

# Leaf quality, predators, and stochastic processes in the assembly of a diverse herbivore community

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**Abstract.** Ecological communities are structured by both deterministic, niche-based processes and stochastic processes such as dispersal. A pressing issue in ecology is to determine when and for which organisms each of these types of processes is important in community assembly. The roles of deterministic and stochastic processes have been studied for a variety of communities, but very few researchers have addressed their contribution to insect herbivore community structure. Insect herbivore niches are often described as largely shaped by the antagonistic pressures of predation and host plant defenses. However host plants are frequently discrete patches of habitat, and their spatial arrangement can affect herbivore dispersal patterns. We studied the roles of predation, host plant quality, and host spatial proximity for the assembly of a diverse insect herbivore community on *Quercus alba* (white oak) across two growing seasons. We examined abundances of feeding guilds to determine if ecologically similar species responded similarly to variation in niches. Most guilds responded similarly to leaf quality, preferring high-nitrogen, low-tannin host plants, particularly late in the growing season, while bird predation had little impact on herbivore abundance. The communities on the high-quality plants tended to be larger and, in some cases, have greater species richness. We analyzed community composition by correlating indices of community similarity with predator presence, leaf quality similarity, and host plant proximity. Birds did not affect community composition. Community similarity was significantly associated with distance between host plants and uncorrelated with leaf quality similarity. Thus although leaf quality significantly affected the total abundance of herbivores on a host plant, in some cases leading to increased species richness, dispersal limitation may weaken this relationship. The species composition of these communities may be driven by stochastic processes rather than variation in host plant characteristics or differential predation by insectivorous birds.

**Key words:** bird predation; community assembly; insect herbivore; leaf quality; Missouri; niche; *Quercus alba*; similarity.

## INTRODUCTION

The assembly of ecological communities is often described as being driven by two types of processes. Deterministic, niche-based processes such as competition predict similar community compositions when sites with similar environmental conditions are “populated” by species from the same regional species pool (Condit et al. 2002, Chase and Leibold 2003). Stochastic processes, including random dispersal, local extinction, and the resulting ecological drift (Bell 2001, Hubbell 2001, Chave 2004), can produce very different species compositions at sites with otherwise matching conditions. Recently ecologists have acknowledged that both types of processes operate concurrently (Adler et al.

2007, Chase 2007, Chase et al. 2009), and have begun to ask a more nuanced question: under what conditions are deterministic or stochastic processes more important to community assembly?

Herbivorous insects are nearly ubiquitous in terrestrial systems and can form phenomenally diverse communities, but understanding the factors that influence the patterns of diversity in these communities remains a significant challenge (Lewinsohn et al. 2005). While a number of researchers have empirically assessed the roles of deterministic and stochastic processes in natural communities (e.g., Thompson and Townsend 2006, Chase 2007, Ellwood et al. 2009), very few insect herbivore communities have yet been evaluated in this way (but see Novotny et al. 2002, Rominger et al. 2009).

Essentially all herbivores face two antagonistic forces, predation and host plant defenses, each of which can affect herbivore abundance and diversity (Matson and Hunter 1992, Walker and Jones 2001). Herbivores are consumed by a variety of predators, including arthropods and vertebrates. Insectivorous birds, as endotherms, require large amounts of food to maintain their

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metabolism and that of their offspring during the nesting season. Although many bird exclusion experiments have studied predation effects on overall herbivore abundance and herbivory (Van Bael et al. 2008, Mooney et al. 2010), few have examined bird impacts on herbivore communities (but see Forkner and Hunter 2000, Gruner and Taylor 2006, Mooney 2006, 2007). Predation can act as a deterministic force, either by reducing the number of species able to colonize a site (the realized species pool; Chase et al. 2009) or by enhancing diversity through prevention of competitive exclusion (Paine 1966, Boege and Marquis 2002). However predators may also alter colonization–extinction dynamics, thus driving stochastic processes (Ryberg and Chase 2007, Chase et al. 2009).

Foliage quality of host plants can have strong effects on the abundance and performance of insect herbivores. Leaf quality often varies among individuals within a community (e.g., Marquis 1992, Hemming and Lindroth 1995, Fincher et al. 2008, Zehnder et al. 2009), and if herbivore host preferences reflect this variation, their density should vary predictably with host traits (Abrahamson et al. 2003, Forkner et al. 2004, Ricklefs 2008). As a result, leaf quality can act as a deterministic force in herbivore community assembly, and individual plants with similar foliage characteristics should be utilized by similar herbivore assemblages.

Because many herbivores complete their larval development on a single plant, host plants can represent discrete habitat patches (Gripengberg and Roslin 2005), and the spatial distribution of these patches can affect community composition. Dispersal limitation between plants can affect the spatial distribution of species in a community. Dispersal may be performed by foraging herbivores or, perhaps more commonly for species with limited mobility as larvae, such as many Lepidoptera, by ovipositing females. The likelihood of a species dispersing from one plant to another decreases as the distance between the plants increases, so colonization of a plant by a particular species is more likely if the source plant is nearby. This will lead to a patchy distribution of the species across the landscape: a species may be present in one group of adjacent host plants but absent from others, even if they are suitable hosts, because of dispersal limitation (Gripengberg and Roslin 2007). When all herbivore species in the community are taken into account and their distributions are overlaid, the similarity of the species assemblage on two plants should decrease with distance between the plants (Chave and Leigh 2002, Chase et al. 2005). This similarity distance-decay indicates the importance of stochastic dispersal dynamics in the assembly of the herbivore community.

Although predation and host plant quality have been shown to influence insect herbivore communities and their impacts on plants, these factors often explain only a small proportion of the intraspecific between plant variance. Leaf traits rarely explain more than 30% of the variation in damage (e.g., Sagers and Coley 1995),

abundance (Basset 1991, Hunter et al. 1997, Boege 2005), and community composition (Wold and Marquis 1997, Forkner et al. 2004). Stochastic factors, which have not been the target of previous study by plant–herbivore ecologists, may contribute to the unexplained variance. We evaluated the impacts of predation, host leaf quality, and host spatial proximity at a local scale on the abundance and composition of a diverse but well-described oak herbivore community. To understand how deterministic processes act on ecologically differing species, we categorized herbivores into guilds based on feeding behavior and diet breadth. We predicted that, if deterministic factors are important in structuring this community, these guilds would be affected differently by predation and host plant quality, and the composition of the herbivore community on individual plants would reflect these variations. Alternatively, if stochastic processes predominate, similarity of communities among oaks would follow a simple distance-decay pattern and be unrelated to either bird exclusion or plant characteristics.

#### METHODS

We studied the composition of the leaf-chewing herbivore community on *Quercus alba* L. (white oak) at Tyson Research Center near Eureka, Missouri. *Quercus alba* is a canopy co-dominant in the mature oak-hickory forest at this site. Other common canopy species in the study area include *Q. velutina* (black oak) and *Carya* spp. (hickory). The understory tree community is dominated by *Cornus florida* (flowering dogwood), *Cercis canadensis* (Eastern redbud), and *Amelanchier arborea* (downy serviceberry). We chose 60 *Q. alba* of canopy or mid-story height with accessible understory branches (<3 m from ground). The experimental trees were growing along a rocky southwest-facing slope with shallow soil. The slope was approximately 700 m long, 100–200 m wide, and spanned around 40 m in elevation from trees at the bottom of the slope to those at the top. The trees were distributed across approximately 11 ha, and distances between trees varied from 3 to 643 m (mean 257 m, median 227 m). This is roughly the same area studied by Marquis and Whelan (1994). While there were other *Q. alba* interspersed among the experimental trees, these 60 trees represented the majority of understory *Q. alba* foliage in the study area, as saplings were very rare.

To manipulate predation, we constructed bird exclosures consisting of PVC pipe frames covered with monofilament gill netting around understory branches of 30 randomly selected trees (Barber and Marquis 2009). Exclosure dimensions varied by tree, but were generally 2–3 m tall and 2–3 m wide on each side. Exclosures were constructed in late winter 2007 so that netting was in place before budburst. Exclosures were maintained year-round until the conclusion of the experiment.

We censused the arthropod community on each tree three times in each of years 2007 and 2008. These censuses took place during known peaks in *Q. alba* herbivore abundance, in May, early July, and late August–early September. These peaks also have distinct species compositions with little or no overlap of individual herbivores from one peak to the next, thus representing semi-independent assemblages (Marquis and Whelan 1994, Marquis and LeCorff 1997, Forkner et al. 2004). Following census protocols in Forkner et al. (2004), we searched tops and bottoms of leaves on experimental branches and identified all leaf-chewing herbivores encountered. We counted the leaves inspected and searched approximately 400 leaves per branch, and abundances were standardized as densities per m<sup>2</sup> leaf area using a mean leaf size of 58.7 cm<sup>2</sup> (Le Corff and Marquis 1999). Identification of these herbivores to species or morphospecies level is possible because of past work in conjunction with the Missouri Ozark Forest Ecosystem Project (Marquis and LeCorff 1997, Marquis et al. 2002a). We also identified arthropod predators encountered to either order or family.

To assess host plant characteristics, we collected three leaves from each experimental tree following each census. We measured leaf traits known to affect herbivore abundance and performance: leaf toughness, specific leaf area, and percent content of water, condensed tannins, hydrolyzable tannins, carbon, and nitrogen (Feeny 1970, Coley 1983, Forkner et al. 2004, Yarnes et al. 2008, Cornelissen and Stiling 2008, Fincher et al. 2008; see Appendix A for detailed methodology of leaf measurements).

## STATISTICAL ANALYSES

### *Leaf quality*

Because leaf-quality characteristics often covary, we used principal components analysis (PCA) to describe the variation in leaf traits in a smaller number of variables (prcomp, package stats; R Development Core Team 2007). Following Ricklefs (2008), we log-transformed leaf quality measurements to homogenize variances and linearize relationships between variables. Variables were scaled to have unit variance, and analyses were performed on the correlation matrix (see documentation of prcomp for details). We performed six individual PCAs to independently describe the leaf quality in each of the six censuses. To ease interpretation and discussion, we reversed signs of some PCs so that relationships between high-loading foliage characteristics and PCs were in the same direction in all censuses.

### *Herbivore density, richness, and guild structure*

To determine how bird predation and leaf quality affect herbivore density, richness, and the density of feeding guilds, we used MANCOVA with bird exclusion as a fixed factor and the first two leaf quality principal components (PCs) in each census as covariates. We used just these first two PCs because they described the

majority of variation in leaf quality (see *Results*) and to avoid loss of statistical power by over-parameterizing models. Data from repeated censuses are usually analyzed using mixed models to account for lack of independence of replicates between censuses, but this was not possible because leaf quality changes greatly from one census to the next. For example, condensed tannin content increases sixfold from May to September; during this same time, toughness increases 54%, water content declines 17%, and nitrogen content declines 30% (N. A. Barber and R. J. Marquis, *unpublished data*). Because of these large changes in leaf quality it would be inappropriate to include a covariate that incorporated September leaf measurements when analyzing May herbivore density. Instead we analyzed responses in separate MANCOVAs for each census; this approach is further justified by the distinct communities in each census in which few, if any, individual insects are present in more than one census and most species occur only once (Appendix B). In each census we analyzed eight response variables: total herbivore density, total richness, density of each of the four feeding guilds (free-feeding, shelter-building, and leaf-mining herbivores; we also included arthropod predators as a guild), and the density of the two host breadth guilds (oak specialists, species that feed only on *Quercus* spp., and generalists, species that feed on at least one other plant genus). Categorization of herbivores by feeding guild and host breadth is based on information in Covell (1984), Forkner et al. (2004), and Wagner (2005). Effects of bird exclusion, leaf quality, or interactions in MANCOVAs with  $P < 0.05$  were followed by examination of individual ANCOVAs. Because the nonnative Asiatic oak weevil (*Cyrtopistomus castaneus*) dominated the community in July censuses and strongly influenced model results, we analyzed July communities with this species excluded from total herbivore, free-feeders, and oak specialists. Weevil density was analyzed independently with separate ANCOVAs. Finally, we examined bubble plots of residuals (Zuur et al. 2009) for all ANCOVAs to determine if densities were strongly affected by covariates not accounted for in the models, which would be suggested by spatial patterns in the residuals. All MANCOVAs and ANCOVAs were carried out in R, and bubble plots were created using package gstat (Pebesma 2004).

### *Herbivore species composition*

To test the impact of bird predation on community composition, we used multi-response permutation procedures (MRPP), a nonparametric method that compares distances within and between groups defined a priori to test the null hypothesis that distances within groups are smaller than expected by chance (McCune and Grace 2002). MRPP produces a statistic,  $A$ , that varies from  $A = 1$  (all replicates within a group are identical) to  $A = 0$  (heterogeneity within groups equal to that expected by chance) or  $A < 0$  (more heterogeneity

TABLE 1. Leaf-quality variable loadings on first and second principal components (PC1 and PC2, respectively) for each census.

Variable	May 2007		Jul 2007		Aug 2007		May 2008		Jul 2008		Sep 2008	
	PC1	PC2	PC1	PC2	PC1	PC2	PC1	PC2	PC1	PC2	PC1	PC2
Toughness	-0.516	-0.072	-0.300	-0.030	-0.257	0.123	-0.404	0.391	-0.037	0.218	-0.188	0.612
Water	0.057	0.689	0.469	0.281	0.493	0.038	0.397	-0.156	0.523	0.061	0.484	0.160
Specific leaf area							-0.538	-0.192	-0.531	0.039	-0.518	0.090
Condensed tannins			-0.362	0.562	-0.324	0.525	-0.316	0.291	-0.193	0.002	-0.245	-0.675
Hydrolyzable tannins	-0.583	0.094	-0.558	-0.162	-0.564	-0.099	-0.186	-0.624	-0.524	0.222	-0.453	0.138
Carbon	-0.140	0.704	-0.265	0.672	-0.140	0.702	-0.324	0.286	-0.100	0.772	0.046	-0.343
Nitrogen	0.609	0.126	0.421	0.356	0.498	0.453	0.387	0.479	0.348	0.549	0.442	-0.006
Total variance (%)	38.2	25.3	29.6	18.4	31.8	21.2	33.1	26.0	36.7	18.0	42.9	17.9

Notes: Condensed tannins were excluded from May 2007 because of laboratory error (see *Methods*). Specific leaf area was measured in 2008 but not 2007. Percentage of total variance is the proportion of the total variation in leaf quality accounted for by each PC.

within groups than expected by chance). We used Bray-Curtis distances based upon data of individual herbivore species and natural  $\log(x + 1)$ -transformed abundances, following the recommendations of McCune and Grace (2002). Trees on which no herbivores were recorded (a small number in May 2007 only) were excluded.

We compared exclosure vs. control trees in each of the six censuses individually using PC-ORD 4.25 (MjM Software, Gleneden Beach, Oregon, USA). Significant community differences in *A* according to MRPP were visualized using nonmetric multidimensional scaling (NMDS). We compared the influences of host plant quality and spatial factors on herbivore community similarity using partial Mantel tests (Tuomisto and Ruokolainen 2006). These tests produce a correlation coefficient for two distance matrices while controlling for a third matrix and provide a test of significance without inflating the probability of type I error. We tested the relationship between each community similarity matrix and two independent variable matrices: (1) host plant quality similarity and (2) distance between host plants. We tested each independent variable matrix while controlling for the other for each of the six censuses. Partial Mantel tests were necessary because the two independent matrices were correlated in some surveys (Appendix C). The community matrix consisted of all pairwise Bray-Curtis distances between trees. To create an index of host plant quality similarity, we used the PCAs described above. For each tree, the score of each principal component was weighted by the amount of variance explained by that component, and weighted scores were summed. This is similar to the defense index used by Fine et al. (2006), except that the summed values (principal components) describe variation in the multivariate leaf quality space, and these values are weighted so that those explaining the most variation have a greater impact on the final host plant quality index. Thus these values created a one-dimensional axis of leaf quality, and the host plant similarity matrix was composed of pairwise differences between trees on this axis. The spatial distance matrix was created using GPS coordinates of each tree to calculate all pairwise interplant distances (in m), which were log-transformed.

## RESULTS

### Leaf quality

Individual PCAs for each census verified strong correlation structure within leaf-quality measurements (Table 1). The first two PCs explained >50% of the variation in leaf quality in five of the six censuses, and 48% of the variation in July 2007. In July and August/September, water, hydrolyzable tannins, and nitrogen content were frequently strongly correlated; increased water tended to be correlated with high nitrogen and low hydrolysable tannins. In 2008, these trees tended to have low specific leaf area (SLA) as well. This combination of variables was represented in the first PC for all four of these censuses. High nitrogen and low hydrolysable tannins also contributed to May 2007 PC1 and May 2008 PC2. These components were all significantly positively correlated (all  $P < 0.006$ ), indicating that relative leaf quality among trees was constant within and between years. Because only these principal components (PC1 in mid- and late-season censuses) affected herbivore densities (see *Herbivore density, richness, and guild structure*), we will hereafter refer to these components as "leaf quality." Second PCs in July and August 2007 represented positive correlations between condensed tannins and carbon content but relationships were more varied in 2008.

### Herbivore density, richness, and guild structure

We recorded 1478 leaf-chewing herbivores of 71 species or morphospecies in 2007 and 2415 herbivores of 77 species in 2008 (Appendix B). Bubble plots of residuals revealed no spatial patterns that would suggest other important variables missing from models. MANCOVAs revealed significant impacts of leaf quality in July 2007, August 2007, and September 2008 censuses. Bird exclusion had no significant effects, and there were no significant interactions between birds and leaf quality (Appendix D). Total herbivore density increased with leaf quality in both of the late season censuses, although the relationship was marginally significant in September 2008 (Table 2, Fig. 1). Species richness also increased with leaf quality in both of these surveys (Table 2).

TABLE 2. Results of herbivore density, richness, and guild structure ANCOVAs.

	df	Birds <i>F</i>	Lq 1 <i>F</i>	Lq 2 <i>F</i>	Birds × Lq1 <i>F</i>	Birds × Lq2 <i>F</i>	$\eta^2$
July 2007							
Generalists	1,52	5.837	5.278*	1.283	0.035	0.278	0.20
Arthropod predators	1,52	0.603	4.902*	1.086	0.067	0.147	0.12
August 2007							
Total herbivores	1,54	0.026	10.213**	4.304	2.241	0.935	0.25
Richness	1,54	0.018	4.124*	2.209	0.444	0.104	0.11
Free-feeders	1,54	1.679	4.377*	1.310	0.477	0.437	0.13
Leaf miners	1,54	2.075	6.481*	1.465	0.174	0.015	0.16
Generalists	1,54	0.524	8.477*	0.139	0.245	0.087	0.15
September 2008							
Total herbivores	1,51	0.757	3.153†	1.578	0.954	3.427	0.24
Richness	1,51	0.848	11.957**	2.401	0.338	2.972	0.27
Leaf miners	1,51	0.741	5.341*	0.006	0.332	3.033	0.16
Arthropod predators	1,51	0.459	7.902**	4.599*	0.012	2.087	0.23
Specialists	1,51	0.063	2.989†	2.474	0.929	5.932	0.20

Notes: For simplicity, censuses and response variables that were not significantly affected by bird predation or leaf quality are excluded. In all cases presented, density decreased with leaf quality (less abundant on trees with higher tannin content and low nitrogen content). Leaf quality 1 (Lq1) and Leaf quality 2 (Lq2) are the first and second principal components, respectively, from the leaf quality PCA;  $\eta^2$  is the proportion of variance explained.

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; †  $P < 0.1$ .

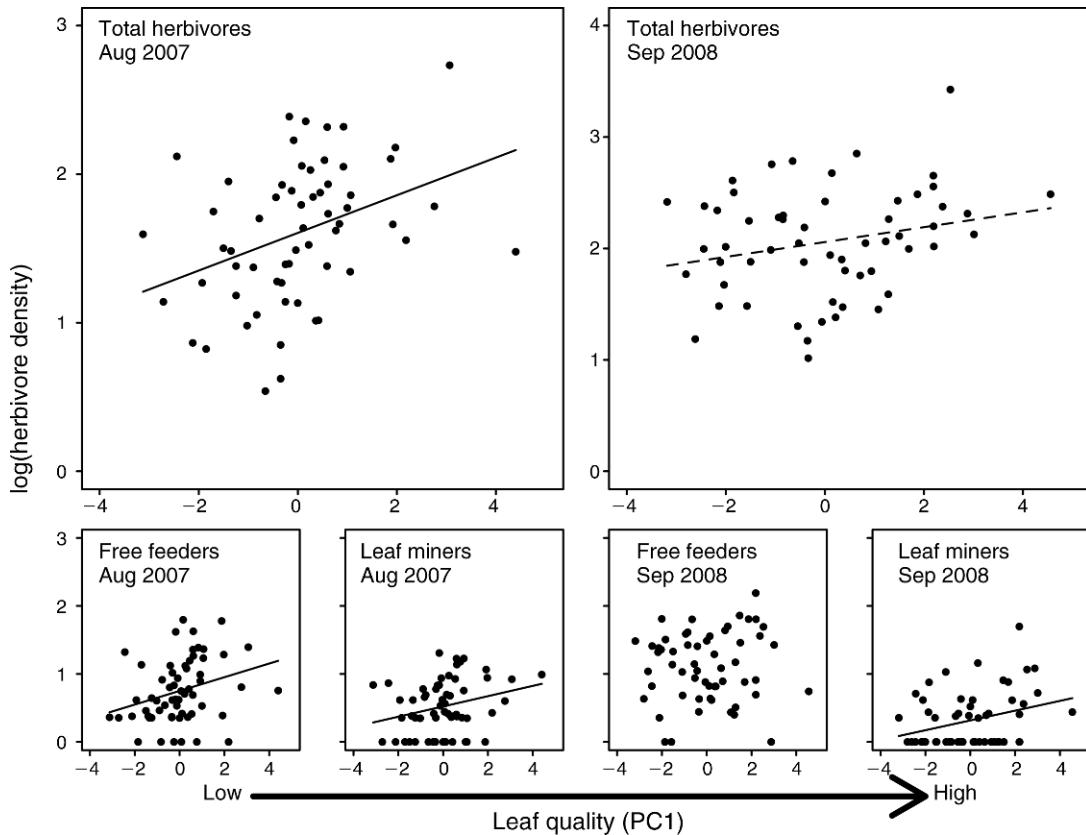


FIG. 1. Relationship between leaf quality (PC1) and density of total herbivores (measured as individuals/m<sup>2</sup>), free feeders, and leaf miners in late-season censuses. In the 2008 total herbivores plot, the dashed line indicates that the relationship was marginally significant; in the 2008 free feeders plot, the relationship was not statistically significant.

TABLE 3. Results of multi-response permutation procedures (MRPP) analyzing the effects of bird exclusion on herbivore community composition for each census.

Censuses	<i>A</i>	<i>P</i>
May 2007	-0.005	0.814
Jul 2007	0.008	0.085
Aug 2007	-0.001	0.496
May 2008	0.010	0.063
Jul 2008	<b>0.014</b>	<b>0.012</b>
Sep 2008	0.002	0.312

Note: Boldface type indicates partial MRPP *A* where *P* < 0.05.

Herbivore feeding guild structure was influenced only in late-season censuses (Table 2), but the groups responding were not identical in both years. Free-feeders were more abundant on high-quality trees in 2007, while leaf miners were more abundant on high quality trees in both years (Fig. 1). Arthropod predator density was also positively associated with higher leaf quality in September 2008. Abundance of shelter-builders never correlated with leaf quality.

Density of insect herbivores categorized by host breadth guild (generalist vs. specialist) was significantly affected by leaf quality in July 2007 and late-season censuses (Table 2). Generalists in July and August 2007 were more abundant on trees with high leaf quality. Oak specialist density was marginally significantly (positively) correlated with leaf quality in September 2008. Asiatic oak weevil densities were not affected by birds or leaf quality in July 2007, but were positively correlated with leaf quality in July 2008 ( $F_{1,51} = 9.377$ ,  $P = 0.004$ ).

#### Herbivore species composition

Bird exclusion had few and weak effects on herbivore species composition. Differences between enclosure and control trees were marginally significant in July 2007 and May 2008 and significant in July 2008 (Table 3). However *A* was <0.02 in each of these cases, suggesting weak differences, and examination of NMDS ordination plots reveals no strong differences between trees with and without bird predation (Appendix E). Neither eliminating rare species (present on <5% of trees) nor relativizing species abundances qualitatively affected results (McCune and Grace 2002).

Partial Mantel tests showed consistent and usually significant correlations between community similarity and spatial proximity of host plants. In five of six censuses, similarity declined with distance between trees. Three of these were statistically significant, and the other two were marginally significant (Table 4). In August 2007, communities on proximate trees tended to be less similar than more distant communities. In no census was the similarity of host plant leaf quality significantly correlated with community similarity. Tests using other similarity measures (Jaccard, incidence-based Sørensen) were qualitatively similar (results not shown).

#### DISCUSSION

This is the first study to compare the importance of individual host plant characteristics to stochastic processes in structuring insect herbivore communities. Our results indicate that host plant leaf quality, a deterministic factor, affects abundance of herbivores but has weak impacts on community composition. In contrast, similarity patterns in community composition are more consistent with stochastic processes such as dispersal limitation. Predation by insectivorous birds had almost no detectable effect on either herbivore abundance or community composition. This suggests that, while foliage characteristics may affect leaf consumption by herbivores and therefore their impacts on plants (Coley 1983, Dudd and Shure 1994), the role of bottom-up forces in diversity patterns is limited to effects on abundance and resultant richness but not species composition.

Leaf quality effects on herbivore abundance were remarkably consistent across different groups of herbivores and the community phenology of two seasons. The covariation of leaf quality characteristics itself was consistent through time, as evidenced by the similar variable loadings in the six PCAs. For example, leaf nitrogen and phenolic content were always negatively correlated. In five of the six PCAs, the component encompassing the largest portion of leaf quality variation described an axis of negatively correlated nitrogen and tannin content. This axis also tended to describe leaf toughness, thickness, and water content. Thus while the leaf quality of an individual plant changes greatly through the growing season, the

TABLE 4. Results of partial Mantel tests of correlation between community similarity and leaf quality similarity or spatial distance.

Census	Leaf quality   spatial distance		Spatial distance   leaf quality	
	Partial Mantel <i>r</i>	<i>P</i>	Partial Mantel <i>r</i>	<i>P</i>
May 2007	-0.075	0.086	<b>-0.095</b>	<b>0.013</b>
July 2007	0.050	0.212	<b>-0.093</b>	<b>0.010</b>
Aug 2007	0.062	0.218	<b>0.057</b>	<b>0.045</b>
May 2008	-0.001	0.464	-0.043	0.082
July 2008	0.019	0.417	<b>-0.074</b>	<b>0.028</b>
Sep 2008	0.052	0.199	-0.047	0.090

Notes: Effects of each independent matrix (leaf quality or distance) are correlations controlling for the other independent matrix. Boldface type indicates partial Mantel *r*'s where *P* < 0.05.

relationship between individual leaf traits remains similar. Every grouping of herbivores that was significantly correlated with leaf quality followed the same correlational pattern: herbivores were more abundant on high-nitrogen, low-tannin trees. It is noteworthy that these patterns were strongest in the end-of-year census (August 2007 and September 2008). These results mirror a previous study in a closely related system (Forkner et al. 2004), in which total abundance of herbivores on *Q. alba* was most strongly negatively associated with condensed tannin content in late summer. Given the decline in oak foliage quality through a growing season (Feeny 1970), as nitrogen content declines and phenolics increase, insect herbivores late in the season will encounter low quality food and may be under the greatest selective pressure to choose suitable host plants. The significant effects on richness in August 2007 may be a sampling effect; when the influence of total herbivore density on richness is removed, richness no longer correlates with leaf quality ( $t_{58} = 0.781$ ,  $P = 0.438$ ). In September 2008, however, the significant positive correlation still exists ( $t_{55} = 3.143$ ,  $P = 0.003$ ,  $R^2 = 0.137$ ).

The overall weak impacts of bird predation are surprising considering the strong direct effects of birds documented in this (Marquis and Whelan 1994) and other systems (Van Bael et al. 2008, Mooney et al. 2010). Excluding birds from trees did not result in higher densities of total herbivores as expected, and no feeding guild was affected. In this experiment, concealed feeding behavior by structure-building herbivores or leaf miners did not confer any special protection from avian predators relative to free-feeding herbivores. This weak predation pressure also did not translate to differences in community composition; the only MRPP result of statistical significance (July 2008) was of such low effect size that it was likely of little biological significance. The impacts of bird predation have been shown to interact with leaf quality in some systems (e.g., Sipura 1999), but we found no such interaction in our experiment.

Shelter-building caterpillars seem to represent a special case, as they were the only feeding guild whose abundance was never affected by leaf quality. Previous work in this system has demonstrated that leaf-tying caterpillar density is strongly related to plant architecture (Marquis et al. 2002b). This trait is likely more important than food quality for host plant choice by these insects. The most abundant leaf-tier (*Pseudotelphusa* sp.: Gelechiidae) can also act as a deterministic force in affecting the richness and composition of the *Q. alba* herbivore community (Lill and Marquis 2003). Since we did not measure architectural traits in our experiment, they may account for a portion of the unexplained variation in community similarity. However, given the ubiquity of leaf-tying caterpillars (present on 87–100% of trees in the July and late-season censuses), their influence on community composition

may have been fairly consistent across the experiment so that we were still able to detect a spatial signal.

Similarity between communities was most consistently correlated with geographic distances between plants, while leaf quality, even after controlling for the influence of spatial effects, never correlated with similarity (Table 4). In five of six censuses, trees in close proximity had more similar herbivore communities than distant trees. In the one exception, August 2007, the opposite pattern seems to have been driven by inexplicably similar communities on a small number of trees at both the extreme north and extreme south ends of the research area (>600 m apart). These results parallel those of Gripenberg and Roslin (2005) who demonstrated that spatial configuration of oaks better explained occurrence of a leaf miner than variation in host plant quality. Forkner et al. (2004) also found no significant relationships between community composition and *Q. alba* leaf quality (condensed tannins) despite an effect on total herbivore abundance. A shortcoming of Mantel  $r$  is that it cannot be used to accurately estimate a coefficient of determination in the way Pearson  $r$  typically is because it tends to underestimate explained variance (Legendre et al. 2005). We await other studies of herbivore community spatial variation with which to compare the strength of our community-similarity-geographic-distance relationship. We acknowledge that our investigation of leaf quality and bird predation does not encompass the full range of deterministic factors influencing herbivore distribution. Other factors, such as attack by parasitoid wasps and flies (Le Corff et al. 2000), pupal predation while pupae are in the soil (Tanhuanpää et al. 1999), or fine-scale abiotic variations not reflected in leaf quality (for example, canopy openness that potentially influences ballooning and subsequent survival of certain caterpillar species [Hunter and Elkington 2000]), can vary spatially and could contribute to spatial patterns in the herbivore community observed here.

A distance-decay in community similarity is consistent with assembly by stochastic processes such as dispersal limitation. Detailed estimates of dispersal abilities of forest moths (which accounted for 84% of the species we encountered) are difficult to acquire, and as a result, are available for only a few species. Nieminen (1996) performed a mark-recapture study of several moth species in an archipelago and reviewed other studies that quantified moth movements, finding that most species moved <1 km and few >100 m. Our study area was about 700 m long, so if Nieminen's (1996) findings apply to moths in this system, few herbivores in the present study would disperse the length of the study area, which would contribute to the spatially structured community patterns detected. Had we studied trees more widely spaced (e.g., up to several km), the distance-decay may have been even stronger.

Dispersal may also be related to diet breadth. It has long been recognized that Lepidoptera with flightless adult females tend to be generalists (Hackman 1966,

Barbosa et al. 1989), and a detailed study has found that flightless females may move very short distances when ovipositing (Doak 2000). These species often rely on ballooning by larvae to reach new hosts. The May censuses in this study recorded several species (families Geometridae, Lymantriidae) that follow this limited dispersal strategy, which may have contributed to the spatial structuring of the spring community. Species with flying females are likely capable of longer-distance dispersals, and among specialists selection may favor individuals that disperse farther because they are more likely to locate scattered hosts. Conversely, generalists will be able to colonize a greater number of plants in an area and may not need long dispersal distances to reach suitable hosts.

A long tradition of studies of oak leaf miners indicates that dispersal is important in determining presence and abundance on individual host plants (Connor et al. 1983). Mopper et al. (2000) extirpated leaf miners from individual oaks, and the trees were rapidly recolonized by the next insect generation, but these effects were studied at a fairly small scale (mostly <50 m). Gripenberg et al. (2008) modeled the dispersal of a specialist oak leaf miner across a large area and found a mean dispersal distance of 87 m. This resulted in a patchy distribution determined in part by the spatial distribution of the host trees, consistent with our results. Little is known about the dispersal of structure-building Lepidoptera that roll or tie leaves. Most in this study are small-bodied and could be more dispersal-limited than larger free-feeding species.

In summary, the effects of leaf quality on the *Q. alba* herbivore community patterns were limited to influencing the density and richness of herbivores, and bird predation had little effect. These deterministic factors had no impact on the species composition of individual *Q. alba* herbivore communities. Rather, the compositional similarity between pairs of trees was correlated with the distance separating pairs, suggesting that stochastic processes may determine the identities of herbivore species on oaks.

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#### APPENDIX A

Detailed methodology of leaf trait measurements (*Ecological Archives* E092-058-A1).

#### APPENDIX B

Herbivore species recorded, feeding guild, diet breadth, and census recorded (*Ecological Archives* E092-058-A2).

#### APPENDIX C

Results of Mantel tests correlating spatial arrangement of trees with leaf quality similarity (*Ecological Archives* E092-058-A3).

#### APPENDIX D

Results of MANCOVAs assessing the impact of bird exclusion, leaf quality, and interactions on herbivores (*Ecological Archives* E092-058-A4).

#### APPENDIX E

Nonmetric multidimensional scaling plots of community composition (*Ecological Archives* E092-058-A5).