] occasionally form small, isolated stands. In upland sites, beaked hazel, *Corylus cornuta* Marsh., often forms a thick understory. Other common understory shrubs include red raspberry (*Rubus idaeus* L.), red osier dogwood (*Cornus stolonifera* Michx.), Bebb's willow (*Salix bebbiana* Sarg.) wild rose (*Rosa* spp.), saskatoon (*Amelanchier alnifolia* Nutt.), and pin cherry (*Prunus pennsylvanica* L.). Wetlands, primarily sedge (*Carex* spp.) and cattail, *Typha latifolia* L., marshes, are common throughout the study area. Nonforested land cover is largely the result of agricultural clearing for forage crops (hay and alfalfa, *Medicago sativa* L.) and pastureland for cattle grazing.

At the landscape scale, light trapping sites were selected to provide a range of surrounding forest (versus nonforest) cover as a measure of forest fragmentation. Sites ranged from 20 to 90% fragmented (proportion of nonforest to forest) at three spatial scales, measured in concentric circles with radii of 200, 400, and 600 m. Because the regional forest structure at Ministik Hills is more characteristic of a perforated landscape (sensu Hunter 1992) rather than discrete, isolated patches, we used stand context (percentage of nonforest versus forest) as a measure of fragmentation. Forest structure was defined as the spatial context in which the study sites occurred, at scales between 200 and 600 m. Fragmentation was measured at three scales, because there were no a priori predictions for the scale at which moths would respond to fragmentation most strongly, and because response to fragmentation is known to be scale-dependent for other insects (Roland and Taylor 1997, Hamer and Hill 2000). Landscape structure was classified visually into forest and nonforest from 1:20,000 aerial photographs taken between 1994 and 1997. Landscape cover classified as nonforest consisted primarily of agricultural land (pasture, canola crops, and cereal crops). Subsequent forest cover parameters were calculated using ImageTool for Windows 2.00 (University of Texas Health Science Center, San Antonio, TX). Twelve sites were sampled in 1999, with an additional 12 added in 2000. Sites were separated from one another by a minimum distance of 1.7 km. Because local topography can affect light trap catch (Waring 1994), trap locations with similar microtopography and surrounding vegetation structure were chosen. Traps were located in upland sites at or near the top of the local topography (maximum relief within a 250-m^2 area is ≈10 m). To minimize the effects of local vegetation on moth species composition, sites dominated by a trembling aspen canopy and a beaked hazelnut understory were selected.

Specimen Collection and Processing. UV light traps (12 V, 12-W DC, BioQuip Products, Gardena, CA), operated using rechargeable, 7 amp-hour batteries (Global and Yuasa Battery Co., Korea), were used to sample moths at each site. Traps were suspended by a rope between two trees, at 1.5–2 m above the ground. Traps were placed at least 3 m from the nearest tree, and a minimum of 20 m from the nearest forest edge to control for effects of sampling variation owing to stand structure. The effective attraction distance of most UV-emitting lights to moths is between 3 and 10 m (Baker and Sadovy 1978). Vegetation cover further prevented the light from being visible outside of the forest stand. During 1999, all 12 sites were sampled on the same nights to control for the effect of weather on trap catch (Morton et al. 1981). Because time restrictions did not permit sampling of all 24 sites in one night during 2000, one grid of 12 sites each was sampled on one of two consecutive nights to minimize phenological and meteorological effects. Sampling was conducted approximately once every 7 d, between mid-May and early October (1999) and late May to early September (2000), depending on local weather conditions. Traps were not operated on cold or clear, moonlit nights because trap catch is known to be significantly lower under these conditions (Morton et al. 1981). Traps were operated from dusk until dawn. Specimens were collected from the traps the next morning and stored frozen in airtight containers until processed. Lepidopteran nomenclature follows that of Troubridge and Lafontaine (2003). Nomenclature of the dipteran and hymenopteran parasitoids of forest tent caterpillar follows Williams et al. (1996). Moth species were identified using the available literature, the University of Alberta Strickland Museum insect collection and private collections. Only macrolepidopteran species were recorded, making up the Drepanoidea, Geometroidea, Bombycoidea, Sphingoidea, and Noctuoidea. Voucher specimens are deposited in the University of Alberta Strickland Entomological Museum.

Functional Groups. Moth species were assigned to one of two feeding groups based on larval host plant use, consisting of those species either being dependent or not dependent on woody plants. Species dependent on woody plants included those that fed on trees, shrubs, leaf litter, and lichens (hereafter referred to as arboreal species). Although detritovores and lichen feeders are not directly dependent on trees, leaf litter and lichens are strongly correlated with forested habitat in the boreal region, and we therefore treated these species as woody plant dependent. Those species not dependent on woody plants (hereafter nonarboreal species) included those that fed on grasses, herbaceous plants, and host generalists. Generalists feeding on both herbaceous and woody plants consisted primarily of noctuids in the subfamilies Hadeninae and Noctuinae. Cutworms (Noctuinae) are primarily nocturnal feeders that burrow into the soil or plant litter by day and ascend plants at night to feed, and they are often habitat limited more by soil type than by host plant association (Lafontaine 1998). Both Hadeninae and Noctuinae are most diverse in nonforested habitats, and for these reasons we treated these generalists as not being dependent on woody plants. Assignment of host plant use was based on published life history information, primarily from the Moths of North America series (see Dominick et al. 1976; Prentice 1962, 1963, 1965; McGuffin 1972, 1977, 1981, 1987; Handfield 1999; Wagner 2005).

The third functional group included those species that were known hosts of forest tent caterpillar parasitoids. Forest tent caterpillar parasitoid host records were compiled primarily from the tachinid host catalog of Arnaud (1978) and from Krombein et al. (1979) for the Ichneumonidae. Additional records were obtained from numerous literature sources (Schmidt 2001), and unpublished data (Canadian Forest Service, Sault St. Marie, Ontario; J. Lill, personal communication). Of the 40 parasitoid species that have been reared from forest tent caterpillar in the prairie region (Williams et al. 1996), we limited the analysis to the 17 species reported for Alberta by Parry (1995). The term “alternative host” is used here to refer both to those hosts that are obligately used by multivoltine forest tent caterpillar parasitoids, and those hosts that may be used facultatively by univoltine parasitoids.

Statistical Analyses. Moth species richness (d) at each site was calculated using the Margalef Index (Magurran 1988):

$$d = (S - 1)/ln\, N$$

where S is the number of species recorded, and N is the total number of individuals. This index provides a simple measure of species richness corrected for sample size, and species richness-based indices such as this have a greater discriminatory ability than do evenness- or dominance-based indices (Magurran 1988). Because the number of sites sampled differed between 1999 and 2000 (12 versus 24), only the 2000 data were used to calculate d.

We fit three different models to assess the shape of the response to fragmentation, each reflecting a different hypothesis for the effect of fragmentation on diversity: 1) a linear model under the assumption that loss of species is proportionate to the amount of habitat lost; 2) a second order polynomial, on the assumption that there may be a peak of diversity at intermediate levels of fragmentation owing to mixing of both forest and nonforest fauna; and 3) a threshold model under the assumption that there is an effect of fragmentation only beyond some critical level of habitat loss and fragmentation. Models were fit using S-Plus software (Insightful 2000). The response variable (d) is distributed normally (Magurran 1988). Models were fitted separately to forest cover data at each of the three spatial scales to determine at which scale forest structure had its greatest effect. Model fit was assessed using both the residual deviance and the Akaike Information Criterion (AIC) of the respective models. For the threshold model, arbitrary values for the threshold level of fragmentation had to be imposed; we assessed the fit using a series of such values, and used the one that was again associated with the smallest residual deviance and AIC. Quasi-likelihood models were used for regressions on total abundance, because the count data were overdispersed.

For the alternative host functional group, we modeled the effect of forest fragmentation on species abundance, by using generalized linear model regressions with Poisson-distributed errors (Agresti 1996). Abundance was modeled separately for each species as a function of forest structure measured at each of three scales of forest fragmentation (200, 400, and 600 m), by using the S-Plus software package (Insight-

Table 1. Summary of moths sampled in 2000

Family	No. species	No. individuals	Arboreal	Nonarboreal
Arctiidae	16	1,110	4	12
Drepanidae	7	130	7	0
Geometridae	66	6,395	46	20
Lasiocampidae	2	78	2	0
Lymantriidae	2	15	2	0
Noctuidae	151	14,263	58	93
Notodontidae	14	1267	14	0
Saturniidae	1	95	1	0
Sphingidae	4	904	4	0
Uraniidae	1	321	1	0
Total	264	24,578	139	125

Nonarboreal and arboreal indicate the number of species assigned to each functional group, respectively.

ful 2000). Because some data were overdispersed (dispersion parameter [Φ] $>$ 1, where Φ is variance: mean), the analysis was adjusted by standardizing observed values of x_i, that is x_i/Φ (Connor et al. 1997). Because count data (with a Poisson distribution) are truncated at zero, analysis of abundance changes of rare species (those which were not present at many sites) is not likely to yield meaningful results. Therefore, species with low total counts (arbitrarily set at $<$20) were not included in this analysis, but they were included in the logistic regression analysis of species presence/absence. Species that were represented by at least one individual at 25% or more of the sites were included.

Results

We sampled a total of 264 species and 24,578 specimens in 2000, representing 10 macrolepidopteran families (Table 1). The families Geometridae and Noctuidae were the most speciose, with 66 and 151 species, respectively. The total number of species assigned as either arboreal or nonarboreal were roughly equal, although disproportionately distributed among families with most Geometridae being arboreal and most Noctuidae being nonarboreal species (Table 1). All three regression models tested (linear, second order polynomial, and threshold) best explained overall species richness as a function of forest fragmentation when fragmentation was measured at 200 m, compared with 400 and 600 m (data not shown). Both the polynomial and threshold models performed better than the linear model, but there was little difference between the polynomial and threshold model based on the *P* value, Akaike information criterion, and the amount of explained variance (Table 2). Total species richness remained constant or increased slightly up to fragmentation levels of ≈60% (Figs. 1 and 2), with a marked decrease in diversity beyond fragmentation levels of 60% (Fig. 1) to 80% (Fig. 2). Species richness of the arboreal group showed a marked negative relationship with increasing fragmentation, with a polynomial model at a scale of 200 m best explaining variation in richness (Table 2). Species richness declined markedly at fragmentation levels of greater than ≈50% (Fig. 3). Similarly, total abundance of arboreal species remained constant up to a threshold of 50% fragmentation, beyond which abundance declined (Fig. 4; Table 2). The 50% threshold model at the 400-m scale best explained variation in arboreal species abundance (Table 2). In contrast, diversity of nonarboreal species showed no significant change at all scales with all models (data not shown), with the exception of a polynomial model at 400-m scale, which showed a marginally significant relationship (Table 2; Fig. 3). This model suggested a slightly higher diversity of nonarboreal species at moderate fragmentation levels (50–70%) than at either low (20–50%) or high (>80%) fragmentation (Fig. 3). Abundance of nonarboreal species however, increased at higher fragmentation levels (Fig. 5), with a 60% threshold model at 600 m explaining the most variation (Table 2). For

Table 2. Summary statistics for regressions of species richness and abundance on forest fragmentation.

Dependent variable[a]	Model[b]	Scale (m)[c]	*P* value	AIC	r^2
d_T	Linear	200	<0.0002	101.12	0.159
d_T	Poly.2	200	<0.00001	95.29	0.394
d_T	Thresh.80	200	<0.00001	95.52	0.334
d_A	Poly.2	200	0.00022		0.551
d_{NA}	Poly.2	400	0.0477		0.251
n_A	Thresh.50	400	0.003		0.659
n_{NA}	Thresh.60	600	0.03		0.810

[a] *d* is Margalef Index of species richness, where d_T is all species, d_A is arboreal species, and d_{NA} is nonarboreal species. *n* is total abundance of arboreal species (d_A) and nonarboreal species (d_{NA}).

[b] Regression model used, where poly.2 is second order polynomial and thresh is model with threshold set at percentage of fragmentation indicated by decimal number.

[c] Radius in meters at which forest fragmentation was measured.

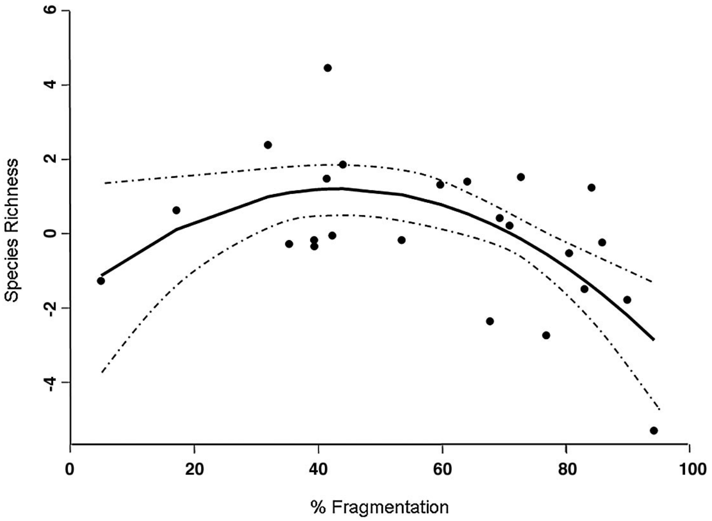

Fig. 1. Regression for fit of total species richness as a function of forest fragmentation. Model is second order polynomial, with fragmentation measured at 200-m scale. Dotted line indicates 95% confidence limit.

nonarboreal species, all tested models explained more variation (in both richness and abundance) at scales greater than the corresponding variable in arboreal species, i.e., nonarboreal versus arboreal richness exhibited optimal scales of 400 and 200 m, respectively, and nonarboreal versus arboreal abundance exhibited optimal scales of 600 and 400 m, respectively (Table 2).

Of the 17 forest tent caterpillar parasitoid species listed by Parry (1995), nine (four Diptera and five Hymenoptera) had lepidopteran hosts reported in the literature that were sampled in this study (Table 3). This alternative host group consisted of 14 species from eight families, host to at least one and as many as three parasitoids. Ten of the 14 alternative hosts were classified as arboreal and four as nonarboreal species (Table 3). Regressions on the abundances of the individual alternative hosts as a function of fragmentation showed significant negative relationships for 10 species in at least one of the sampling years. Only one species [*Pyrrharctia isabella* J.E. Smith] showed a positive relationship as a function of fragmentation in at least 1 yr, albeit with significance at $P = 0.09$. Three species showed no significant change in abundance with increasing fragmentation in either year (Table 4). An increase in sampling sites from 12 to 24 between 1999 and 2000 was correlated with a greater number of significant regressions (Table 4).

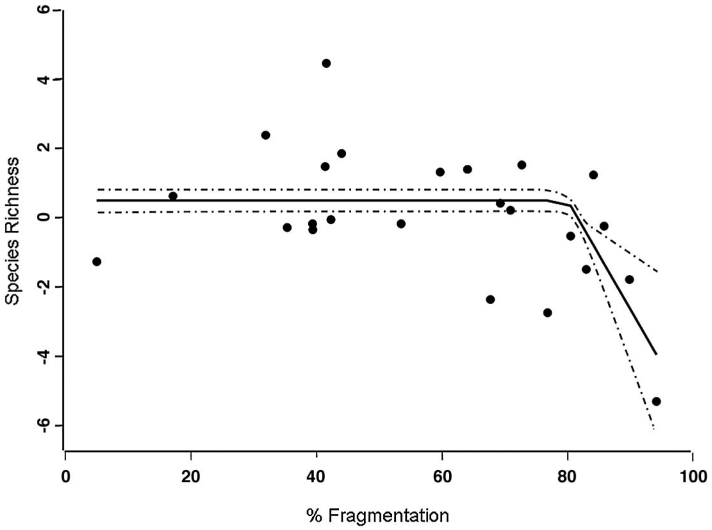

Fig. 2. Regression for fit of total species richness as a function of forest fragmentation. Model is 80% threshold model, with fragmentation measured at 200-m scale. Dotted line indicates 95% confidence limit.

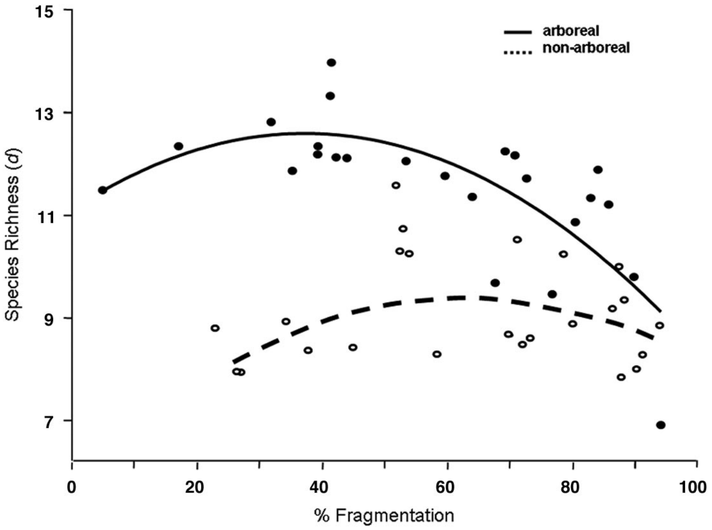

Fig. 3. Regression for fit of arboreal and nonarboreal species richness as a function of forest fragmentation. Model is polynomial, with fragmentation measured at 200-m (for arboreal) and 400-m (for nonarboreal) scale. Confidence limits omitted for clarity.

Discussion

Species richness of the total moth community declined disproportionately with increasing forest fragmentation. Richness declined significantly at fragmentation levels >60–80%, below which diversity remained relatively constant. In contrast, the two functional feeding groups showed individual responses differing both from each other and from the total richness; species dependent on trees and shrubs showed a marked decrease in both species richness and abundance beyond fragmentation levels of 50%. Species not dependent on woody plants showed a marginal decrease in richness, coupled with higher abundance levels, when fragmentation was greater than ≈70%. This has several important implications for moth community structure in the boreal forest. First, total species richness may not be a good indicator of change in community structure, because our data suggest that arboreal species are more sensitive to fragmentation than nonarboreal species, and effects of decreasing tree–shrub obligates are masked by constant or slightly increased levels of richness in forb–grass feeders. At moderate forest fragmentation levels, impoverishment of arboreal species is therefore offset by an influx of species from the landscape matrix. This pattern of community change is similar to that seen in

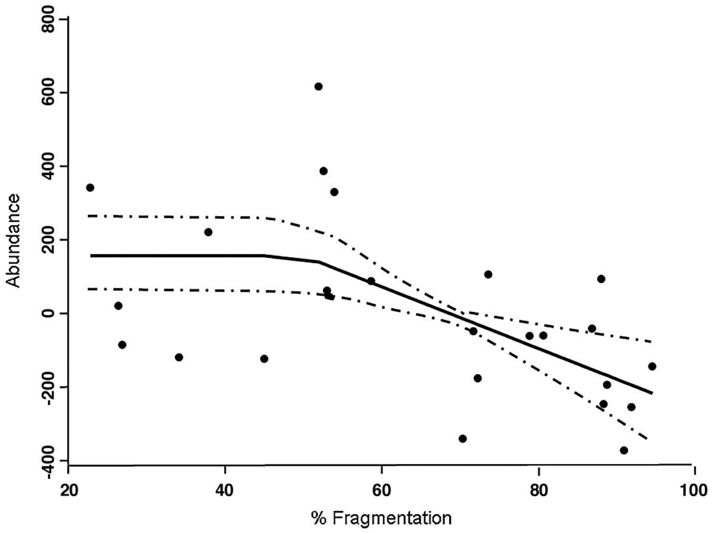

Fig. 4. Regression for fit of arboreal species abundance as a function of forest fragmentation. Model is 50% threshold model, with fragmentation measured at 400-m scale. Dotted line indicates 95% confidence limit.

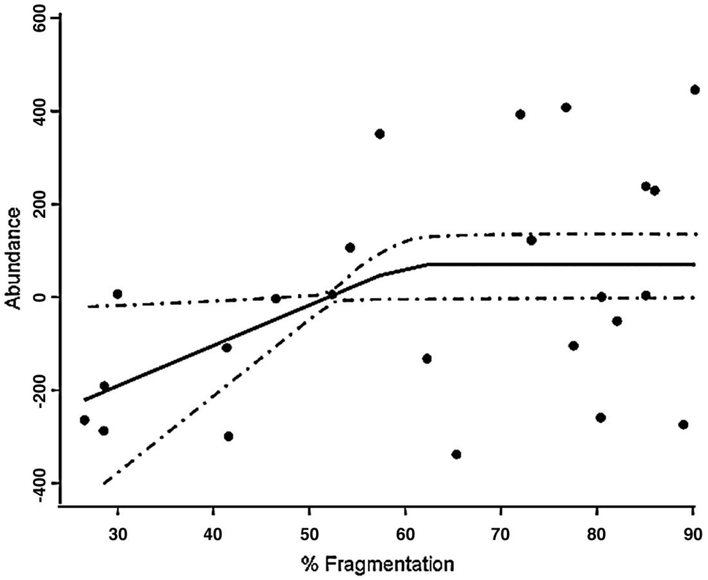

Fig. 5. Regression for fit of nonarboreal species abundance as a function of forest fragmentation. Model is 60% threshold model, with fragmentation measured at 600-m scale. Dotted line indicates 95% confidence limit.

eastern deciduous forests (Summerville and Crist 2003, 2004). At the highest levels of fragmentation (>80%), the greatest change in community structure is evident: diversity of both feeding groups decreases; abundance of arboreal species also decreases, but in nonarboreal species abundance remains constant. Total diversity therefore seems to be driven primarily by an impoverished woody plant feeding group and disproportionately overabundant species of herb–grass feeders. An overabundance of agricultural crop–forage feeders in smaller forest fragments within an agricultural matrix has been noted previously in eastern deciduous forests (Summerville 2004a) and in tropical forests (Ricketts et al. 2001).

Moth community structure within a forest stand is dependent on the local stand context, i.e., the amount of surrounding forest has a significant effect on community structure. This is particularly evident in arboreal species richness. The scale at which the local forest context is measured is taxon dependent: in both richness and abundance, the optimal landscape scale for arboreal species was smaller than for nonarboreal species. The arboreal group consisted largely of geometrid moths with slender bodies and broad wings, compared with the Noctuidae with broad thoraces and relatively slender wings. This may be reflective of dispersal ability in moths, where better dispersers respond to landscape structure at a greater scale than poor dispersers.

Almost all species of the host group of forest tent caterpillar parasitoids showed a marked overall decline in abundance (or probability of occurrence) with increasing forest fragmentation. Most of the host species were tree or shrub feeders, probably reflective of parasitoid host search strategies; parasitoids with multiple hosts tend to specialize on hosts in similar ecological niches rather than hosts closely related taxonomically (Belshaw 1994). This also suggests that alternative hosts of forest tent caterpillar, despite the poor state of knowledge of alternative hosts use in parasitoids, are very likely a subset of the arboreal group. Although the functional group of parasitoid hosts considered here was too limited to draw conclusions about changes in species richness as a function of forest fragmentation, the overall pattern seen in response of arboreal species richness also may well reflect changes to a subset of that group, such as the parasitoid host guild. If forest fragmentation has an overall negative impact on parasitoid host diversity, the diversity of generalist parasitoids is in turn likely higher in contiguous forest. Although depauperate parasitoid diversity mirrors host diversity (Kruess and Tscharntke 2000, Tscharntke 2000), the effects on parasitism rates and subsequent population dynamics are not necessarily intuitive. Whether this decrease in parasitoid diversity results in lower forest tent caterpillar parasitism rates remains to be determined, but this prediction is consistent with longer forest tent caterpillar outbreaks in more fragmented forests (Roland 1993). Lower host abundance and diversity would, however, compound the effects of increased mortality (Mitchell 2001) and lower host-finding success in fragmented landscapes (Roland and Taylor 1997). When these factors are taken into account, in addition to possible adult nectar source limitations in fragmented landscapes (Kruess and Tscharntke 1994), it is perhaps not surprising that habitat fragmentation has a greater negative impact on parasitoids than on their herbivorous hosts (Kruess and Tscharntke 2000).

Parasitoids that are entirely dependent on forest tent caterpillar as a host, such as *Leschenaultia exul* (Townsend) and *Patelloa pachypyga*, (Aldrich &

Table 3. Reported lepidopteran hosts of *M. disstria* parasitoids in central Alberta (indicated with an X)

Host			Parasitoid								
			Diptera				Hymenoptera				
Family[a]	Feeding group[b]	Species	*Euexorista futilis*	*Exorista mella*	*Lespesia frenchii*	*P. pachypyga*	*Isoropus stercorator*	*I. conquisitor*	*Phobocampe clisiocampae*	*Pimpla pedalis*	*Theronia atalantae*
Ar	A	*Lophocampa maculata* Harris								X	
Ar	NA	*Ctenucha virginica* (Esper)					X			X	
Ar	A	*Pyrrharctia isabella* (J. E. Smith)	X	X						X	
Ar	NA	*Spilosoma virginica* (F.)		X	X						
Dr	A	*Oreta rosea* (Walker)									X
Ge	NA	*Nematocampa resistaria* (Henrich-Schäffer)						X			
Ge	A	*Protoboarmia porcelaria* (Guenée)								X	
La	A	*Phyllodesma americana* (Harris)		X							
Nc	A	*Enargia decolor* (Walker)				X					
Nt	A	*Oligocentria semirufescens* (Walker)						X			
Nt	A	*Schizura unicornis* (J. E. Smith)							X		
Sa	A	*Antheraea polyphemus* (Cramer)	X		X						
Sp	A	*Smerinthus cerysii* Kirby			X						
Sp	A	*Smerinthus jamaicensis* (Drury)			X						

[a] Ar, Arctiidae; Dr, Drepanidae; Ge, Geometridae; La, Lasiocampidae; Nc, Noctuidae; Nt, Notodontidae; Sa, Saturniidae; Sp, Sphingidae.
[b] A, arboreal; NA, nonarboreal.

Table 4. Regression results for abundances of parasitoid alternative hosts as a function of forest fragmentation

Species	Family[a]	1999							2000							Slope	
		Total catch	*P* value	Model[b]	Intercept	Slope	Dev. expl.[c]	Scale (m)[d]	Total catch	*P* value	Model[b]	Intercept	Slope	Dev. expl.[c]	Scale (m)[d]	1999	2000
Ctenucha virginica	Ar	208	<0.001	Poisson	2.32	-0.028	0.57	200	61	N.S.	Pois					−	N.S.
Lophocampa maculata	Ar	66	N.S.	Poisson					66	0.040	Pois	0.95	−0.021	0.19	400	N.S.	−
Pyrrharctia isabella	Ar	4	0.090	Log	−4.89	0.067	0.21	400	4	N.S.	Log					+	N.S.
Spilosoma virginica	Ar	82	0.002	Poisson	2.21	-0.022	0.47	200	50	<0.001	Pois	1.78	−0.027	0.39	200	−	−
Oreta rosea	Dr	26	N.S.	Poisson					26	0.027	Log	2.76	−0.044	0.15	200	N.S.	−
Nematocampa resistaria	Ge	112	N.S.	Poisson					64	0.002	Pois	1.39	−0.025	0.27	200	N.S.	−
Protoboarmia porcelaria	Ge	26	0.024	Poisson	1.30	-0.029	0.36	200	34	0.019	Pois	1.15	−0.022	0.20	400	−	−
Phyllodesma americana	La	25	N.S.	Poisson					39	N.S.	Pois					N.S.	N.S.
Enargia decolor	Nc	61	N.S.	Poisson					144	N.S.	Pois					N.S.	N.S.
Oligocentria semirufescens	Nt	20	N.S.	Poisson					4	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.S.	
Schizura leptinoides	Nt	11	0.007	Log	6.74	−0.132	0.44	200	34	0.043	Pois	0.44	−0.027	0.21	200		−
Schizura unicornis	Nt	66	N.S.	Poisson					100	0.027	Pois	1.52	−0.014	0.18	400	N.S.	−
Antheraea polyphemus	Sa	21	N.S.	Poisson					95	0.013	Pois	2.21	−0.010	0.22	400	N.S.	−
Smerinthus cerisyi	Sp	190	N.S.	Poisson					626	N.S.	Pois					N.S.	N.S.
Smerinthus jamaicensis	Sp	267	N.S.	Poisson					259	0.022	Pois	1.69	−0.011	0.17	200	N.S.	−

[a] Ar, Arctiidae; Dr, Drepanidae; Ge, Geometridae; La, Lasiocampidae; Nc, Noctuidae; Nt, Notodontidae; Sa, Saturniidae; Sp, Sphingidae.
[b] Regression model used in analysis: Poisson, regression on total trap catch; Log, logistic regression on presence or absence of species.
[c] Proportion of the deviance explained by the model, i.e., [(Null Dev. − Residual Dev.)/Null Dev].
[d] Spatial scale at which the model provided the best fit the data.

Webber) are arguably not influenced by alternate host availability, even though they are a significant mortality agent during and subsequent to forest tent caterpillar population outbreaks. However, parasitoids with a broader host range are expected to have more stable populations (Hassell 1978), because they are able to switch hosts when forest tent caterpillar densities become exceedingly low and should therefore be relatively more important than specialist parasitoids during the endemic phase of the forest tent caterpillar cycle. Although little data exist on parasitism of forest tent caterpillar at low densities, preliminary results suggest that there is a much higher incidence of parasitism by generalist species at endemic forest tent caterpillar densities; the highest parasitoid-caused mortality of pupae is attributable to ichneumonid wasps, primarily *Itoplectis conquisitor,* (Say) *Theronia atalantae* (Poda), and *Gambrus canadensis* (Provancher) (J.R., unpublished data). *I. conquisitor* also causes higher parasitism rates in the early stages of an outbreak (Parry 1995). These ichneumonid species have a broader host range than do the tachinid flies prevalent during outbreaks. Because the host assemblages of the Ichneumonidae in this study showed a marked decrease in abundance with forest fragmentation, ichneumonid wasps would be predicted to cause higher rates of forest tent caterpillar parasitism in large, continuous forest stands. This parallels the notion that generalist parasitoids are better suited to searching for hosts in late successional habitats (Price 1994).

A leading concern for both conservation biology and forestry has been how forest fragmentation affects biodiversity, and how, at the landscape level, forest harvest regimes can minimize diversity losses. Here, we assessed landscape-level changes in moth species richness and abundance in relation to forest fragmentation, measured at multiple scales by using three regression models. Total species richness showed a significant decline as a function of fragmentation at all measured spatial scales; both polynomial and threshold models explained more variation than linear models, suggesting that there is little to no change in overall moth diversity between low and moderately fragmented stands. However, changes in diversity patterns within arboreal versus nonarboreal species showed that measures of total species richness may mask changes in community structure. Changes in overall diversity were driven largely by a decrease in species richness of tree- and shrub-feeding moths, although forb- and grass-feeding moths also showed marginally lower species richness at high fragmentation levels. Most species of the parasitoid host group decreased in abundance with increasing fragmentation. These findings show that overall diversity measures can mask important community changes and that the optimal landscape scale at which these changes are measured is taxon dependent. Finally, the decrease in host availability to *M. disstria* parasitoids in fragmented forests may exacerbate population outbreaks of *M. disstria.* Our findings also highlight the need for additional information on such basic natural history information as parasitoid host use, without which it is not possible to interpret important functional changes as a result of landscape changes and the resulting impact on insect community structure.

The effect of habitat fragmentation on insect diversity has been a popular field of research over the past two decades. However, the functional consequences of reduced diversity resulting from habitat fragmentation are more difficult to determine. In this study, we investigate the effects of landscape-driven changes in lepidopteran diversity, and the implications for a well-known parasitoid–host system of the boreal forest. The observed changes in the community of lepidopteran parasitoid hosts support the notion that defoliating insects such as forest tent caterpillar exhibit longer or more severe outbreaks in fragmented landscapes. This study also highlights the value of and additional need for parasitoid host records, particularly for lepidopteran species that are not of economic importance, but also for outbreaking species during endemic population phases.

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