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DIVERSITY, ECOSYSTEM FUNCTION, AND STABILITY OF PARASITOID–HOST INTERACTIONS ACROSS A TROPICAL HABITAT GRADIENT

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Abstract. Global biodiversity decline has prompted great interest in the effects of habitat modification and diversity on the functioning and stability of ecosystem processes. However, the applicability of previous modeled or mesocosm community studies to real diverse communities in different habitats remains ambiguous.

We exposed standardized nesting resources for naturally occurring communities of cavity-nesting bees and wasps and their parasitoids in coastal Ecuador, to test the effects of host and parasitoid diversity on an ecosystem function (parasitism rates) and temporal variability in this function. In accordance with predictions of complementary host use, parasitism rates increased with increasing diversity, not simply abundance, of parasitoids. In contrast, parasitism decreased with increasing host diversity, possibly due to positive prey interactions or increased probability of selecting unpalatable species. Temporal variability in parasitism was lower in plots with high mean parasitoid diversity and higher in plots with temporally variable host and parasitoid diversity. These effects of diversity on parasitism and temporal stability in parasitism rates were sufficiently strong to be visible across five different habitat types, representing a gradient of increasing anthropogenic modification. Habitat type did not directly affect parasitism rates, but host and parasitoid diversity and abundance were higher in highly modified habitats, and parasitoid diversity was positively correlated with rates of parasitism. The slope of the richness–parasitism relationship did not vary significantly across habitats, although that for Simpson's diversity was significant only in rice and pasture. We also show that pooling data over long time periods, as in previous studies, can blur the effect of diversity on parasitism rates, and the appropriate spatiotemporal scale of study must be considered.

Key words: agriculture; arthropod; bee; ecosystem services; insect; managed land; multiple scale; predator–prey interactions; trap nest; wasp.

Introduction

The modification of landscapes through human exploitation of the environment continues to reduce biodiversity on a global scale (Vitousek et al. 1997). This dramatic anthropogenically mediated decline in biodiversity has led to concern over the potential loss of important ecosystem processes (Foley et al. 2005, Kremen and Ostfeld 2005), and the need for a clearer understanding of the ways in which diversity affects ecosystem functioning (Chapin et al. 2000, Daily et al. 2000, Hooper et al. 2005) and variability in this functioning over time (Rodriguez and Hawkins 2000, Halpern et al. 2005). The tenet that diversity increases ecosystem functioning has itself engendered some controversy (e.g., Huston 1997, Tilman et al. 1997, Naeem 2002), and several authors have argued for a clearer understanding of the interactions between abiotic factors and the diversity–function relationship (e.g., Loreau et al. 2001).

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Much recent work has focused on the relationship between diversity and productivity in plant communities (e.g., Mouquet et al. 2002, Pfisterer and Schmid 2002, Cardinale et al. 2004, van Ruijven and Berendse 2005); however, there is some evidence that the dominant impacts of biodiversity change on ecosystem functioning are trophically mediated by consumers (Duffy 2003). A recent link has therefore been made between the body of work relating to ecosystem function and that relating to predator–prey interactions (Ives et al. 2005).

Diversity effects on consumer–resource interactions have until now been examined using modeled (Fox 2004, Ives et al. 2005) or simplified communities in the laboratory (Gamfeldt et al. 2005) or in field cage environments (Cardinale et al. 2002, 2003, Finke and Denno 2004, Straub and Snyder 2006). While this work has been critical to understanding the mechanisms through which diversity may affect ecosystem processes, the structure and diversity of experimental communities often differs markedly from the communities actually providing ecosystem services within real landscapes (Sih et al. 1998, Kremen 2005). Therefore, uncertainty remains as to how the results of such experiments scale up to landscapes and generalize across different spatiotemporal scales and habitat types (Loreau et al.

2001, Cardinale et al. 2004). In particular, it has been suggested that different mechanisms may operate in artificial vs. natural environments. The main mechanisms through which consumer diversity may lead to increased consumption can be summarized as: (1) selection/sampling effects, whereby high diversity increases the probability of including an highly efficient consumer (Hooper et al. 2005), (2) facilitation effects, whereby the presence of one consumer species alters the environment in such a way as to improve the efficiency of another species (Cardinale et al. 2002, 2003), and (3) niche partitioning or resource complementarity, whereby a more diverse array of consumers allows greater saturation of niche space and more efficient overall utilization of food resources (Hooper et al. 2005). While resource complementarity has received significant attention in small-scale studies, it has been argued that complementary resource use by different species can only increase overall consumption when a diverse array of niches is available. This mechanism may therefore be more likely to operate in natural environments than in experimental systems, where sampling effects may be more likely (Wellnitz and Poff 2001, Ives et al. 2005).

Related to the diversity–function debate is the effect of diversity on stability of ecosystems and their processes. This subject has received considerable attention (see Pimm 1984, McCann 2000, Cottingham et al. 2001 for reviews), and carries important implications for conservation and sustainable agriculture, as consistency in ecosystem services is required over time. Moreover, diversity effects on ecosystem functioning and stability generally act in concert, so these factors are most meaningful when studied together (Pfisterer and Schmid 2002, Worm and Duffy 2003). As with diversity–function relationships, much of the diversity–stability literature has focused on stability of plant productivity (e.g., Tilman 1996, Tilman et al. 1998, Pfisterer and Schmid 2002, Caldeira et al. 2005). However, the importance of predator diversity for ecosystem stability remains poorly studied (Loreau et al. 2001), despite the importance of these species for biological pest control, and the fact that higher trophic levels frequently suffer more from landscape modification (Kruess and Tscharntke 1994, Klein et al. 2006). Increased stability through temporal complementarity may be expected to occur in a manner analogous to spatial resource complementarity. As consumers become more or less abundant through time, other species that occupy a different temporal niche may compensate, leading to a more stable overall rate of consumption. This "insurance hypothesis" purports that diverse communities are better able to compensate for temporal stochasticity of individual species in variable environments, and comprises a potential future benefit to biodiversity (e.g., Yachi and Loreau 1999). Although there is some evidence from the laboratory (Steiner et al. 2005), the effects of diversity on consumer–resource interactions and stability in real systems remain contentious (Rodriguez and Hawkins 2000, Montoya et al. 2003, Finke and Denno 2004). A recent meta-analysis found a destabilizing effect of predator diversity on herbivore biomass (Halpern et al. 2005), whereas a field investigation of a parasitoid guild showed no effect of diversity on functioning and stability (Rodriguez and Hawkins 2000).

We address this dearth of field evidence by examining the effect of parasitoid diversity on ecosystem functioning (parasitism rates) and stability of parasitism rates through time. We also examine how these effects vary across different habitat types, forming a gradient of anthropogenic modification. We use a diverse guild of cavity-nesting bees and wasps, and their natural enemies (parasitoids and kleptoparasites, hereafter: parasitoids) in coastal Ecuador, and find that increased diversity of parasitoids leads to increased parasitism rates, exceeding the effects of abundance of parasitoids or their hosts. We also show that high mean diversity per month leads to low between month variability in parasitism (i.e., high stability), even though high overall diversity pooled across the entire sampling period had no significant effect on stability. Conversely, temporally variable parasitoid and host diversity led to variable rates of parasitism between months. These effects were found across five different habitat types, representing a gradient of increasing anthropogenic modification. Our results show that consistently high consumer diversity can promote overall consumption and temporal stability, whereas variability in diversity through time is inimical to the maintenance of high parasitism rates.

Materials and Methods

Study region

The 48 study plots were spread across three cantons in the region of Jipijapa (1°19′60″ S, 80°34′60″ W, 259 m above sea level [asl]), Pajan (1°34′00″ S, 80°25′00″ W, 142 m asl), and 24 de Mayo (largest town: Noboa, 1°24′00″ S, 80°23′00″ W, 260 m asl), within the province of Manabi, southwest Ecuador (for individual plot location details and a full description of the region see Tylianakis et al. 2005; a map of the study region is provided in Appendix A). The region falls within the semiarid tropics and is largely dominated by agriculture. Here we examine a gradient of anthropogenic modification using the predominant agricultural systems in the region: an arable crop (rice), pasture, and agroforestry (coffee). We also examine forest fragments and use abandoned coffee agroforests as an intermediate between forest and agricultural systems. Twelve replicates of each managed habitat type were sampled in the study, as well as six abandoned coffee agroforests (abandoned for 10–15 years and now resembling secondary forest) and six forest fragments.

Trap nests

Nine trap nests were positioned (in a 3×3 grid, 25 m between adjacent traps) in the center of each of the 48

PLATE 1. Parasitoids (Hymenoptera: Chalcidoidea) attacking cavity-nesting bees and wasps. (Left) An ectoparasitoid (Leucospidae) on a trap nest. (Right) A host bee pupa parasitized by *Melittobia acasta* (Walk.) (Eulophidae), with adult *Melittobia* (~1 mm length) shown in the inset. Photo credit: J. Tylianakis.

plots, to provide nesting sites for naturally occurring bee, wasp, and parasitoid communities. Exposure of standardized trap nests is similar to the exposure of other resources, e.g., phytometer plants, but because the guild of aboveground cavity-nesting species reproduces in these traps, the problem of species appearing as "tourists" in samples is eliminated. It may be argued that in open habitats, where fewer natural nesting sites are available, these trap nests will attract Hymenoptera more than in wooded habitats; however, this has been shown not to be the case. Rather, cavity-nesting species usually build nests very close to the nesting site from which they pupated, and trap nests give an accurate representation of the community normally occurring in a particular habitat (see Tscharntke et al. 1998). Trap nests were constructed according to the methodology of Tscharntke et al. (1998). A PVC tube with a length of 22 cm and a diameter of 15 cm formed the outer case of the nest. Internodes of reeds *Arundo donax* L. (Poaceae) with varying diameter (2–20 mm) and a length of 20 cm were inserted into this tube and provided the nesting sites for bees and wasps. Trap nests were hung from trees in shaded (coffee, abandoned coffee, and forest) systems and suspended from wooden posts in open (rice and pasture) systems. Sticky glue (Tanglefoot, Tanglefoot Company, Grand Rapids, Michigan, USA) was applied every month to the post or attachment point to deter ants. All traps were positioned 1.5 m above the ground.

The parasitoids found in trap nests can be broadly classified as either ectoparasitoids (feed externally on the host), endoparasitoids (feed internally on the host), or kleptoparasites (feed on the host's food resources; Appendix B). All kill the host larva/pupa, and for convenience we simply refer to them collectively as "parasitoids." Host identity was usually determined either from surviving hosts within a parasitized nest or by nest characteristics when all host larvae were parasitized.

A broad spectrum fungicide (Fitoraz 76 PM, Bayer Crop Science S.A., Bayer del Ecuador, Quito, Equador: propineb 21 g/L, cymoxanil 1.8 g/L) that is not toxic to Hymenoptera was applied to each trap with a hand sprayer every month.

Each trap was evaluated every month from June 2003 to October 2004, and all reed internodes that were occupied by Hymenoptera were removed and replaced with new internodes of the same diameter. Occupied reeds were opened, and the larvae were reared to maturity for positive identification to subfamily level following Goulet and Huber (1993) for wasps, and Michener (2000) for bees. Genera and species were identified where possible by J. Gusenleitner and D. W. Roubik, and by the authors using keys and reference collections from the Pontificia Universidad Católica del Ecuador. Remaining species were identified as morphospecies. Data from each of the nine traps per plot were pooled for analyses. A gregarious hymenopteran parasitoid species (*Melittobia acasta* Walk., Chalcidoidea: Eulophidae) occurred in our trap nests (see Plate 1) with up to 1500 individuals in each nesting tube. Because this would overwhelm the 1–5 individuals of other parasitoid species, we defined the abundance of *M. acasta* (and indeed, all parasitoid species) as the number of host larvae parasitized by this species. This accords better with the other observed parasitoid species that in most cases produce one individual per parasitized host. This species also hyperparasitized 10 larvae of another

parasitoid (*Chrysis* sp., Hymenoptera: Chrysididae); however these incidents were not included in analyses.

Data analyses

Diversity–abundance.—Analyses were carried out in Statistica 6.1 (StatSoft 2003). Post hoc tests for differences between habitat types were made using Tukey's pairwise comparisons. Determinants of host and parasitoid diversity (mean species richness and Simpson diversity per month) and abundance were examined using general linear models (GLM). As richness, abundance, and Simpson diversity were intercorrelated for both hosts (Spearman rank, $r > 0.51$, $P < 0.05$ for all comparisons) and parasitoids (Spearman rank, $r > 0.75$, $P < 0.05$ for all comparisons), they were treated as a multivariate response variable in both models. The first model examined the effects of habitat type (fixed factor) on host diversity and abundance. The second model examined the effects of habitat type (fixed factor), mean abundance, and species richness of hosts (covariables) on parasitoid diversity and abundance. Two further models examining the effects of habitat (and host richness) on total richness of hosts and parasitoids, pooled over the entire sampling period, are presented in Appendix C. Model residuals were tested for adherence to a normal distribution.

Diversity–parasitism.—Parasitism rate was defined as the proportion of host individuals that were parasitized or kleptoparasitized per month per plot. Proportion parasitism data were arcsine square-root (+0.5) transformed prior to analysis to meet the assumptions of normality and homogeneity of variances. They were analyzed in three GLMs with backward stepwise elimination and habitat type as a fixed factor. A Bonferroni corrected α of 0.01667 was used in all three models. The first model included host and parasitoid species richness as continuous predictors. Because species richness covaried with abundance (see *Results*), host and parasitoid abundance were tested separately as covariables in a second model. The third model used Simpson's diversity index ($1 - \Sigma[n/N]^2$, where n = number of individuals of a species, and N = the total number of individuals of a species) of hosts and parasitoids as covariables, as this index is less sensitive to differences in abundance than other diversity indices. Interaction effects between habitat type and each of the covariables were included in all three models. A Mantel test was conducted in R (R Development Core Team 2004) to test for spatial autocorrelation of the species richness vs. parasitism model residuals. The test was based on Pearson correlations, using a distance matrix constructed from x and y GPS coordinates, and found no spatial autocorrelation ($r = -0.0008$, $P = 0.702$).

To determine whether any diversity–parasitism relationship was consistent for each host species, as opposed to a combined effect of different parasitoids attacking different host species, we conducted separate analyses on the six most abundant host species. Because sample sizes were much smaller, we pooled species richness across all months and did not include zero values (which were not present in the previous total community analyses, but would bias results toward a positive diversity–parasitism relationship). For each host species we used a GLM with backward stepwise elimination, habitat type as a fixed factor, and parasitoid richness as a covariable.

Diversity–stability.—To determine whether there was significant variation in parasitism rates (response variable) across months, we conducted a repeated-measures ANOVA with habitat type as a predictor and time (month) as a within-factor.

Subsequently, we followed previous authors (e.g., Tilman et al. 1998, Rodriguez and Hawkins 2000, Halpern et al. 2005, Kremen and Ostfeld 2005) by measuring stability using the coefficient of variation (CV, i.e., the standard deviation expressed as a percentage of the mean) in parasitism rates, such that high stability is indicated by low CV (hereafter "variability") through time. To determine the effect of parasitoid and host richness and variability on variability in parasitism rates, we used three GLMs with backward stepwise elimination and a Bonferroni corrected $\alpha = 0.0166$. The response variable in all three models was the CV in parasitism rates (ln-transformed), and habitat type was included as a fixed factor. Interaction effects between habitat and covariables were also included in the models. The first model used the mean species richness of hosts and parasitoids per month as covariables. The relationship between parasitoid richness and stability was found to be logarithmic (see *Results*), so the model was repeated using natural log (ln) parasitoid richness as the covariable. The second model used the total pooled parasitoid richness for the plot, over the entire sampling period, as a covariable. The purpose of this model was to determine whether pooling of data over long periods (as in Rodriguez and Hawkins 2000) yields similar results as when mean monthly richness values are used. The third model used variability (CV) in host and parasitoid species richness across months as covariables, to determine whether stability in richness promotes stability in parasitism rates.

Results

Diversity

Overall, 24 017 individuals of 33 species of bees and wasps (Hymenoptera: Apidae, Megachilidae, Mutilidae, Pompilidae, Sphecidae, and Vespidae) occupied the trap nests. Of these primary occupants (hereafter "hosts"), 5328 were parasitized by 1924 individuals (plus 40 380 individuals of the gregarious *Melittobia acasta*) of nine parasitoid species (Hymenoptera: Eulophidae, Ichneumonidae, Leucospidae, Megachilidae, and Chrysididae; Diptera: Bombyliidae; Appendix B).

Mean host diversity (per month) and abundance varied significantly across habitat types (Wilks' lambda $= 0.30$, $F = 5.26$, df $= 12, 109$, $P < 0.0001$; abundance, $R^2 = 0.577$; richness, $R^2 = 0.500$; Fig. 1; Simpson, $R^2 = 0.160$

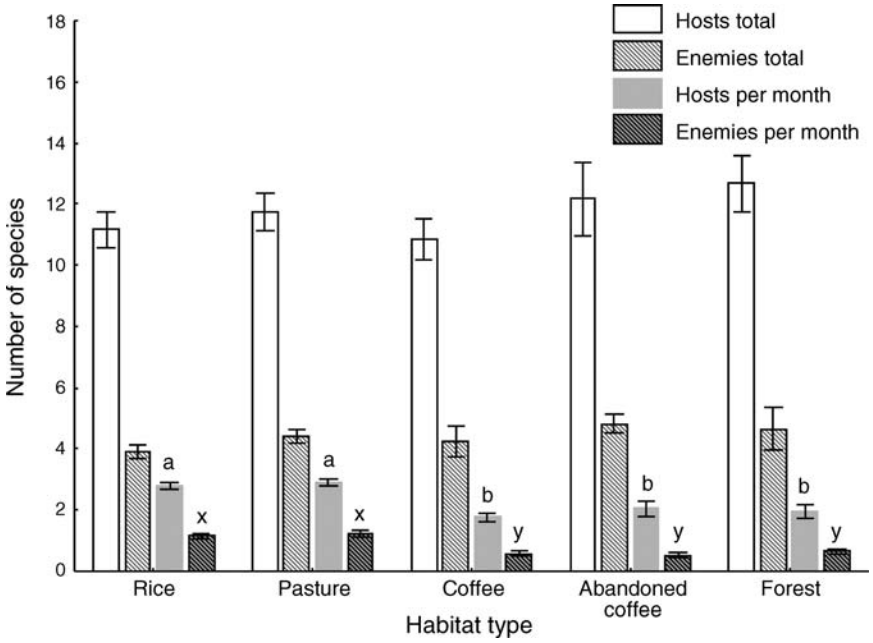

FIG. 1. Total (pooled over the entire sampling period) and mean monthly species richness of hosts and parasitoids in the different habitat types: rice, pasture, coffee, abandoned coffee, and forest. Values are mean ± SE per site. Letters represent significant differences from GLMs (see Table 1). No significant differences were found for total diversity of hosts or parasitoids (Appendix C).

adjusted for ties; Table 1A) and were higher in rice and pasture (the most highly modified habitats) than in the remaining habitat types. Mean diversity and abundance of parasitoids also varied significantly across habitat types (Wilks' lambda = 0.16, df = 12, 104, $F = 8.77$, $P < 0.0001$; overall model, abundance, $R^2 = 0.786$; richness, $R^2 = 0.675$; Fig. 1; Simpson, $R^2 = 0.577$ adjusted for ties; Table 1B), and were positively correlated with host richness (Wilks' lambda = 0.82, $F = 2.92$, df = 3, 39, $P = 0.046$; Table 1B) and abundance (Wilks' lambda = 0.16, $F = 20.34$, df = 3, 39, $P < 0.000$; Table 1B). In contrast to the mean values, total pooled diversity of hosts and parasitoids did not vary significantly across habitats (Appendix C, Fig. 1).

Diversity–parasitism

Rates of parasitism and kleptoparasitism (hereafter "parasitism") per month were significantly positively correlated with mean parasitoid species richness per month (Fig. 2) and weakly negatively correlated with host richness (Table 2A). Overall, the model explained 54.6% of the variance in parasitism rate (adjusted for ties). Not surprisingly, abundance of parasitoids was also significantly and positively correlated with parasitism rate (Table 2B); however, abundance explained less variance (39.4% adjusted for ties) than did species richness. In the absence of interaction effects, Simpson's diversity index was positively correlated with rates of parasitism ($F_{1,46} = 22.32$, $P < 0.0001$, $R^2 = 0.312$ adjusted for ties). However, this positive relationship was only significant in rice and pasture, and when interaction effects were included in the model, the interaction between habitat type and parasitoid Simpson diversity was significant (Table 2C), and the direct effect of parasitoid Simpson diversity disappeared (overall model, $R^2 = 0.359$ adjusted for ties). Rates of parasitism did not vary significantly across habitat types in any of the models, and habitat type did not significantly interact with the effects of parasitoid richness or abundance on parasitism rates, so the slope of these relationships did not vary significantly across habitats.

In the analyses of individual host species, parasitism rates on two of the six most abundant hosts were significantly positively correlated with species richness of their parasitoids (Appendix D). No significant effects of parasitoid richness were found for the remaining species.

Diversity–stability

Parasitism rates showed significant temporal variation (Table 3), and this variation was not consistent across habitat types (time × habitat interaction effect), although again, habitat type did not directly affect rates of parasitism (graphs of temporal variation in parasitism rates, host and parasitoid richness and abundance for each habitat type are available in Appendix E). Temporal variability in parasitism rates (the inverse of stability) was significantly negatively correlated with the mean species richness of parasitoids per month, such

TABLE 1. Univariate results from general linear models testing effects of habitat type on abundance, species richness (mean per month), and Simpson diversity index (mean per month) of (A) hosts and (B) parasitoids.

Model and variable	df	SS	MS	F	P
Model A, hosts					
Abundance					
Habitat	4	2 362 522	590 631	17.05	<0.0001
Error	43	1 489 455	34 638		
Richness					
Habitat	4	11.47	2.87	12.73	<0.0001
Error	43	9.69	0.23		
Simpson					
Habitat	4	0.09	0.02	3.24	0.021
Error	43	0.28	0.01		
Model B, parasitoids					
Abundance					
Habitat type	4	165 449	41 362	27.14	<0.0001
Host richness	1	9 305	9 305	6.11	0.018
Host abundance	1	16 989	16 989	63.64	<0.0001
Error	41	62 485	1 524		
Overall model	6	271 743	45 290	29.72	<0.0001
Richness					
Habitat type	4	4.48	1.12	20.95	<0.0001
Host richness	1	0.23	0.23	4.22	0.046
Host abundance	1	0.83	0.83	15.55	0.0003
Error	41	2.19	0.05		
Overall model	6	5.50	0.92	29.72	<0.0001
Simpson					
Habitat type	4	0.10	0.03	15.71	<0.0001
Host richness	1	0.00	0.00	0.19	0.665
Host abundance	1	0.01	0.01	7.09	0.011
Error	41	0.07	0.00		
Overall model	6	0.1	0.02	11.69	<0.0001

Notes: Richness, abundance, and Simpson diversity were intercorrelated and therefore treated as a multivariate response variable. Habitat type was a fixed factor in models A and B. In model B (parasitoids), host diversity and abundance (both mean per month) were also used as covariables.

that plots with a high per month richness had greater stability (lower CV) in parasitism rates ($F_{1,46} = 119.39$, $P < 0.0001$, overall model, $R^2 = 0.715$ adjusted for ties); however, the relationship was nonlinear, and a model using ln parasitoid richness explained more variance (Table 4A; overall model, $R^2 = 0.765$ adjusted for ties; Fig. 3A). Surprisingly, there was no significant effect of pooled species richness over the entire sampling period on stability in parasitism (Table 4B). Rather, in the second model, habitat type explained the majority of the variation in stability of parasitism, due to the indirect effect of habitat type on monthly richness (rice and pasture had the highest mean richness; see *Results: Diversity*), and this pooled model explained less of the variability in parasitism (overall model, $R^2 = 0.472$ adjusted for ties) than the model using mean richness per month. In contrast, temporal variability in parasitism rates was positively correlated with temporal variability (CV) in both parasitoid (Fig. 3B) and host species richness (Table 4C; overall model, $R^2 = 0.867$ adjusted for ties).

DISCUSSION

Diversity–parasitism

In our study system, parasitism (an ecosystem function) and stability of parasitism rates across time increased with increasing diversity of parasitoids. Effects of consumer diversity on prey consumption have been predicted by modeled and mesocosm studies of simplified communities (e.g., Cardinale et al. 2002, 2003, Fox 2004, Gamfeldt et al. 2005); however, previous field studies have found no effect (Rodriguez and Hawkins 2000, Straub and Snyder 2006) or even a negative effect (Finke and Denno 2004) of diversity on rates of predation/parasitism. The mixed results of these field studies may have been the result of specific characteristics of the systems examined. For example, Rodriguez and Hawkins (2000) found no effect of parasitoid diversity on rates of parasitism of grass-feeding *Tetramesa* spp., or stability in parasitism. However, these hosts comprised one genus, with one life-history strategy, and all the natural enemies were hymenopteran larval parasitoids (Chalcidoidea). In contrast, our study system contained a diverse parasitoid and host community, and a high functional diversity of natural enemies (e.g., solitary parasitoids, gregarious parasitoids, kleptoparasites), an element of diversity that is very important for ecosystem functioning (Diaz and Cabido 2001) and emergent effects of multiple consumers (Sih et al. 1998). The parasitoid species in our study all required host resources for development, and although there were (very few) instances when more than one species of parasitoid attacked a host nest, parasitoids could not survive only by consuming other parasitoids unless the latter had already consumed a host. Therefore, the extent of intraguild predation that may lead to reduced predation in diverse consumer guilds (e.g., between spider species; Finke and Denno 2004) did not occur in our system (only 10 instances of hyperparasitism were recorded out of a total of 5328 parasitism events).

The effect of parasitoid diversity on parasitism rates of individual hosts was generally positive, but somewhat idiosyncratic, with significant relationships observed for only two out of the six most abundant host species. Further studies of individual hosts, using greater replication may serve to elucidate whether the diversity–parasitism relationship is driven by multiple parasitoids using different hosts, increased attack rates on individual host species, or both.

We also emphasize the importance of examining diversity–function relationships at the spatiotemporal scales at which interactions take place (Cardinale et al. 2004). Pooling long-term data on species richness neglects the importance of temporal turnover in species, such that all of the species recorded in a site over a year may not necessarily have the opportunity to interact with each other. This is especially important if there is a high temporal turnover in species, as is shown by the difference between the total and per-month species

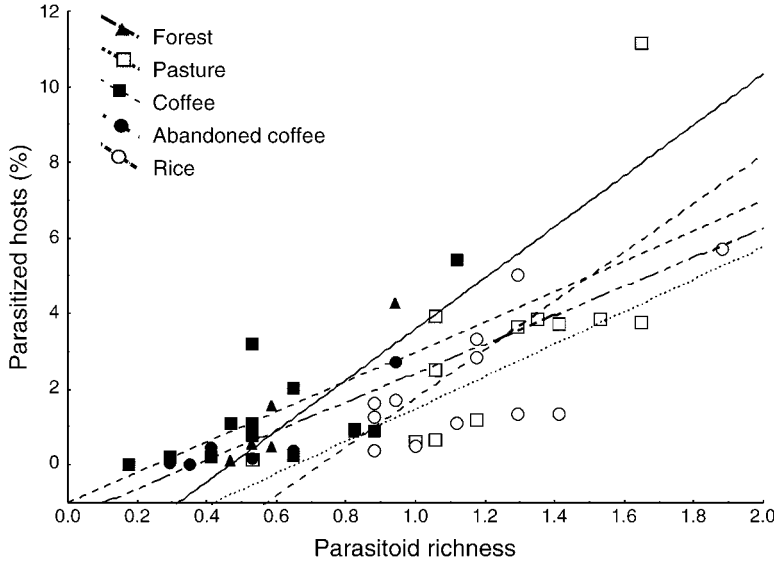

FIG. 2. Mean percentage of host individuals parasitized vs. mean species richness of parasitoids per month for each plot. Habitat types are shown separately; however, the diversity–parasitism relationship did not significantly differ between types (Table 2A).

richness in Fig. 1 (see also Tylianakis et al. 2005). The effect of parasitoid diversity on parasitism rates and stability was much stronger when measured each month, than when diversity and parasitism rates were pooled over the entire sampling period, as in previous studies (Rodriguez and Hawkins 2000). Therefore caution is required when examining large-scale patterns based on small-scale processes, as diversity, parasitism, and stability may all vary with the spatiotemporal scale examined.

A recent meta-analysis of consumer–resource experiments found that consumer effects tended to decrease as diversity of the prey assemblage increases (Hillebrand and Cardinale 2004), in accordance with the negative

TABLE 2. General linear models testing the effects of habitat type and host and parasitoid (A) diversity (mean species richness per month), (B) abundance (mean number of individuals per month), and (C) Simpson's diversity index, and interactions on rates of parasitism (mean per month).

Model and predictor variable	df	SS	MS	*F*	*P*
Model A, diversity–parasitism					
Parasitoid diversity	1	0.008908	0.01	44.03	<0.00001
Host diversity	1	0.001308	0.00	6.46	0.015
Habitat type	...	...	...	...	...
Habitat × parasitoid diversity	...	...	...	...	...
Habitat × host diversity	...	...	...	...	...
Error	45	0.009104	0.00		
Overall model	2	0.011847	0.01	29.28	<0.00001
Model B, abundance–parasitism					
Parasitoid abundance	1	0.00853	0.01	31.58	<0.00001
Host abundance	...	...	...	...	...
Habitat type	...	...	...	...	...
Habitat × parasitoid abundance	...	...	...	...	...
Habitat × host abundance	...	...	...	...	...
Error	46	0.01242	0.00		
Overall model	1	0.00853	0.009	31.58	<0.00001
Model C, Simpson's diversity–parasitism					
Parasitoid Simpson	...	...	...	...	...
Host Simpson	...	...	...	...	...
Habitat type	...	...	...	...	...
Habitat × parasitoid Simpson	4	0.00867	0.00	7.59	0.0001
Habitat × host Simpson	...	...	...	...	...
Error	43	0.01228	0.00		
Overall model	4	0.00867	0.00	7.59	0.0001

Note: Ellipses indicate nonsignificant variables removed from the model during backward stepwise elimination (Bonferroni corrected $\alpha = 0.0166$).

TABLE 3. Repeated-measures ANOVA to determine variation in parasitism rates across time (17 sampling dates), habitat types, and interaction of the two.

Predictor variable	df	SS	MS	*F*	*P*
Habitat type	4	0.79	0.20	1.21	0.330
Error	27	4.38	0.16		
Time	16	5.62	0.35	3.44	0.000009
Time × habitat type	64	11.64	0.18	1.78	0.0005
Error	432	44.16	0.10		

effect of food web complexity on parasitism shown by Montoya et al. (2003). Our results support this pattern; however, whether the potential mechanisms proposed for this effect (increased possibility of selecting unpalatable species, or positive prey interactions), operated in our particular system is unclear. Although host richness had a negative direct effect on parasitism rates in our cavity-nesting communities, host diversity appeared to provide a varied niche base, supporting a higher diversity of parasitoids, which in turn correlated with increased parasitism rates. Therefore, there may be positive indirect effects of host diversity on rates of parasitism.

Diversity–stability

Species diversity has been shown to increase stability in plant biomass production (Worm and Duffy 2003, Caldeira et al. 2005) and crop pollination (Klein et al. 2003, Kremen and Ostfeld 2005), two important ecosystem services. In simplified aquatic systems, diversity has been shown to enhance community-level food-web stability (Steiner et al. 2005); however, a previous field study of a parasitoid–host system found no influence of parasitoid diversity on temporal stability in rates of parasitism (Rodriguez and Hawkins 2000). Here we used a diverse host and parasitoid community to examine parasitism rates, and found that parasitism rates varied significantly across time. We found that temporal variability in parasitism was lower when average parasitoid diversity was high, but increased with high temporal variability in host and parasitoid diversity. High overall pooled diversity (as measured by Rodriguez and Hawkins 2000) was not associated with reduced variability in rates of parasitism. Rather, overall stability in parasitism increased with constantly high diversity in each month. High spatiotemporal species turnover (beta diversity) has been shown previously to lead to higher overall diversity in unmanaged habitat types in our study system (Tylianakis et al. 2005). However, high total pooled diversity that results from high temporal turnover in species did not increase stability in parasitism rates. The relationship between parasitoid diversity and stability was logarithmic, such that increasing parasitoid diversity gave diminishing returns in terms of stability in

TABLE 4. General linear models testing effects on temporal variability (log CV) in parasitism rates. (A) Mean host and natural log of parasitoid diversity (mean species richness per month), (B) total host and parasitoid diversity (pooled over entire sampling period), and (C) temporal variability (CV) in host and parasitoid diversity.

Model and variable	df	SS	MS	*F*	*P*
Model A, variability in parasitism					
Log parasitoid diversity (mean)	1	3.20	3.20	154.16	<0.00001
Host diversity (mean)	...	...	...	...	...
Habitat type	...	...	...	...	...
Habitat × log parasitoid diversity	...	...	...	...	...
Habitat × host diversity	...	...	...	...	...
Error	46	0.9558	0.02		
Overall model	1	3.20	3.20	154.16	<0.00001
Model B, variability in parasitism					
Habitat type	1	2.15	0.54	11.52	<0.0001
Parasitoid diversity (total)	...	...	...	...	...
Host diversity (total)	...	...	...	...	...
Habitat × parasitoid diversity	...	...	...	...	...
Habitat ×host diversity	...	...	...	...	...
Error	43	2.01	0.05		
Overall model	2	2.15	0.54	11.52	<0.0001
Model C, variability in parasitism					
Parasitoid richness CV	1	1.28	1.28	109.00	<0.0001
Host richness CV	1	0.11	0.11	9.15	0.004
Habitat type	...	...	...	...	...
Habitat × parasitoid richness CV	...	...	...	...	...
Habitat × host diversity CV	...	...	...	...	...
Error	45	0.53	0.01		
Overall model	2	3.63	1.82	154.47	<0.0001

Notes: Habitat type was a fixed factor in all models, and interactions between habitat type and covariables were included. Ellipses indicate nonsignificant variables removed from the model during backward stepwise elimination (Bonferroni corrected $\alpha = 0.0166$).

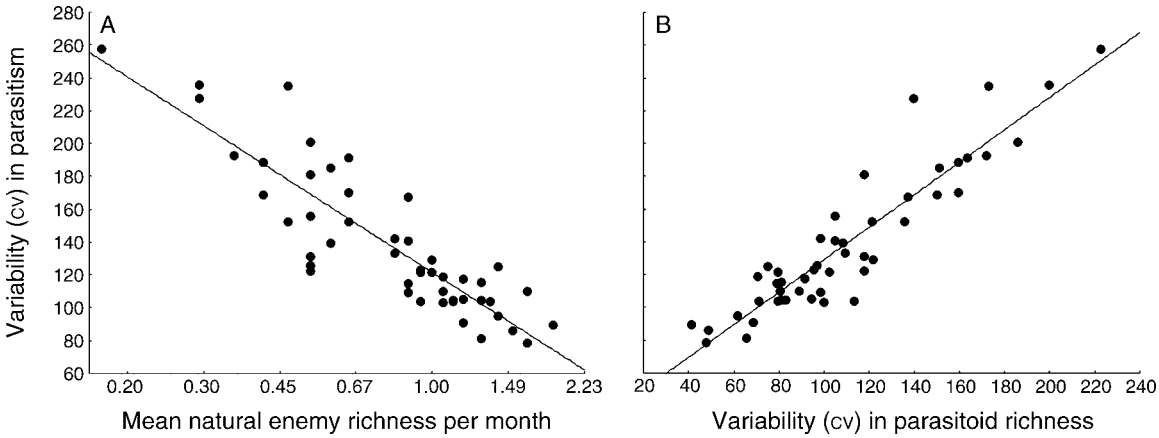

FIG. 3. Variability (coefficient of variation, CV) in parasitism rates between months (A) decreases with natural log of the mean parasitoid diversity per month (backtransformed on log scale), and (B) increases with monthly variation (CV) in parasitoid species richness.

parasitism. This indicates that there may be a threshold diversity necessary to maintain stability in parasitism rates, and that increasing richness beyond this point makes little difference to stability. A similar logarithmic relationship between diversity and stability has also been shown for pollination (Kremen and Ostfeld 2005), and although this may indicate a degree of functional redundancy beyond a threshold of diversity, the longer-term benefits of diversity for ensuring ecosystem services in a changing environment remain uncertain (Yachi and Loreau 1999).

Effects of habitat

Surprisingly, the effects of diversity on parasitism and temporal stability were identifiable over the noise of environmental variation across habitats, which has been predicted to mask local effects of diversity on ecosystem function (Loreau 2000). Habitat type (level of anthropogenic disturbance) did not have a significant effect on parasitism rates. Moreover, the slope of the richness–parasitism relationship did not vary across habitat types, despite predictions from theoretical modeling that this slope should decrease with increasing habitat disturbance (Cardinale et al. 2000). In contrast, the Simpson diversity–parasitism relationship was contingent on habitat type, with a significant positive relationship only occurring in rice and pasture. Additionally, habitat affected diversity of parasitoids and their hosts, which in turn strongly affected parasitism rates, and both of these variables were highest in rice and pasture.

Kremen and Ostfeld (2005) examined the effects of organic vs. conventional farming on stability in pollination services and found no effect of management practice. The proportion of natural habitat in the landscape surrounding the sites was found to significantly affect pollen deposition; however, it is unclear whether this effect was mediated through bee diversity, as bee abundance may have been a confounding factor.

Conclusions

We showed that the positive effects of diversity on parasitism rates and stability were not simply the result of increased abundance of parasitoids being correlated with diversity, but rather an effect of diversity itself. Models using Simpson's diversity (which is relatively insensitive to differences in abundance) and species richness both explained a greater proportion of variance in rates of parasitism than did abundance of individuals, although the effect of Simpson's diversity was mediated by habitat. Diversity itself, and the functions it provides may vary across time and space, and knowledge of the processes affecting diversity across ecosystems is essential for conservation and management (Loreau et al. 2003), and determination of the scales at which studies should be conducted. We recommend the further use of field-based studies to test predictions of models and experimental studies, and urge caution when extrapolating effects across habitats, community types, and multiple spatiotemporal scales.

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APPENDIX A

Map of the study region showing study plots (*Ecological Archives* E087-183-A1).

APPENDIX B

Parasitoid species/morphospecies, mode of attack, hosts parasitized in our study, and the habitat types in which they were found (*Ecological Archives* E087-183-A2).

APPENDIX C

Table for general linear models testing the determinants of host and parasitoid species richness pooled over the entire sampling period (*Ecological Archives* E087-183-A3).

APPENDIX D

Table for general linear models testing the effect of parasitoid diversity pooled over the entire sampling period on rates of parasitism for the six most common host species (*Ecological Archives* E087-183-A4).

APPENDIX E

Graphs showing variation in parasitism rates, parasitoid (natural enemy) species richness and host species richness, and parasitoid (natural enemy) and host abundance per plot through time for each habitat type (*Ecological Archives* E087-183-A5).