REPORT

Diversity, function and stability in parasitoid communities

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Abstract

The parasitoid assemblages associated with grass-feeding chalcid wasps in Great Britain were used to examine the relationships between diversity (species richness), community function (total parasitism rate) and stability (variability in parasitism rate over time). Species-rich communities did not generate higher parasitism rates than species-poor communities, nor was temporal variation of parasitism rates related to parasitoid community richness. The mechanisms underlying hypotheses linking species richness and community function and stability are discussed in the light of these results. Because all parasitoid species represent a single functional group, a lack of complementarity in the ways they use their resources may explain why diversity is not linked to function or community stability. A second likely reason is that these parasitoid communities are under bottom-up control, thus exerting little or no influence on total system function and variability. This is likely to be common in parasitoid communities.

Keywords

Bottom-up, density compensation, diversity-function, diversity-stability, parasitoids, portfolio effect, top-down.

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INTRODUCTION

The nature of the relationship between the species diversity of a community and its stability is a long-standing problem in ecology (see Pimm 1984 for a review, and McCann *et al.* 1998 for a recent theoretical approach). A closely related question is whether or not diversity is also related to ecosystem function (e.g. see the reviews by Huston 1997 and Grime 1998). The answers to both questions remain unresolved, although the field is advancing rapidly. Even so, the arguments are based either on data and experiments from the first trophic level (McNaughton 1977; Frank & McNaughton 1991; Rodríguez & Gómez-Sal 1994; Tilman & Downing 1994; Tilman 1996; Hooper & Vitousek 1997; Tilman *et al.* 1997; Wardle *et al.* 1997; Symstad *et al.* 1998), or from studies of model webs in which stability and/or function are integrated across all trophic levels (Naeem *et al.* 1994; Naeem & Li 1997). Although the final answer will depend on an understanding of complete ecosystems, there is value in studying how diversity within specific trophic levels contributes to total community function. In this paper we examine the relationships between diversity (species richness), stabi-

lity and function using a group of communities representative of a major component of terrestrial ecosystems, namely communities of insect parasitoids.

The importance of parasitoids is widely recognized, as is their functional role as major mortality sources for herbivorous insects and as agents in the biological control of pests. On the other hand, whether or not the species richness of parasitoid complexes bears any relationship with the levels of host mortality they inflict or with the stability of their communities is not well studied. Hawkins & Gagné (1989) and Hawkins & Gross (1992) found that parasitoid species richness and total parasitism rates were positively associated across many host species, but Hawkins (1994) subsequently found the association was not causally linked and concluded that in the majority of parasitoid-host communities, one or perhaps a few parasitoid species were driving the dynamics of the system, and additional species present contributed little.

Here we use a comparative approach to further address several aspects of function and stability in parasitoid communities. We ask two general questions. First, is the species richness of parasitoid communities related to the levels of mortality they inflict on their host populations, i.e. is diversity related to function? Second, what

relationship, if any, exists between the diversity of a parasitoid community and its stability? The data we use to address these questions comprise the parasitoid communities associated with *Tetramesa* spp. (Hymenoptera: Eurytomidae) in Great Britain. These data represent the highest quality parasitoid community data collected from multiple host species currently available and are appropriate for investigating the relationships between the diversity of the third trophic level and variability in function and stability.

METHODS

The data

The data represent parasitoid–host associations generated by H. A. Dawah over a 12-year period. Sixteen grass-feeding *Tetramesa* spp. were sampled in up to 24 sites in England, Wales and Scotland from 1980 to 1992 (see Dawah *et al.* 1995) by cutting at ground level all grass stems in 1–7 m^2 plots and dissecting them in the laboratory. All insect larvae encountered were subsequently reared to adulthood and identified. The complete data set is based on the dissection of ≈ 165 000 grass stems, in which ≈ 65 000 feeding relationships were observed. However, not all sites were sampled all years. So we selected a subset of the data comprising 13 host species sampled in 14 sites at least 70 km apart in the period 1981–83, 1985 and 1989 (nonsequential years were selected to maximize the number of host species sampled, and there is no reason, even in principle, why samples must be sequential). Because multiple host-parasitoid communities occurred at some sites, the data set includes a total of 30 local parasitoid assemblages. For statistical purposes we considered local assemblages co-occurring at sites as being independent, as all are dominated by monophagous parasitoid species, and hence there is minimal interaction among them.

The questions

We treat community function and stability as closely related concepts. The first question we ask is, is the number of parasitoid species in a community related to overall "function", which means the levels of host mortality all species induce (i.e. total parasitism rate)? To answer this we first correlate the number of parasitoid species in each sample and parasitism rates in that sample to determine if there is a relationship at the local community level. We then test for a relationship across whole systems by examining the total number of parasitoid species each host species supports

and system-wide parasitism rates pooled (we use arithmetic means) over all sites and years. A lack of a relationship at both levels indicates that diversity and function are not related.

The second question is, is diversity related to the stability of the parasitoid communities? That is, are parasitism rates more or less variable in more diverse communities? Because measuring parasitism rates is equivalent to estimating both host mortality levels and total parasitoid abundance, the relationship between diversity and community stability is also equivalent to testing the relationship between diversity and variability in function. The aspect of stability we examine is temporal variation in total parasitism rate (aggregate variability, *sensu* Micheli *et al.* 1999). We consider parasitoid communities exhibiting high temporal variability to be less stable than those showing less variability. Aggregate variability was measured as the coefficient of variation in total parasitism rates in each community across the 5 years for which we have data. The relationship between aggregate variability and species richness was tested using correlation. To better understand the underlying causes of a relationship between diversity and stability, or the lack thereof, we also examined patterns of covariance among the parasitoid species comprising each community, using Schluter's (1984) variance ratio (V). This statistic measures species associations as the ratio of the variance in total parasitism rates (equivalent to total parasitoid relative abundance) and the sum of the variances of parasitism rates by individual species (equivalent to relative abundances of each parasitoid species), and tests the null hypothesis that species abundances do not covary among samples. The ratio makes no assumptions about the biological causes of covariation (see Schluter 1984). We calculated net covariances for each parasitoid community consisting of more than one species ($n = 27$), and then tested them against parasitoid species richness and variability in parasitism rate using Spearman rank correlation.

RESULTS

Diversity and function

Local parasitoid species richness varied between 1 and 8 (Mean = 4.00, SD = 1.94, Mode = 4), although 87% of the 30 local communities had 3–8 species. The species richness of the parasitoid communities was not associated with total parasitism rates, either when all local communities were considered separately ($r = 0.047$, $P = 0.807$, Fig. 1a), or when independent *Tetramesa* systems were compared ($r = -0.021$, $P = 0.947$, Fig. 1b). Thus, there was no relationship between the diversity of the parasitoid complexes and the level of their "function".
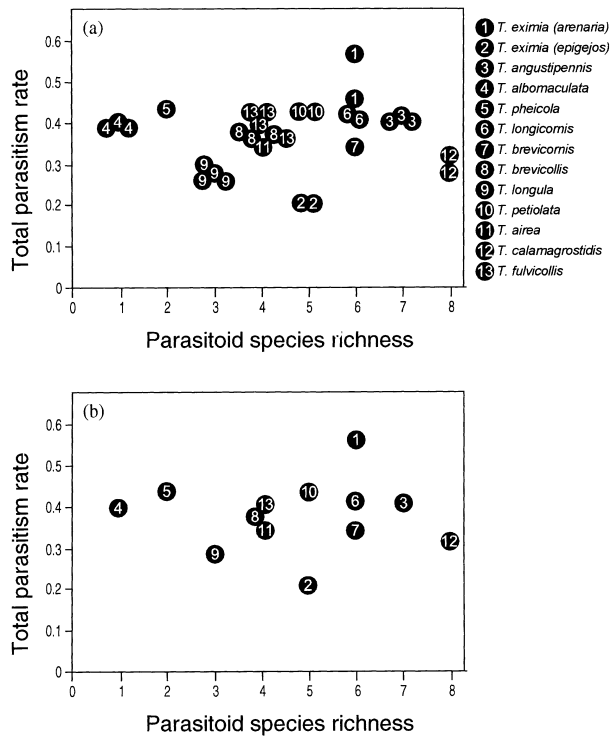
Figure 1 Relationships between the species richness of parasitoid communities and the total parasitism rate they inflict on host populations. (a) Data for 30 local communities, each pooled over 5 years. (b) System-wide data for each of 13 *Tetramesa* species (sites and years pooled). The identities of the host species are indicated along side of part (a) (see Dawah *et al.* 1995 for additional information). Some data points have been displaced slightly along the *x*-axis for clarity.

Diversity and stability

There was also no relationship between aggregate variability (variability in total parasitism rates) and parasitoid species richness ($r = 0.146$, $P = 0.442$, Fig. 2). Even so, aggregate variability increased as net covariance became more positive ($r_s = -0.577$, $t = 3.54$, $P < 0.002$, Fig. 3a), and net covariance became more positive as parasitoid species richness increased ($r_s = 0.397$, $t = 2.16$, $P = 0.040$, Fig. 3b).

DISCUSSION

We found no evidence of a link between parasitoid diversity and their ability to inflict mortality of host populations, suggesting, in these systems at least, that diversity and function are independent. This raises the obvious question as to why the diversity of parasitoid communities might not be linked to this aspect of their function. A positive effect of parasitoid species richness on host mortality is expected if two conditions are met by
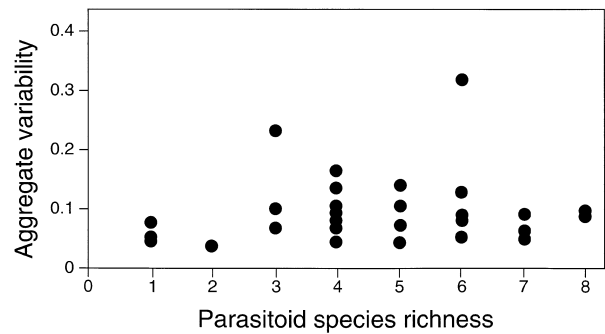

Figure 2 Relationship between parasitoid community richness and aggregate variability (temporal variability in total parasitism rate). See text for statistics.
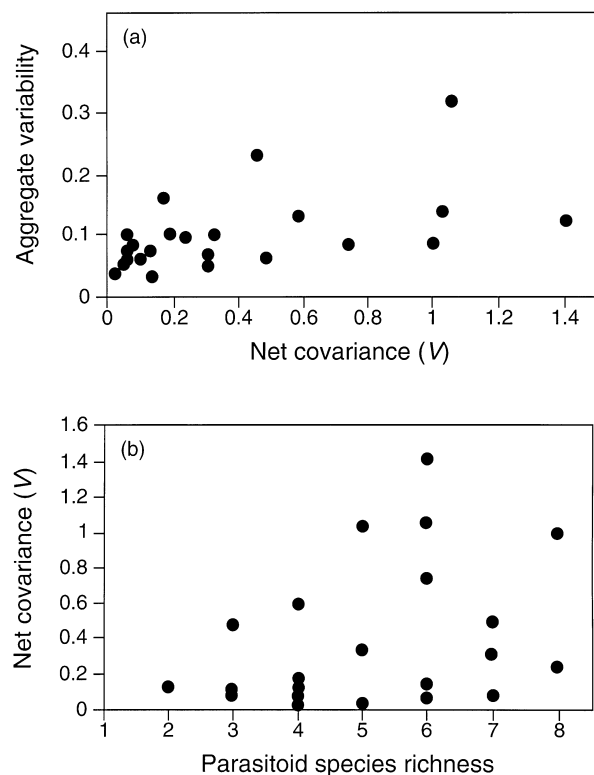

Figure 3 Relationships between (a) aggregate variability (temporal variability in total parasitism rate) and net covariance ratios (V), and (b) net covariance ratios and parasitoid species richness. Ratios < 1 represent net negative covariance and ratios > 1 represent net positive covariance (Schluter 1984).

the parasitoid complexes. First, the parasitoid species have complementary resource use (cf. Hooper & Vitousek 1997). This complementarity could occur in space, for example, because of differences in host-searching capabilities in different habitats in which the host occurs; or in time, for example, because of temporal

segregation across either host stages or host generations. If true, then greater parasitoid species richness potentially allows access to a greater proportion of available hosts, leading to increased total parasitism rates. However, this appears not to be the case in *Tetramesa*-parasitoid communities, because all local communities support every parasitoid species that attacks that host species, and all parasitoids attack similar host stages and at the same time of year (Dawah *et al.* 1995).

The second condition is that the parasitoid assemblages exert top-down control on host populations. If they do not, then any variation due to differences in parasitoid species richness will be trivial and dynamically irrelevant to total system function. It is possible that the *Tetramesa*-parasitoid communities of Great Britain are indeed under bottom-up control, or at least top-down control is not being exerted by the parasitoids on their hosts. Although experimental evidence is needed to quantify levels of top-down control by natural enemies, strong linear relationships between local and regional species richness (Dawah *et al.* 1995) and independent fluctuations in the abundances of most of the parasitoid species (Dawah *et al.* 1995 and see below) both suggest that host densities are not limited by the parasitoids. Furthermore, this may be very common in parasitoid communities centred on endophytic hosts (Hawkins 1992). Whether or not there is a relationship between parasitoid species richness and the level of top-down control of hosts is a contentious area in biological control, but the biological control record suggests that in the majority of cases only a single, key parasitoid species is required for strong top-down control (Myers *et al.* 1989). It has also been suggested that the dynamics of the majority of host-parasitoid systems is driven by one or a few parasitoid species (Hawkins 1994), and many of the additional parasitoids that may be present are opportunists taking advantage of an available resource. If so, then the pattern for *Tetramesa*-parasitoid communities may be widespread, and diversity and function will not be directly linked in many host-parasitoid systems. The notion that one or a few key species are largely responsible for ecosystem function, rather than diversity *per se*, has also been argued for plant communities (Grime 1998).

We also found no relationship between parasitoid species richness and levels of community variability (i.e. stability). To understand this we analysed the logic of two stability hypotheses that can be addressed with our data. The diversity-stability hypothesis relies on complementarity among competing species to establish a link between diversity and stability which is driven by density compensation. This hypothesis states that more diverse ecosystems are more likely to contain species that can thrive during adverse environmental conditions and thus maintain aggregate properties by compensating the losses of abundance experienced by other species (Tilman & Downing 1994; Tilman 1996). Assuming that a footprint of density compensation is net negative covariance, under this hypothesis (i) aggregate variability will decrease as net covariance becomes more negative, (ii) net covariance will become more negative as species richness increases and, consequently, (iii) aggregate variability will decrease with species richness. Although the first pattern was found in our data (see Fig. 3a), the second one did not hold, as net covariance actually became more positive as parasitoid richness increased (see Fig. 3b). Therefore, it is not surprising that aggregate variability was not related with richness (see Fig. 2). In other words, the data suggest that the conditions necessary to establish the causal link between diversity and stability proposed by the hypothesis did not occur in these communities.

The theory of consumer–resource interactions provides an alternative way of viewing the diversity-stability hypothesis. This view emphasizes ecological complexity, which is determined not only by the number of species present in a community, but also by the strength of the species interactions within it. Using a set of nonlinear models, McCann *et al.* (1998) have recently explored and developed this hypothesis. Briefly, it predicts that multi-trophic systems dominated by strong resource–consumer interactions are likely to exhibit strong fluctuations in species abundances and therefore are more prone to lose species. Conversely, those systems comprising many weak links between species should be more stable. Weak links seem to act by inhibiting oscillations between consumers and resources, thus maintaining population densities away from zero and decreasing the probability that populations will become extinct. In general, it is expected that weak interactions become more frequent as species richness increases and, consequently, that species-rich communities are more stable than species-poor ones. However, as mentioned above, it is likely that the *Tetramesa*-parasitoid communities are under bottom-up control, which means that strong per-capita parasitoid–host interactions are probably not present. If true, increasing the number of species (and weak links) should not have any noticeable effect on stability. This is what we observed.

The second hypothesis we investigated, the "portfolio effect", relies on a different linking mechanism between species richness and aggregate variability (Doak *et al.* 1998). This hypothesis states that random fluctuations in the abundances of individual species may be as or more important than species interactions (such as those leading to density compensation) in creating diversity-stability relationships. That is to say, the hypothesis assumes that aggregate variability will decrease with increasing species richness, even if density compensation (i.e. net negative

covariance) is independent of species richness. However, since species richness and aggregate variability were not associated in the *Tetramesa*-parasitoid communities, a basic condition necessary for this effect is absent. Furthermore, in these communities positive covariances became predominant as species richness increased. Therefore, if any statistical effects of species richness on variability existed, they were overridden by other effects causing the species in the species-rich communities to exhibit greater positive covariance.

In summary, we are unable to identify a clear functional role of species richness in these parasitoid assemblages. Species-poor assemblages can be just as effective mortality agents as species-rich assemblages, and the number of coexisting parasitoid species has no effect on temporal variation in community structure. Of course we cannot be sure just how representative *Tetramesa*-parasitoid communities are. We have no reason to believe that they are fundamentally different from other parasitoid communities centred on endophytic hosts, but until other parasitoid-host systems are analysed, we cannot be sure. One thing to bear in mind is that, effectively, all parasitoid species represent a single functional group. Much of the debate about diversity and ecosystem function is based on the potential importance of the number of functional groups in a system rather than the number of species (Lawton & Brown 1993; Naeem & Li 1997). If this is true, then there may not be enough variation among parasitoid species to matter to function or stability. Even so, we do not conclude from this analysis that parasitoid diversity is unimportant in nature; only that diversity and function need not be associated in all communities at all trophic levels.

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BIOSKETCH

Miguel Á. Rodríguez's main interests include the study of factors and processes conditioning biodiversity at local, regional and global scales, and the detection of evolutionary effects of global warming on organisms, particularly *Drosophila*.