richness and either woody debris volume or leaf litter depth. It seems likely that higher richness of carabids in primary forests is the result of increased woody resources and higher potential for niche diversification. However, more study will be required to evaluate the spatial scale that is most relevant to carabids, and to separate the effects of coarse woody debris from other factors that covary with it.

Our data indicate that woody debris volume is more important for the diversity of ground beetles than for their abundance. The ability of both forest types to sustain similar beetle abundance might imply that the resource base of the two forests is comparable, and that species richness in the secondary forest is limited by low resource heterogeneity rather than low resource supply. Specific aspects of resource heterogeneity that might be relevant to carabid diversity include physical structure of substrate, predation risk and prey availability. Other measures of habitat complexity such as heterogeneity of soil fungi and soil litter may also contribute to this pattern. Further research is required to analyze the relative importance of these potential factors.

Because Coleoptera are important elements of forest food webs and are also sensitive to habitat alteration, Coleopteran diversity has often been used as an indicator of general habitat quality and ecosystem diversity (Berry et al. 1994, Rykken et al. 1997). In this context, our results imply that logging and grazing can depress habitat heterogeneity and faunal diversity for at least twenty years, which is longer than required for the development of a closed canopy forest. Future research in these forests may offer further insights into the time scale for re-establishment of diversity in forest floor communities, as well as the patterns of species succession following disturbance.

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Internal and External Herbivory on a Common Rubiaceae Shrub in Primary and Secondary Cloud Forest

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Abstract: High biodiversity could be associated with low parasitism, which would favor increased stability. We tested for relationships between diversity and parasitism by comparing one class of parasitism, insect herbivory, on a species of Rubiaceae that occurs within both a diverse primary forest and an adjacent, but less diverse, secondary forest in Monteverde. We examined amounts of leaf-miner infection, or internal herbivory, and more general external herbivory. We did not find differences in host species density between primary and secondary forest. Additionally, parasitism by leaf-miners and external folivores was not related to density of conspecifics. For leaf-miners, host-plant density does not appear to be limiting population size. Although external herbivory was not related to density of conspecifics, leaf damage decreased with increasing plant size in the primary forest and was independent of plant size in the secondary forest, suggesting different herbivores. It appears that diversity does not affect parasitism by a specialist leaf-miner and external folivores on a common plant species, thus providing evidence for a more narrow application of the diversity-parasitism postulate.

Key Words: biodiversity-stability theory, diversity, folivores, leaf-miners, parasitism, resistance

Introduction

Increasing evidence suggests that higher biodiversity is associated with greater ecosystem stability. One postulate of the biodiversity-stability hypothesis is that systems with greater diversity are less susceptible to disease and parasitism. Higher diversity is associated with less abundant dominants (Guariguata 2000). The comparatively low density of each species in these diverse systems could limit the transmission of specialist parasites. If so, this could reduce the chances of parasite epidemics and increase the stability of the community. Studies demonstrating decreased pathogen transmission are based on less-diverse grassland ecosystems. The general applicability of the diversity-parasitism hypothesis to other ecosystems and to other classes of parasitism is not well documented. We evaluated the relationship between diversity and parasitism for the case of two types of plant parasites, internal leaf-miners and external folivores, that feed on a single species of plant that occurs within tropical forest communities of differing diversities.

In tropical forests, secondary-growth forest is generally less diverse than primary-growth forest (Guariguata 2000), with greater abundance of a few individuals (Haber 2000). Our focal plant was a species of Rubiaceae that occurred within primary and secondary forests and experienced significant herbivory from one species of leaf-miner (probably Diptera: Agromyzidae) and one or more species of external folivores. Under the diversity-parasitism hypothesis, herbivory should be greater in secondary-growth forest than in primary forest. We also predicted that herbivory would be positively related to local density of the host plant and negatively related to size of plant.

Methods

On 19 - 20 January 2002, we measured damage from leaf-miners (endoparasites) and external folivores on a shrubby species of Rubiaceae in primary forest and a nearby secondary forest (20 years old) at La Estación Biológica, Monteverde, Costa Rica. We walked the Quitirrí Trail through secondary forest, and the Principal and Cariblancos Trails through primary forest searching for individuals of the target plant species. The first individual found more than 20 m away from the

last individual surveyed was designated as a focal individual, or if a patch was encountered, an individual was randomly chosen from within the patch. We counted total number of leaves per plant and the number of leaves that were, or had been, infected by leaf-miners. We also sampled 30 leaves (or as many leaves as present in small individuals) near the top of each plant and scored external herbivory on a 0 - 4 scale (0 = no damage, 1 = small amount of damage, 2 = ≥25% of leaf eaten, 3 = ≥50% of leaf eaten and 4 = ≥75%). We estimated local density by counting conspecific plants within a 5 m radius of the focal plant. We measured nearest neighbor distance (NN1) from the focal plant to the closest conspecific and measured total number of leaves, leaf-miner damage and leaf damage (external herbivory) for NN1. Then we measured the distance from NN1 to its nearest neighbor (NN2) and recorded total leaves and leaf-miner damage for NN2. Our sampling included 9 focal plants in the primary forest and 10 in the secondary forest.

We performed linear regression analysis of both the proportion of leaves mined and external herbivory score versus number of conspecifics within 5 m. We compared forest types with respect to mean and variance in density of (1) conspecifics and (2) nearest neighbor distances. Mean proportions of miners in primary and secondary forest were compared using a t-test. We used least-squares regression to determine rates of leaf-miner parasitism (number of miner-infected leaves versus number leaves), and then compared the linear regressions. Mean amount of external herbivory for primary and secondary forests was analyzed with a t-test, where herbivory index was calculated with the following formula:

$$\sum_{i=0}^{4} \frac{(i)(\#\ of\ affected\ leaves\ of\ rating\ i)}{number\ of\ leaves\ counted}$$

Linear regressions of herbivory score on number of leaves were compared between primary and secondary forests.

Results

Neither density of conspecifics nor size of plant was related to the presence of leaf-miner parasitism. The proportion of leaves infected by miners was independent of the local density of conspecifics ($r = 0.00$, $n = 19$, $P = 0.92$), and tended to be negatively related to number of leaves per plant ($r = -0.26$, $n = 53$, $P = 0.06$). Similarly, external leaf damage was independent of local density of conspecifics ($r = 0.00$, $n = 20$, $P = 0.88$), although it was negatively related to number of leaves per plant ($r = 0.39$, $n = 38$, $P = 0.02$).

Contrary to our expectations, local density of the focal species did not differ between primary and secondary forest ($t = 0.59$, $df = 17$, $P = 0.56$; Table 1). Average leaf damage declined with individuals in the secondary forest and was more clumped than in primary forest ($F_{9,8} = 3.28$, $P = 0.05$ for test of equal variances in density; Table 1). Mean nearest neighbor distance was not used, because for one case in the primary forest and three cases in the secondary forest we could not find a neighbor within 10 m.

Mean leaves parasitized by leaf-miners did not differ between primary and secondary forest ($t = 0.07$, $df = 51$, $P = 0.95$). There was no difference between primary and secondary forests in the relationship between incidence of leaf-miners and plant size (Fig. 1). Average leaf damage scores did not differ between forests ($t=1.63$, $df=36$, $P=0.11$; Table 1). Average leaf damage scores declined with number of leaves per plant in the primary forest, but not in the secondary forest (Fig. 2).

TABLE 1. Density and dispersion, leaf-miner damage and external herbivory score (mean ± SE) for a common Rubiaceae shrub in primary and secondary forest at Monteverde, Costa Rica.

Forest Type	Conspecifics/ 25 m^2	Dispersion Index*	Leaves with Miners (%)	Herbivory Score
Primary	3.22 ± 0.97 (9)	2.63	4.8 ± 0.8 (27)	0.90 ± 0.08 (18)
Secondary	4.40 ± 1.67 (10)	6.31	4.9 ± 1.2 (25)	0.73 ± 0.28 (20)

*Variance/mean; values > 1 indicate aggregation.

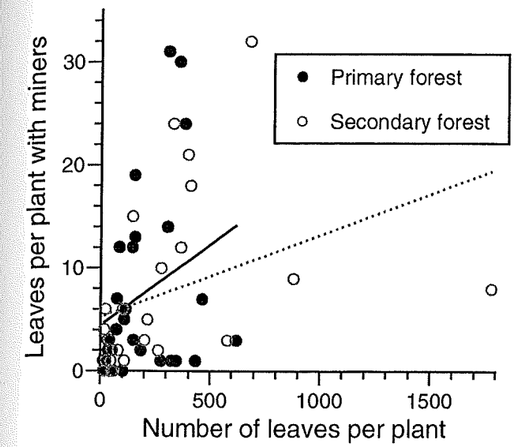

FIG 1. Comparison between forest types of leaf miner incidence as a function of plant size. Regressions did not differ between forest types ($F_{2,49} = 0.31$, $P = 0.77$) and neither regression was significant by itself ($r^2 = 0.08$, $df = 26$, $P = 0.16$ and $r^2 = 0.13$, $df = 25$, $P = 0.07$ for primary and secondary forests, respectively).

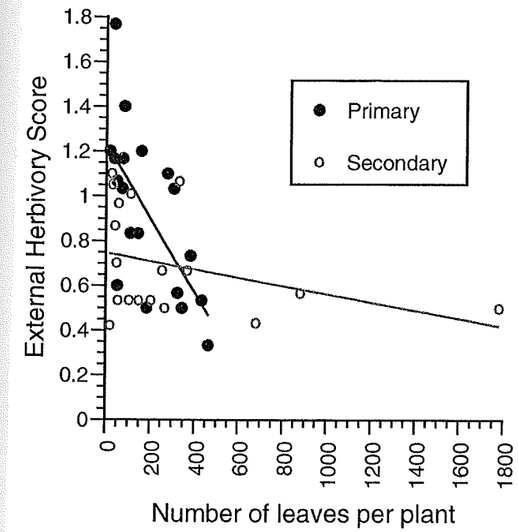

FIG. 2. Comparison between forest types of external leaf damage scores as a function of plant size. Regressions differed strongly between forest types ($F_{2,34} = 5.34$, $P < 0.01$). The individual regressions were significant for the primary forest ($r^2 = 0.43$, $df = 17$, $P < 0.01$), but not the secondary forest ($r^2 = 0.09$, $df = 16$, $P = 0.25$).

Discussion

Contrary to the hypothesis that increasing diversity leads to decreasing parasitism, internal herbivory on our study species did not differ between primary and secondary forests (Table 1). Presumably, a different herbaceous species might exhibit lower densities in the more diverse primary forest. However, this does not necessarily lead to lower parasitism because there was no relationship between local density of our study species and incidence of leaf-miners (Fig. 1). This suggests that leaf-miner abundance is influenced primarily by factors that are independent of host density. These results are contrary to the general hypothesis that parasitism increases with decreasing biodiversity. It would be informative to quantify the relationship between biodiversity and species-specific densities in primary versus secondary forests at Monteverde. Looking at host plant density at a larger spatial scale (beyond the 5 m radius employed in this study) could reveal meaningful relationships between host density and parasitism frequency in Rubiaceae. Presumably, the relevant spatial scale depends in part upon the mobility of leaf-miner adults and whether local abundance is influenced more by search behavior of individuals or population demographics.

The diversity-parasitism hypothesis was further refuted by the finding that leaf-damage scores were independent of host density and forest type. Forest types did differ in the relationship between leaf damage and

number of leaves on the plant (Fig. 2). One possible explanation is that herbivore encounters with shrubs are independent of shrub size, in which case larger shrubs would sustain less damage per leaf than smaller shrubs. This could explain the pattern in Fig. 2 if herbivore search patterns differ between primary and secondary forests, perhaps because they are different species or because of the increased aggregation of shrubs in the secondary forest (Table 1). Additional studies should investigate the relationship between biodiversity and parasitism by pathogens and other classes of parasitism, especially as they affect species whose densities vary across diversity gradients of forest ecosystems.

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