Ecological Specialization and Susceptibility to Disturbance: Conjectures and Refutations

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ABSTRACT: Niche breadth of species has been hypothesized to be associated with species' responses to disturbance. Disturbance is usually believed to affect specialists negatively, while generalists are believed to benefit from disturbance; we call this the "specialization-disturbance" hypothesis. We also propose an associated hypothesis (the "specialization-asymmetry-disturbance" hypothesis) under which both specialization and asymmetry of interactions would explain species' responses to disturbance. We test these hypotheses using data from a plant-pollinator system that has been grazed by cattle (i.e., a biological disturbance) in southern Argentina. We quantified specialization in species interactions, specialization of interaction partners, and species' responses to disturbance. We found no relationship between degree of specialization and a species' response to disturbance. We also found that plant-pollinator interactions tend to be asymmetric in this system; there was no relationship between the degree of specialization of a given species and the degree of specialization of its interaction partners. However, asymmetry of interactions did not explain the variability in species' responses to disturbance. Thus, both hypotheses are rejected by our data. Possible reasons include failure to assess crucial resources, substantial direct effects of disturbance, inaccurate measures of specialization, difficulty detecting highly nonlinear relationships, and limitations of a nonexperimental approach. Or, in fact, there may be no relationship between specialization and response to disturbance.

Keywords: asymmetric interactions, cattle, disturbance, generalization, grazing, mutualism, plant-pollinator interactions, specialization, temperate forests of the southern Andes.

In fact, specialization is arguably the most fundamental concept in the history of thought on extinction risk. (M. L. McKinney 1997, p. 500)

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Understanding what factors are important for species persistence when ecosystems are subject to change is of paramount importance for ecology. Why are some species negatively affected by disturbance, while others respond positively or are not affected at all? Can any ecological characteristics of species help to predict how they will respond to disturbance?

One possible answer to the above questions is that the niche breadth of a species is related to its response to disturbance. It is usually believed that specialists are negatively affected by disturbance, while generalists benefit from it (e.g., Preston 1962; Baker 1965; Wilson and Willis 1975; Parrish and Bazzaz 1979; McKinney 1997; Hobbs 2000); throughout this article, we will call this the "specialization-disturbance hypothesis." This is what Den Boer (1968) called "spreading the risk." Den Boer hypothesized that species can spread the risk of extinction in at least four different ways: phenotypically, by having high phenotypic variation among individuals; temporally, by having low synchronization of developmental times among individuals; spatially, by using different kinds of habitats; and in terms of the interactions with other species, for example, by being polyphagous as opposed to monophagous. It is this last way of spreading the risk that we analyze here.

Specialization in interspecific interactions has been hypothesized to affect species in several ways. First, populations of specialists might be more temporally variable than generalists, as originally hypothesized by MacArthur (1955). Population variability (one of many possible measures of stability; see Pimm 1984, 1991) is usually believed to be positively correlated with probability of extinction (Pimm et al. 1988; Pimm 1991; but see Tracy and George 1992). However, the evidence for MacArthur's hypothesis has been ambiguous. Redfearn and Pimm (1988) and Morin and Lawler (1996) found niche breadth and population stability to be positively correlated, while Watt (1964, 1965) and Rejmánek and Spitzer (1982) found them to be negatively correlated. All these studies dealt with predation; none of them analyzed specialization in terms

of other kinds of interactions (e.g., mutualism) or other "niche axes."

Second, specialists might have more restricted distributions than generalists (Brown 1984) and thus be at a higher risk of extinction. The probability of extinction of a population is believed to be related to its geographic range, with range-restricted populations being more prone to extinction than wide-ranging populations (e.g., Manne et al. 1999; Chown and Gaston 2000). Thus, specialists could be more prone to extinction than generalists because they tend to have more restricted distributions. However, the study of the relationship between niche breadth and geographic range is methodologically problematic; because geographically widespread and locally abundant species tend to be represented more in samples, a positive correlation between niche breadth and these two variables is expected simply as a by-product of sampling. The few studies that have controlled for this sampling effect have failed to find a positive correlation between niche breadth and geographic range size (Burgman 1989; Kouki and Häyrinen 1991; Gaston et al. 1997).

Regardless of the mechanism, according to the specialization-disturbance hypothesis, specialists should be more vulnerable to disturbance than generalists. Below we point out some conceptual problems with the specialization-disturbance hypothesis and propose an alternative hypothesis. To our knowledge, there have been only two attempted tests of this hypothesis, which we also briefly discuss below. Finally, we test these hypotheses with data from our work on plant-pollinator interactions in the temperate forests of the southern Argentine Andes.

The Hypotheses

The specialization-disturbance (S-D) hypothesis can be described mathematically as

$$A_i = b_0 + b_1 s_i^f, \tag{1}$$

where A_i is an index of abundance change of species i with disturbance with range $A_i = [-1, 1]$ (negative values of A_i mean negative effects of disturbance, while positive values mean positive effects), s_i is the niche breadth of species i (low values of s_i mean narrow niche breadth, i.e., high specialization), f is a constant with range $f = [0, 1]$, and b_0 and b_1 are constants that can take any value. When $f = 1$, A_i is a linear function of s_i; however, when $f < 1$, the relationship is nonlinear. This relationship is shown in figure 1a.

The constant f can be thought of as representing the degree of redundancy of plant-pollinator interactions. When $f = 1$, there is no redundancy, and each new mutualist species adds a little, resulting in a linear relationship

between s_i and A_i. Thus, when $f = 1$, it will always be beneficial to be a generalist when disturbance occurs, and a broad generalist has a substantial advantage over a moderate generalist. However, when $f \ll 1$, plant-pollinator interactions are highly redundant and the relationship between s_i and A_i is strongly nonlinear; then the only strong negative effect of disturbance will be on those species with extremely narrow niches, and having an extremely broad niche will not be much more advantageous than having a moderately broad one.

One implicit assumption of the S-D hypothesis is that disturbance does not affect species directly by increasing their mortality; instead, it affects species indirectly by changing the resource availability, as shown in figure 2a. Therefore, because specialists depend more on specific resources than generalists, they should be on average more likely to be affected by disturbance. However, this assumption may be unrealistic in many cases; disturbance may affect species not only indirectly through their resources but also directly through an effect on mortality, as shown in figure 2b. The relative importance of direct versus indirect effects of disturbance will determine whether a relationship between specialization and disturbance is actually observed. Thus, if disturbance does affect species directly, then a main assumption of the S-D hypothesis will be false, and a true effect of specialization on response to disturbance may be hidden by the direct effect of disturbance on mortality. The importance of the violation of this assumption will depend on the relative importance of the direct effect of disturbance on mortality and the indirect effect through the modification of resource availability.

In the particular case of plant-pollinator mutualisms analyzed here, species are at the same time "focal species" for the analysis (i.e., the species for which specialization and response to disturbance are being studied) and resources for their interaction partners. The S-D hypothesis also assumes that the chain of effects is unidirectional, causing disturbance to affect resources, which in turn affect species; we have just mentioned that disturbance can affect species directly. However, when resources are also focal species, it is likely that there will be a reciprocal effect from species to the resource (fig. 2c); in this case, the flow of effects is no longer unidirectional because species can affect their resources. This means that an effect of disturbance on the resource (e.g., plants) will affect species (pollinators), but this effect on pollinators will also affect plants since pollinators are a resource from the plants' perspective.

This reciprocal effect is expected if the degree of specialization of species is also reciprocal (i.e., if there is a correlation between the degree of specialization of species and their partners so that specialists tend to interact with specialists and generalists tend to interact with generalists).
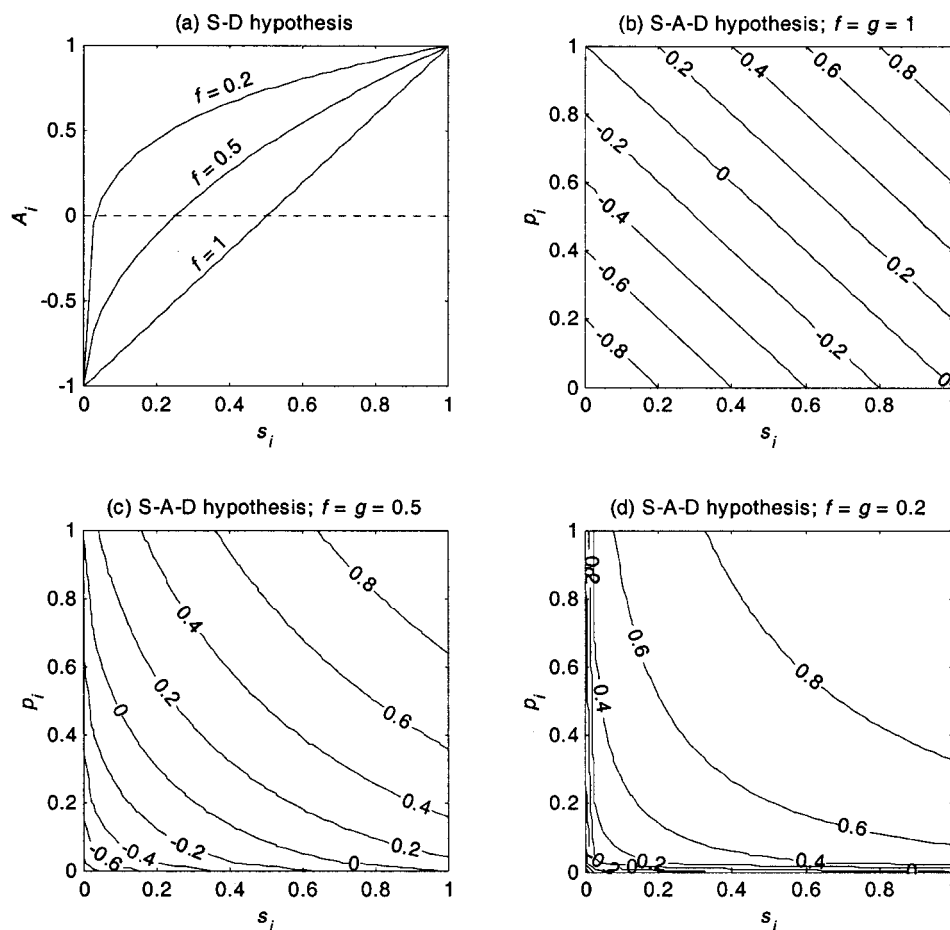
Figure 1: *a*, Specialization-disturbance hypothesis. According to this hypothesis, response to disturbance should go from negative to positive as niche breadth increases, as described by $A_i = b_0 + b_1 s_i^f$, where A_i is some measure of the response of species i to disturbance, s_i is the interaction specialization of species i, f is a constant with range $f = [0, 1]$, and b_0 and b_1 are constants that can take any value (see text for details). *b–d*, Specialization-asymmetry-disturbance hypothesis. Here, for a given species, species response to disturbance is expected to go from negative to positive as both its degree of specialization and some measure of the specialization of its interaction partners increase, as described by $A_i = b_0 + b_1 s_i^f + b_2 p_i^g$, where A_i and s_i are defined as above, p_i is the specialization of interaction partners, b_0, b_1, and b_2 are constants that can take any value, and f and g are constants with range $f = [0, 1]$ and $g = [0, 1]$. Therefore, a decreasing susceptibility to disturbance is expected as one goes away from the lower left corner of the graph. Values for A_i are represented by transverse straight isolines in *b* and by concave isolines in *c* and *d*.

However, reciprocity is not expected if specialization is not symmetrical (i.e., if specialists tend to interact with generalists and vice versa). Thus, a combination of both specialization of a given species and its interaction partners would determine its response to disturbance. We call this new, modified hypothesis the specialization-asymmetry-disturbance (S-A-D) hypothesis. This hypothesis can be described mathematically as

$$A_i = \varphi(s_i, p_i), \qquad (2)$$

where A_i and s_i are defined as above, p_i is degree of specialization of interaction partners, and $\varphi(s_i, p_i)$ is some

function of s_i and p_i. One possible explicit form of equation (2) is an additive model such as

$$A_i = b_0 + b_1 s_i^f + b_2 p_i^g, \qquad (3)$$

where b_0, b_1, and b_2 are constants that can take any value and f and g are constants with range $f = $ range $g = [0, 1]$ (fig. 1*b*–1*d*). As for s_i, low values of p_i mean high specialization of interaction partners. When both f and g are large (i.e., equal to or close to 1; fig. 1*b*), negative values of the response to disturbance A_i are expected when both s_i and p_i are moderately to extremely low, as with the S-D hypothesis (A_i values are represented by transverse
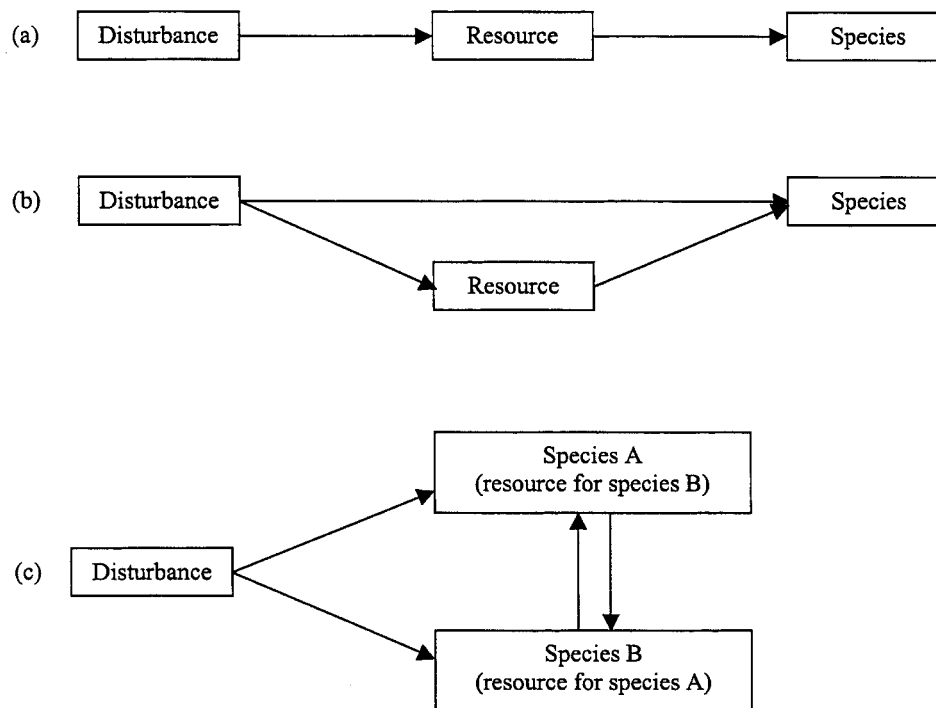
Figure 2: Three possible ways in which species can be affected by disturbance. *a*, According to the specialization-disturbance hypothesis, disturbance affects species only indirectly through their resources. *b*, More realistically, disturbance could affect species not only indirectly through their resources but also directly through an effect on mortality. *c*, When resources are also focal species, it is likely that there will be a reciprocal effect between species and their resources.

straight isolines in fig. 1*b* and by concave isolines in fig. 1*c*, 1*d*); however, even if s_i is relatively large (i.e., species have relatively broad niches), negative values of A_i are still possible so long as p_i is low enough. As f and g decrease, the A_i isolines become increasingly concave. As a result of this concavity, negative values of A_i are clumped in the neighborhood of the figure axes; the lower the values of f and g, the higher the degree of clumpiness of the isolines in the neighborhood of the axes. Clearly, a strongly nonlinear relationship between s_i, p_i, and A_i greatly restricts the range of possible values of s_i and p_i necessary to obtain a negative response to disturbance; only extremely specialized species whose interaction partners are also extremely specialized will be negatively affected by disturbance when this relationship is highly nonlinear.

Previous Tests of the Specialization-Disturbance Hypothesis

Kitahara and Fujii (1994) and Kitahara et al. (2000) tested the S-D hypothesis with data from lepidopteran communities in central Japan. Kitahara and Fujii (1994) studied communities of lepidopteran larvae feeding on plants

in nine sites in three forested areas of varying degrees of human disturbance in or around Tsukuba City; they surveyed lepidopteran larvae along transects in each site to estimate their abundance. Kitahara et al. (2000) censused adult butterflies along transects in five grassland sites of increasing human disturbance on the Asagiri Plateau at the western foot of Mount Fuji. In both cases, using literature reports, they also assigned species to one of two specialization categories (specialist or generalist) according to two different niche axes (time and food). They considered uni- or bivoltine species to be temporal specialists and multivoltine species to be temporal generalists. They considered lepidopteran species whose larvae were known to feed on 10 or fewer plant species belonging to the same family as trophic specialists, and species feeding on >10 plant species of the same family or on plants belonging to different families as trophic generalists. Finally, they considered those species that were both time and food specialists as specialists and those that were both time and food generalists as generalists; they did not analyze the remaining species. In both cases, they found that the number of specialist species increased with decreasing disturbance, while the number of generalist species did not

change significantly. Thus, their results support the specialization-disturbance hypothesis.

A possible problem with the analyses of Kitahara and Fujii (1994) and Kitahara et al. (2001), as with most other analyses of specialization, is how they measured specialization. First, their measure of food specialization seems too coarse; for example, they put in the same specialist category a species feeding on as many as 10 plant species, as long as the plants were in the same family, and a species feeding on only one plant species, while they considered to be generalist a lepidopteran species feeding on just two plant species, as long as the plants belonged to different families. Second, they did not consider relative frequency of use of resources; thus, a lepidopteran species found 95% of the time on a single plant species but with records on two other plant species of different families would be considered a generalist. It would be interesting to see whether their results hold when these conventions are changed.

In this article, we propose a different measure of specialization that we think is more reliable than that of Kitahara and Fujii (1994) and Kitahara et al. (2000). Using this measure, we test whether the degree of specialization in plant-pollinator interactions is related to the response of species to the presence of cattle (a biological disturbance; Huntly 1991). We also develop a simple measure of specialization of interaction partners (p_i, the weighted average of specialization of interaction partners) and use it to test whether the degree of symmetry in interactions can help explain the variability in species' responses to disturbance.

Methods

Study Area and Sites

The study was conducted in Nahuel Huapi National Park and surrounding areas in Río Negro, Argentina. This park lies in the eastern range of the temperate forests of the southern Andes, limited by the Patagonian steppe in the east; it encompasses a striking gradient of decreasing humidity from west to east (Dimitri 1962; Cabrera and Willink 1973). These temperate forests are known for their high incidence of plant-animal mutualisms (Aizen and Ezcurra 1998). For example, in Chile >90% of woody plants have animal-pollination syndromes (Smith-Ramírez and Armesto 1994), and >70% have animal seed-dispersal syndromes (Armesto and Rozzi 1989). Interestingly, although species richness decreases substantially and species composition changes greatly along the humidity gradient from west to east, there is no decrease in the incidence of animal pollination (Aizen and Ezcurra 1998). Because so many plants depend on animal mutualists, disturbance is likely to affect species not only directly but also indirectly through the disruption of plant-animal mutualisms.

Introduced vertebrate herbivores are a main source of anthropogenic alteration of the forests on the Argentinean side of the subantarctic forests. Cattle have been present for about two centuries (see references in Veblen and Alaback 1996). In Nahuel Huapi National Park, cattle are found today in 56% of the total area of the park suitable for cattle (i.e., excluding lakes and mountaintops; Lauría Sorge and Romero 1999). Cattle have important effects on native vegetation and habitat structure (Veblen et al. 1989, 1992; Relva and Veblen 1998).

We have selected four pairs of forested sites for the study, each pair consisting of one site with cattle and one without. Site area ranges between 6 and 12 ha. All sites are dominated by coihue (*Nothofagus dombeyi*) and are usually accompanied by Chilean cypress (*Austrocedrus chilensis*); these two tree species are known to be wind pollinated. In contrast, a number of species in the understory and ground cover are insect pollinated. The four pairs of sites (fig. 3) are (1) Llao Llao (*nc*) and Cerro López (*c*), (2) Safariland (*nc*) and Arroyo Goye (*c*), (3) Lago Mascardi (*nc*) and Lago Mascardi (*c*), and (4) Quetrihué (*nc*) and Quetrihué (*c*) (*nc* = without cattle, *c* = with cattle). The paired sites are contiguous in two sets (i.e., Mascardi and Quetrihué) and are separated by a few kilometers in the other two. We worked with pairs of sites instead of unmatched replicates because of the strong longitudinal gradient in humidity that characterizes the area. It is important that, in order to be comparable, all sites be located at the same longitude; since it was impossible to find a set of sites that met this criterion, a better alternative was to work with paired sites similar in everything except presence of cattle.

Study Organisms

We included all animal-pollinated plants growing in the understory and ground cover that were abundant enough to allow replication; these totaled 15 species, 12 of which had enough visits by pollinators to allow statistical treatment of the data. Plant species are listed in table A1.

Because of the sampling methods, we could not select a priori the insect species to study. Rather, we included all species visiting any of the plant species studied. However, because most pollinator species were too rare to allow statistical analysis of their specialization and abundance (see below), we analyzed only 31 of the 131 recorded species. Most bee and syrphid fly species and all bombilid and nemestrinid fly species were identified to species or genus. Species in other groups were usually identified to family and assigned to "morphospecies" categories. Insect species are listed in table A2. Late in the flowering season
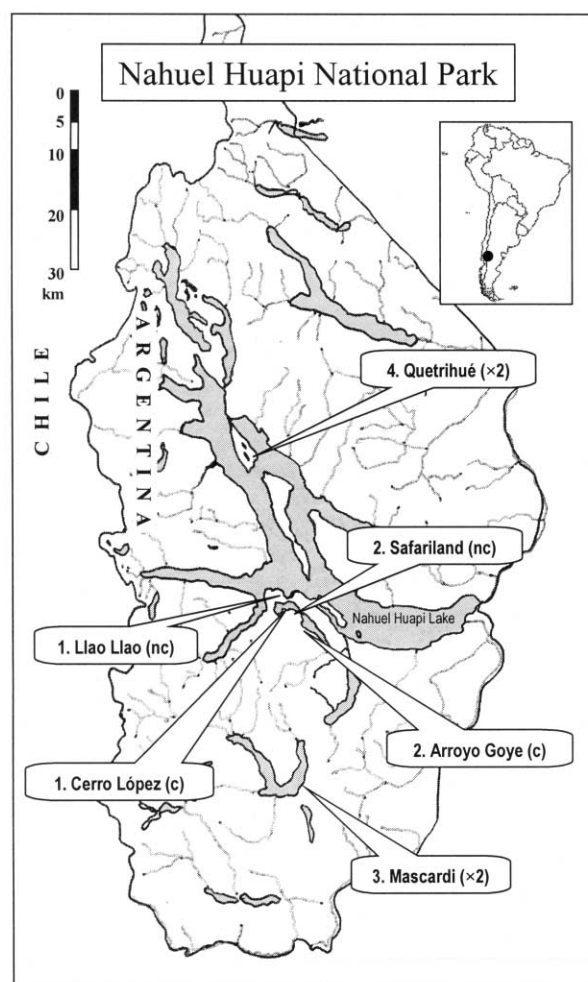
Figure 3: Four pairs of sites selected for the study: (*1*) Llao Llao (*nc*) and Cerro López (*c*), (*2*) Safariland (*nc*) and Arroyo Goye (*c*), (*3*) Lago Mascardi (*nc*) and Lago Mascardi (*c*), and (*4*) Quetrihué (*nc*) and Quetrihué (*c*); *nc* = without cattle, *c* = with cattle. Sites in pairs 1 and 2 were separated by a few kilometers; sites in pairs 3 and 4 were contiguous (indicated as " × 2").

we realized that one syrphid fly morphospecies actually contained two species (see *Allograpta hortensis*, *Toxomerus vertebratus* in table A2). We are confident that the rest of the morphospecies included in this study represent single taxonomic species.

Abundance Estimation

To estimate plant abundance, we examined 30 20-m² rectangular quadrats separated by a fixed distance along transects in each site, and we counted the number of individuals of each species per quadrat. Because the density of understory vegetation was too high to permit walking in some cases (especially in sites without cattle), forest walking paths served as transects in all sites. Transect length varied between ~300 m (Quetrihué [*nc*]) and ~700 m (Llao Llao); therefore, interquadrat distance also varied (~10–23 m). Because we used preexisting forest trails as transects, transect shape also varied among sites, ranging from one single, nearly linear transect to irregular, S-shaped transects.

We took the number of insect individuals visiting any plant species at any time during the flowering season as an estimate of insect-pollinator abundance in each site. Thus, the abundance estimates depend partly on the abundance of the plant species sampled. However, because we sampled virtually all animal-pollinated plants growing in our sites throughout the entire flowering season and sampled with similar effort in paired sites, we believe this is a reliable estimate of abundance. (We also used Malaise

traps to sample the insect fauna. However, for most pollinator species, the catch was too low for statistical analysis.) Pollinators visiting flowers of each species were sampled in 10-min periods. Paired sites were always simultaneously sampled by different observers. A total of 2,710 10-min observation periods were conducted for all sites and plant species. The numbers of sampling periods per site and plant species are given in table 1; these numbers varied across species and sites because species differed in their abundance, duration of flowering period, and flowering time overlap with other species. For each visiting pollinator, we recorded species name, number of flowers visited, and whether it contacted flower reproductive parts (anthers or stigmas). When the pollinator species was unknown, we collected the specimen and identified it in the laboratory. A reference collection from the collected material has been deposited in the Laboratorio Ecotono at the Universidad Nacional del Comahue in Bariloche, Río Negro, Argentina (some bee specimens were also placed in the Museo Argentino de Ciencias Naturales in Buenos Aires).

Fruit Set

Fruit set was calculated as the proportion of flowers that set fruit. We marked individuals of most plant species in all sites where they were present, recording the number of flowers per individual (herbs) or per branch (shrubs, trees, and vines). We then counted the number of fruits produced. Fruit set could not be measured for four species

(*Maytenus chubutensis, Mutisia decurrens, Rosa eglanteria,* and *Digitalis purpurea*).

Response Variables

We evaluated the response of plants to the presence of cattle by comparing species abundance between grazed and ungrazed sites. However, because abundance in plants may take a long time to change, and because the resource we considered is expected to affect abundance only through an effect on reproduction, we also used fruit set as a more direct measure of plants' responses to cattle.

To quantify species' responses to cattle, we developed a normalized index that measures the change of species abundance in response to disturbance:

$$A_i = \frac{1}{n}\left(\sum_{j=1}^{n}\frac{\delta_{ij}^a}{\sigma_{ij}^a}\right), \tag{4}$$

where A_i is the differential abundance index of species i with range $A_i = [-1, 1]$, δ_{ij}^a is the difference in abundance of species i between ungrazed and grazed sites of pair j, σ_{ij}^a is the sum of abundances of species i in ungrazed and grazed sites of pair j, and n is the number of pairs of sites ($n = 4$ in all cases). The absolute value of A_i will be maximized when species' responses across pairs of sites are consistent and of high relative magnitudes (i.e., the δ_{ij}^a values have the same signs and are high relative to the σ_{ij}^a values). An important point here is whether n should always equal 4 (the total number of replicates) or instead

Table 1: Number of 10-min sampling periods performed per site and plant species

Species	LL (nc)	CL (c)	S (nc)	AG (c)	M (nc)	M (c)	Q (nc)	Q (c)	Total
Alstroemeria aurea	147	83	151	129	140	57	103	83	893
Aristotelia chilensis	17	23	34	14	23	11	28	0	150
Berberis buxifolia	0	6	0	3	0	10	0	11	30
Berberis darwinii	10	23	19	24	17	23	1	44	161
Calceolaria crenatiflora	28	12	13	24	11	31	8	49	176
Cynanchum diemii	30	41	51	6	0	0	29	7	164
Digitalis purpurea	0	0	0	0	0	0	0	56	56
Gavilea odoratissima	61	31	26	1	17	18	0	14	168
Maytenus chubutensis	4	0	3	0	13	15	0	0	35
Mutisia decurrens	45	89	29	49	35	16	8	19	290
Rosa eglanteria	0	8	2	3	19	17	1	19	69
Ribes magellanicum	42	7	31	10	11	5	12	2	120
Schinus patagonicus	5	18	10	29	6	23	7	5	103
Tristerix corymbosus	15	0	0	0	0	0	16	0	31
Vicia nigricans	66	35	21	42	21	35	20	24	264
Total	470	376	390	334	313	261	233	333	2,710

Note: Taxonomic affiliations and other species' characteristics are given in the appendices. Paired sites without (*nc*) and with (*c*) cattle are listed contiguously.

equal the number of pairs in which a given species was present; we judged the former to be more appropriate because this convention prevents A_i from being inflated for species found in fewer than four pairs.

Similarly, we defined

$$F_i = \frac{1}{n}\left(\sum_{j=1}^{n} \frac{\delta_{ij}^{f}}{\sigma_{ij}^{f}}\right), \tag{5}$$

where F_i is the differential fruit production index with properties similar to A_i, δ_{ij}^{f} is the difference in mean fruit set of species i between ungrazed and grazed sites of pair j, σ_{ij}^{f} is the sum of mean fruit set of species i in ungrazed and grazed sites of pair j, and n is the number of pairs of sites as defined above.

Specialization

Flower visitors differ widely in terms of their effectiveness as pollinators (Lindsey 1984; Schemske and Horvitz 1984), a fact that must be borne in mind when one assesses specialization. The best way to study pollination effectiveness is through experiments. However, in community-wide studies such as this one involving many species of plants and pollinators, the number of experiments necessary to assess specialization would be prohibitive. We thus estimated pollinator effectiveness differently. Each time a pollinator visited a flower, we recorded whether it touched the anthers or the stigma. We used the proportion of visits in which a particular pollinator species contacted the reproductive parts as an estimate of the pollinator's effectiveness; we then calculated the effective number of visits for plants as $e = pt$, where p is the proportion of visits in which the pollinator contacted the reproductive parts of the flower, t is the total number of visits of the particular pollinator species, and e is the estimated number of effective visits. We used e to calculate plant specialization, but we used t for the calculation of insect specialization (from an insect's perspective, it does not really matter whether the insect is an effective pollinator).

The measurement of niche breadth is analogous to the measurement of species diversity. Two main components have to be taken into account for the quantification of species diversity: species richness (i.e., the number of species) and species evenness (i.e., the relative abundance of species). When measuring niche breadth, we define richness as the number of different resource items used by a given species (e.g., the number of pollinators used by a given plant species, or the number of plants visited by a given pollinator species) and evenness as the relative frequency of use of the different resource types (e.g., the frequency of interaction between plants and pollinators).

A third attribute of niche breadth can be taken into account: the relative abundance of resources. Many measures of species diversity and niche breadth have been proposed (see Gotelli and Graves 1996; Krebs 1998). Two major problems with many of the measures of species diversity and niche breadth is that they are biologically difficult to interpret and they are sensitive to sample size (Gotelli and Graves 1996). One alternative is to use the rarefaction technique. Rarefaction allows the comparison of species richness between samples of different sizes, standardizing by sample size (Gotelli and Graves 1996). Furthermore, the shape of the rarefaction curve reflects the evenness of the sample: for any two samples of equal size and richness but differing in evenness, the value of the rarefaction function is lower for the less even sample throughout the entire function domain (Gotelli and Graves 1996). Thus, it is important to note that, although we used species richness as a measure of specialization, the evenness component of diversity is also accounted for by rarefaction: the rarefied expected richness is a function of both the observed number of species and the observed abundance distribution.

To quantify specialization in species interactions, we defined s_i, the interaction specialization of species i, as the rarefied species richness of its interaction partners. Thus, the richness of pollinators visiting a given plant species served as a measure of plant interaction specialization, and we used the number of plant species visited by a given pollinator species as a measure of insect specialization. We used EcoSim software (Gotelli and Entsminger 2000) to perform the rarefaction calculations.

Of the 15 plants originally included in the study, three had e values too low to be used for rarefaction (*Gavilea odoratissima*, 1; *M. chubutensis*, 0; and *Tristerix corymbosus*, 6); therefore, these plant species were not analyzed. For the remaining species, we used the lowest e recorded (i.e., that corresponding to *Calceolaria crenatiflora*) as the rarefaction sample size; this choice allowed us to compare the expected richness each species would have had if it had received 19 visits. To test whether results depended on the sample size chosen for rarefaction, we also used a rarefaction sample size of 67, which was the e value for *Mutisia decurrens*, the species with the next lowest number of visits after *C. crenatiflora*; we then rerarefied for 11 species only, excluding *C. crenatiflora*.

As mentioned above, of the 131 species of insects in total, most were recorded rarely. We included in the analyses only species that had abundances (i.e., number of individuals recorded visiting flowers) of at least 10; thus, we could include only 31 of the 131 species of flower visitors. As we did for plants, we performed the rarefaction simulations for insects using two different sample sizes, 10 and 20; all 31 species were included when simulations

were run using a sample size of 10, while only 20 species where included with a sample size of 20.

Symmetry of Interactions

We also quantified the degree of interaction symmetry, or reciprocity in the degree of specialization between a species and its interaction partners. To quantify the specialization of interaction partners, we calculated the weighted mean specialization of interaction partners; we used the weighted instead of unweighted mean because species differ in their frequencies of interaction. Therefore, the weighted mean specialization of interaction partners (p_i) is

$$p_i = \frac{1}{n}\left(\sum_{j=1}^{m} s_j v_j\right), \tag{6}$$

where s_j is the specialization of interaction partner species j, v_j is the frequency of interaction between species j and species i ($v_j = e_j$ for plants and $v_j = t_j$ for insects), and $n = \sum v_j$.

As an example of how the p_i index works, we consider a community with four species of plants and four species of pollinators, as shown in figure 4. For simplicity, we assume all pollinators are 100% effective (i.e., $e = t$). Using the frequency of visits of pollinators shown in the graph, we have calculated the expected species richness of interaction partners (s_i) for each species, using a rarefaction sample size of 5; we then used equation (6) to calculate p_i. Thus, for example, plant species E has an s_i of 1, which means it is highly specialized in its pollinator (A); however, its p_i value is 2.61, so its pollinator partner is highly generalized.

Statistical Analyses

We tested the fit of our data to the following five nested models:
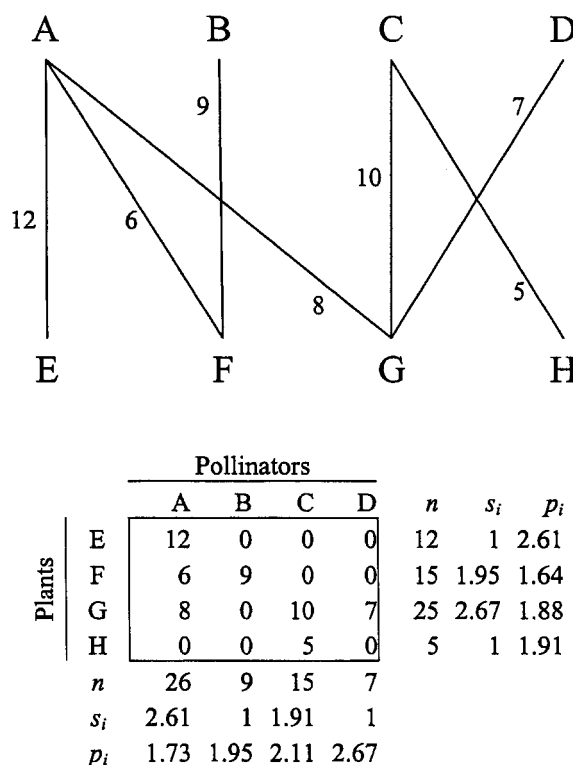
$$\text{Model 1}: A_i = b_0, \tag{7}$$

$$\text{Model 2}: A_i = b_0 + b_1 s_i, \tag{8}$$

$$\text{Model 3}: A_i = b_0 + b_1 s_i^f, \tag{9}$$

$$\text{Model 4}: A_i = b_0 + b_1 s_i + b_2 p_i, \tag{10}$$

$$\text{Model 5}: A_i = b_0 + b_1 s_i^f + b_2 p_i^g. \tag{11}$$

Model 1 (eq. [7]) is the null model of no relationship between A_i, s_i, and p_i, and models 2–5 (eqq. [8]–[11]) are possible forms of this relationship. Because regression analyses of linear models are more straightforward and

Pollinators							
	A	B	C	D	*n*	s_i	p_i
E	12	0	0	0	12	1	2.61
F	6	9	0	0	15	1.95	1.64
G	8	0	10	7	25	2.67	1.88
H	0	0	5	0	5	1	1.91
n	26	9	15	7			
s_i	2.61	1	1.91	1			
p_i	1.73	1.95	2.11	2.67			

Figure 4: Hypothetical community of plants and pollinators illustrating how the specialization of interaction partners (p_i) is calculated. In the example, four pollinator species (*A–D*) visit four plant species (*E–H*) at different frequencies; lines uniting species represent interactions, and numbers beside lines represent frequency of interactions. For simplicity, we assume that all pollinators are 100% efficient (i.e., $e = t$). The s_i values for each species have been calculated using a rarefaction sample size of 5 (see text for explanation).

easier to interpret than equivalent analyses of nonlinear models, we included models 2 and 4 (eqq. [8] and [10]) as special cases of models 3 and 5 (eqq. [9] and [11]), respectively.

To study the fit of our linear models 2 and 4 (eqq. [8], [10]) to the data, we used SAS PROC REG (SAS Institute 1999).

As a more comprehensive confrontation between all models and the data, we used the method of sum of squares (Hilborn and Mangel 1997). We used a computer algorithm written in Matlab (version 5.3, Mathworks) to conduct numerical searches of parameter values within a range of parameters that we judged reasonable. For each combination of parameter values, we calculated the sum of squared deviations between the predicted and the observed values of the dependent variable (A_i); we selected the combination of parameters that minimized the sum of squares as the best fit for the model. However, because increasing

numbers of parameters will tend to decrease the sum of squares, we used a criterion that penalizes the addition of new parameters to compare among models:

$$C = \frac{SSQ}{n - 2m}, \qquad (12)$$

where C is the model selection criterion, SSQ is the sum of squares, n is the sample size (i.e., the number of observations), and m is the number of parameters in the model (Efron and Tibshirani 1993; Hilborn and Mangel 1997; note that this criterion will be meaningful only if $n > 2m$). The model with the lowest C value is judged best. Thus, C rewards increasing sample size and penalizes adding parameters.

Results

Effect of Rarefaction Sample Size on the Estimation of Specialization

The rarefied species richness of interaction partners (i.e., our measure of specialization, s_i) was, as expected, higher for the largest rarefaction sample sizes. However, these values are highly correlated between the two rarefaction sample sizes used (fig. 5). Thus, using different sample sizes for rarefaction should not affect the results, so we used the smallest sample size below.

Symmetry of Interactions

As discussed above, the response of plants and pollinators to disturbance by cattle might be determined not only by specialization (s_i) but also by specialization of interaction partners (p_i; see the S-A-D hypothesis above); this would be particularly true if interactions were not symmetrical, that is, if there were no positive correlation between s_i and p_i.

There is, in fact, no correlation (plants) or a slightly negative correlation (all insects and bees) between s_i and p_i (fig. 7), which indicates a high degree of asymmetry in plant-pollinator interactions in the *Nothofagus dombeyi* forests; specialists do not necessarily interact with specialists, nor generalists with generalists. Furthermore, for insects, there seems to be a slightly negative correlation between s_i and p_i, which means that specialists tend to interact with generalists and generalists with specialists. Finally, for insects, no species combine extremely low values of both s_i and p_i; species with the lowest s_i values have moderate values of p_i, while species with the lowest p_i have only moderate values of s_i. Thus, those species that, ac-
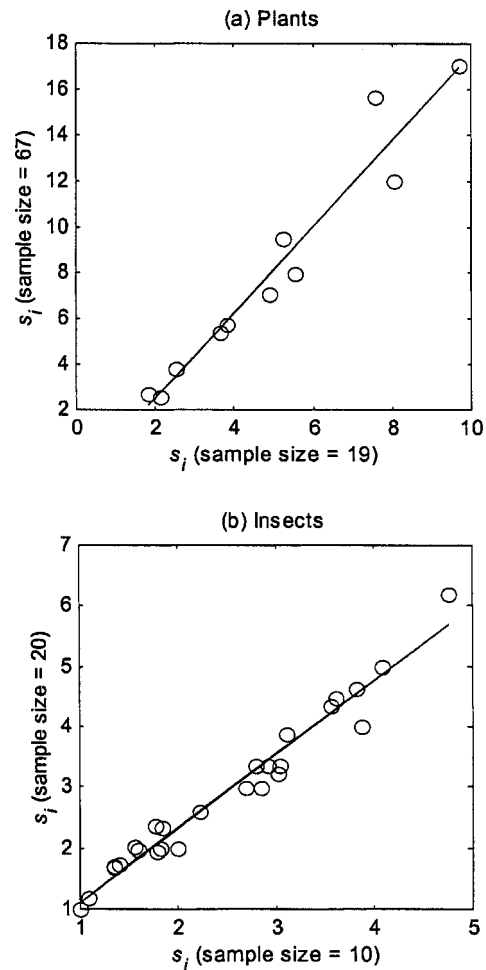

Figure 5: Relationship between s_i values obtained for the two rarefaction sample sizes used. *a*, Plants: $P < .0001$, $r^2 = 0.9418$. *b*, Insects: $P < .0001$, $r^2 = 0.9617$.

cording to the S-A-D hypothesis, should be most affected by disturbance are not represented in our data set.

Testing the Hypotheses

If the S-D hypothesis were correct, model 3 (eq. [9]) or its special case, model 2 (eq. [8]), should provide the best fit to the data; alternatively, if the S-A-D hypothesis were correct, models 4 or 5 (eqq. [10], [11]) should fit the data best. The plots of specialization (s_i) and response to disturbance (A_i; fig. 6) show that there is no relationship between these variables; our data do not follow the S-D hypothesis. Similarly, a plot of s_i, p_i (specialization of interaction partners), and A_i also seems to show that our data do not agree with the S-A-D hypothesis (fig. 7). If
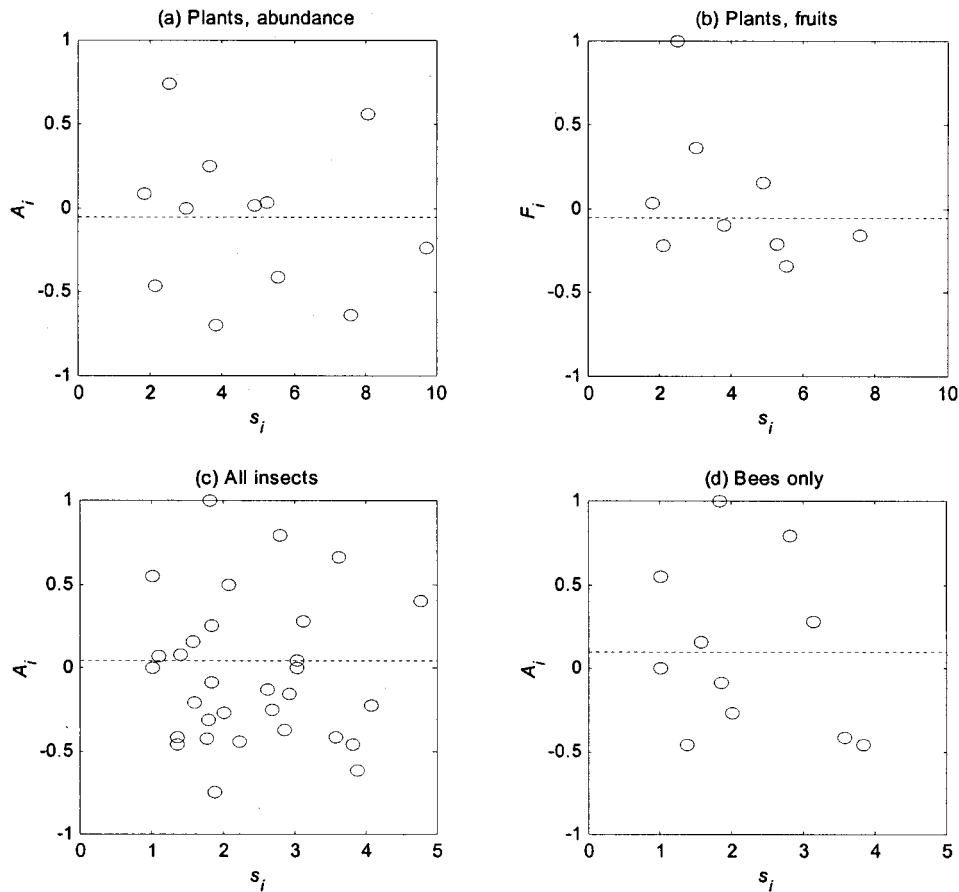
Figure 6: Relationship between abundance index (A_i) and specialization index (s_i); (*a*) plants, abundance; (*b*) plants, fruits; (*c*) all insects; (*d*) bees only. See tables 2 and 3 for statistics. In all cases, the dotted line represents the best fit for model 1 (i.e., the b_0 value that minimized the sum of squares).

this hypothesis were supported by our data, we should see in figure 7 a gradual change from filled diamonds (A_i values close to -1) in the lower left corner of the graph to open diamonds, triangles, or circles (A_i values close to 0), to filled circles (A_i values close to 1) in the upper right corner. However, there seems to be no functional relationship of A_i with s_i and p_i. Furthermore, the results of the linear regressions testing the fit of linear models 2 and 4 (eqq. [8], [10]) are compelling: both models are rejected (table 2); the null hypothesis (model 1; eq. [7]) provides the best fit to the data. These linear regressions formally tell us what we already see in figures 6 and 7: there is no relationship between specialization, specialization of interaction partners, and response to disturbance in our data. This conclusion applies to the two different response variables analyzed for plants (i.e., abundance and fruit set) as well as to insects; even if we consider only bees (which, unlike other pollinators, depend exclusively on flowers as

their food source throughout their entire life cycles; Michener 2000), the pattern is still the same (figs. 6*d*, 7*d*).

However, the above linear analyses do not reject the nonlinear models 3 and 5 (eqq. [9], [11]) described above; that is, we cannot reject the more general forms of the S-D and S-A-D hypotheses. To make the analysis more general, we can refer to the sum of squares method of confrontation described above. The confrontation of the five models using this method gives us the same answer: in all four data sets, the model chosen using *C*, our selection criterion, is model 1 (eq. [7]), the null model (table 3). (Note, however, that for the fruits data set, the selection criterion could not be calculated for model 5 [eq. (11)] because $n < 2m$; nevertheless, model 5 [eq. (11)] had a higher sum of squares than model 4 [eq. (10)], which selects against it.) This result agrees with those obtained in the analysis of the linear models described in the previous paragraph.
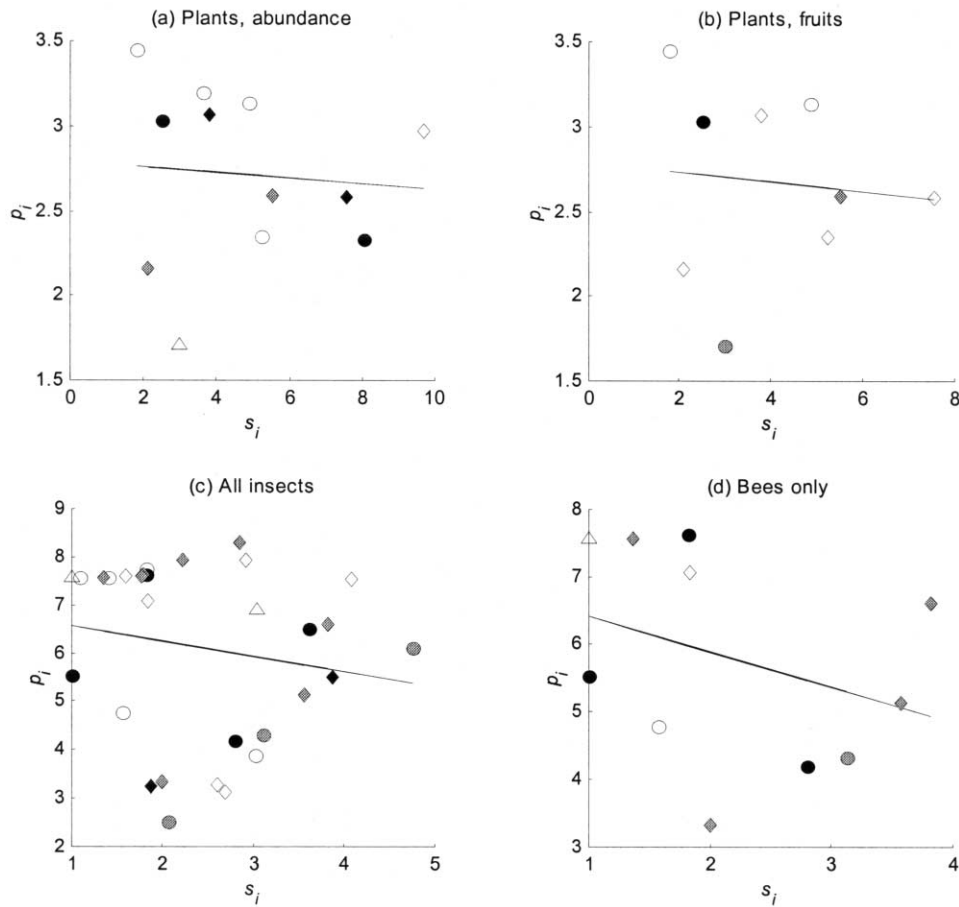
Figure 7: Relationship between specialization index (s_i), specialization of interaction partners index (p_i), and response of species to disturbance (A_i). Symbol shape and shading indicate A_i values; circles represent species that showed a positive response to the presence of cattle (i.e., $A_i > 0$), while diamonds represent species that showed a negative response to the presence of cattle (i.e., $A_i < 0$); species with an A_i value of exactly 0 are represented by triangles; darker colors represent $|A_i|$ values closer to 1, while lighter colors represent $|A_i|$ values closer to 0. Lines are the linear regression curves of p_i versus s_i with the following statistics: plants (*a*) abundance and (*b*) fruits: regression of p_i versus s_i, $P = .8036$, $r = -0.0806$; *c*, all insects: $P = .3525$, $r = -0.1729$; *d*, bees only: $P = .3141$, $r = -0.3348$.

Discussion

Contrary to the specialization-disturbance hypothesis, which is the prevailing view in the ecological and conservation literature, we found no relationship between the degree of specialization of species in plant-pollinator interactions and their response to a biological disturbance (the presence of cattle). This result casts doubt on the generality of the S-D hypothesis.

We also found that, in this system, plant-pollinator interactions tend to be asymmetric (or, at least, they are not symmetric). This is apparently the second time that symmetry of interactions in plant-pollinator systems is quantified (the first time being the study by Petanidou and Ellis 1996). Thus, it is impossible to know how general this pattern is. Nevertheless, it is important to mention two

related pieces of work here: Jordano's (1987) observation that plant-seed disperser systems tend to be highly asymmetric in terms of the dependence of species on this mutualism, and Fonseca and Ganade's (1996) finding of high asymmetry in the dependence of ant-plant mutualists in an Amazonian forest. What Jordano and Fonseca and Ganade call dependence is actually a measure of interaction specialization. They calculate the proportion of all interactions of a given species that involves each of the species' interaction partners, with high proportions meaning high specialization on a given interaction partner and low proportions meaning low specialization. In this respect, their work is more similar to ours than it might seem. In contrast, what they call asymmetry has a somewhat different meaning from ours: they are more interested in a mean

Table 2: Linear regressions using specialization (s_i) and specialization of partners (p_i) as predictors of abundance (A_i) or fruit set (F_i) indices

Taxon/model	n	F	P	R^2
Plants (abundance):				
$A_i = b_0 + b_1 s_i$	12	.19	.6758	.0182
$A_i = b_0 + b_1 s_i + b_2 p_i$	12	.13	.8803	.0279
Plants (fruits):				
$F_i = b_0 + b_1 s_i$	9	1.61	.2448	.1871
$F_i = b_0 + b_1 s_i + b_2 p_i$	9	.75	.5113	.2004
All insects:				
$A_i = b_0 + b_1 s_i$	31	.00	.9988	.0000
$A_i = b_0 + b_1 s_i + b_2 p_i$	31	.25	.7769	.0132
Bees only:				
$A_i = b_0 + b_1 s_i$	11	.56	.4752	.0581
$A_i = b_0 + b_1 s_i + b_2 p_i$	11	.35	.7122	.0813

Note: Regressions were performed using SAS PROC REG (SAS Institute 1999); b_0, b_1, and b_2 are regression parameters.

value of dependence (or specialization), whereas we are interested in the correspondence of the degree of specialization of a given species with that of its interaction partners. Thus, we believe that the findings of Jordano (1987) and Fonseca and Ganade (1996) on symmetry are not comparable to the findings of our work, simply because they have different meanings.

The existence of asymmetry in interaction specialization did not, however, explain the variability in species' responses to disturbance. These results therefore do not support the specialization-asymmetry-disturbance hypothesis; our conjecture was not supported by our data. It is noteworthy that the lower left corner of figure 6 is empty for the insects. Species having a combination of low s_i and p_i (presumably those more likely to be affected by disturbance, according to the specialization-asymmetry-disturbance hypothesis) are lacking.

Faced with these overwhelmingly negative results, we need to ask why specialists are not more affected by disturbance than generalists, which is expected according to the S-D and the S-A-D hypotheses. We briefly discuss several possible explanations.

The resource axes measured are not important ones (*or the most important ones*) *in this case.* The niche axes considered in this analysis were a reproductive resource for plants (i.e., the service of pollinators) and a food resource for pollinators (the rewards obtained in flowers); these resources might not be the key resources for some of our species. For example, Bond (1995) suggested that it is possible that plants compensate for negative effects of pollination specialization by being highly self-compatible or by having a low dependence on pollinators or seeds for reproduction. A similar reasoning could apply to insect pollinators; many species of flower visitors (e.g., flies and

lepidopterans) depend on flowers during only one part of their life cycles (typically the adult phase). However, for bees, for which flowers are indeed a key resource, the pattern (or lack thereof) is still the same. So at least for bees, this explanation is not satisfactory, and we believe that we are considering a crucial resource for them.

Direct versus indirect effect of disturbance. As we discussed above (see fig. 2), disturbance can affect species not only indirectly through the resource but also directly through an impact on mortality rates. It is possible that in our system, direct effects of cattle on mortality were more important than indirect effects transmitted through plant-pollinator interactions. We know that several of our plant species are, to some extent, affected by browsing or trampling; this might in part explain the results obtained for this group. And, although we cannot evaluate this pos-

Table 3: Sum of squares and selection criteria used for confrontation among models

Taxon/model	Model number	m	n	SSQ	C
Plants (abundance):					
$A_i = b_0$	1	1	12	2.2176	**.2218**
$A_i = b_0 + b_1 s_i$	2	2	12	2.1778	.2722
$A_i = b_0 + b_1 s_i^f$	3	3	12	2.1629	.3605
$A_i = b_0 + b_1 s_i + b_2 p_i$	4	3	12	2.1560	.3593
$A_i = b_0 + b_1 s_i^f + b_2 p_i^g$	5	5	12	2.2669	1.1334
Plants (fruits):					
$F_i = b_0$	1	1	9	1.3679	**.1954**
$F_i = b_0 + b_1 s_i$	2	2	9	1.1123	.2225
$F_i = b_0 + b_1 s_i^f$	3	3	9	1.1875	.3958
$F_i = b_0 + b_1 s_i + b_2 p_i$	4	3	9	1.4524	.4841
$F_i = b_0 + b_1 s_i^f + b_2 p_i^g$	5	5	9	1.2592	…
All insects:					
$A_i = b_0$	1	1	41	5.5194	**.1903**
$A_i = b_0 + b_1 s_i$	2	2	41	5.5171	.2043
$A_i = b_0 + b_1 s_i^f$	3	3	41	5.5690	.2228
$A_i = b_0 + b_1 s_i + b_2 p_i$	4	3	41	5.5690	.2228
$A_i = b_0 + b_1 s_i^f + b_2 p_i^g$	5	5	41	5.5614	.2648
Bees only:					
$A_i = b_0$	1	1	11	2.6052	**.2895**
$A_i = b_0 + b_1 s_i$	2	2	11	2.4545	.3506
$A_i = b_0 + b_1 s_i^f$	3	3	11	2.7112	.5422
$A_i = b_0 + b_1 s_i + b_2 p_i$	4	3	11	2.3936	.4787
$A_i = b_0 + b_1 s_i^f + b_2 p_i^g$	5	5	11	2.7110	2.7110

Note: Indices of species abundance (A_i) or fruit set (F_i) were used as response variables, and interaction specialization (s_i) and specialization of interaction partners (p_i) were used as predictors; b_0, b_1, b_2, f, and g are parameters. A computer algorithm written in Matlab (version 5.3, Mathworks) was used to conduct numerical searches of parameter values that minimized the sums of squares. Number of parameters in the model (m), sample size (n), sum of squares (SSQ), and selection criterion (C) are given for each model and data set. Best values of the selection criterion are highlighted in bold type. Ellipses indicate that value cannot be calculated because $n < 2k$.

sibility for insects, the direct effect of disturbance by cattle on mortality could be important. However, our data do not allow us to ascertain the relative importance of direct and indirect effects of cattle.

Specialization was not appropriately measured. It could be that insects used other floral resources (other plant species) flowering outside the study sites, especially those flowering in other forest types not included in the study. This possibility is particularly relevant for species with wide home ranges, such as bumblebees. However, we believe our sites were large enough (typically 6–15 ha) for this problem to be greatly minimized. In any event, our knowledge of the behavioral ecology of the insect species present at our sites is too poor to allow us to evaluate this possibility.

Another caveat in how specialization was measured is that we used only a measure of regional specialization (i.e., using the pooled data for all the sites to quantify specialization). Some species use a wide range of resources over large spatial scales but are relatively specialized locally, while others are both locally and geographically specialized (Fox and Morrow 1981; Hughes 2000). We could not evaluate specialization for each site separately because the rarefaction sample sizes were in most cases too small; thus, our measure of specialization did not discriminate between these different kinds of specialization.

Difficulty of detecting highly nonlinear relationships. Highly nonlinear relationships are usually more difficult to detect than linear ones. First, the number of parameters in nonlinear models is usually higher than that in equivalent linear models (cf. model 2 with model 3 and model 4 with model 5); this higher number of parameters decreases statistical power, as is evident in our selection criterion. Second, in our case, detection of a highly nonlinear relationship (i.e., low values of f and g) depends on the existence of species with very low values of s_i and p_i (e.g., note that all negative values of A_i in fig. 1d are clumped in the neighborhood of the axes). When the species pool is not too large (as in our data set), missing one species will make a big difference. As we pointed out, it is clear from figure 7 that, at least for insects, species with a combination of low s_i and p_i are missing from our data set. Thus, even if there were a relationship between s_i, p_i, and A_i, the absence of species with low s_i and p_i would make detection of this pattern difficult. It might well be that those species were present in the area in the past but were the first ones extirpated by earlier human disturbance in the region. This would mean that, even if the S-D and S-A-D hypotheses were true, the relationship would not be detected because these species were absent. Although this is a possible explanation, we have no way of testing it with our data.

Limitations of nonmanipulative approach. Manipulative experiments are powerful tools that allow direct tests of hypothesized causal relationships between variables. However, manipulation is not feasible in many cases, and other approaches are called for. We chose to take advantage of the preexisting distribution of introduced cattle in our study area. A problem is the possible existence of hidden variables that co-vary with the presence of cattle. For example, natural differences in the precattle vegetation between paired sites could have led to the introduction of cattle in some areas but not others. Although not the most parsimonious explanation, it is possible that these hidden variables could be obscuring real relationships between degree of specialization and response to disturbance.

There is, in fact, no relationship. Since we cannot be sure that the five possible explanations discussed above do not apply in our case, we cannot definitively falsify the S-D hypothesis or its modified version, the S-A-D hypothesis. Furthermore, our test applies only to this particular system, type of specialization, and type of disturbance; thus, it does not universally refute these hypotheses, only invalidates them for this particular case. Therefore, we believe that both hypotheses deserve further attention (and, particularly, further careful, rigorous tests) in other ecological settings before we can discard them.

However, it is possible that such a relationship does not exist, that our hypotheses are indeed false. As Popper (1968, p. 49) put it, "Our propensity to look out for regularities, and to impose laws upon nature, leads to the psychological phenomenon of *dogmatic thinking* or, more generally, dogmatic behavior: we expect regularities everywhere and attempt to find them even where there are none; events which do not yield to these attempts we are inclined to treat as a kind of 'background noise'; and we stick to our expectations even when they are inadequate and we ought to accept defeat." Only careful studies attempting to tease apart the different factors discussed above will let us assess the real importance of ecological specialization for species' response to disturbance.

Acknowledgments

APPENDIX

Table A1: Plant species included in the study

Species	Family	Common name	Life-form	Origin	A_i	F_i	s_i	p_i
Alstroemeria aurea	Alstroemeriaceae	Amancay	Herb	Native	−.64	−.16	7.56	2.58
Aristotelia chilensis	Eleocarpaceae	Maqui	Understory tree	Native	−.46	−.22	2.10	2.16
Berberis buxifolia	Berberidaceae	Calafate	Shrub	Native	.74	1.00	2.50	3.03
Berberis darwinii	Berberidaceae	Michai	Shrub	Native	.01	.15	4.88	3.14
Calceolaria crenatiflora	Scrophulariaceae	Topa-topa	Herb	Native	.00	.36	3.00	1.71
Cynanchum diemii	Asclepiadaceae	…	Vine	Native	−.41	−.34	5.52	2.59
Digitalis purpurea	Scrophulariaceae	Dedalera	Herb	Exotic	.25	…[a]	3.62	3.20
Gavilea odoratissima	Ochidaceae	Orquídea	Herb	Native	.20	.52	…[b]	…[b]
Maytenus chubutensis	Celastraceae	Chaurilla	Shrub	Native	.00	…[a]	…[b]	…[b]
Mutisia decurrens	Asteraceae	Mutisia	Vine	Native	.56	…[a]	8.05	2.33
Ribes magellanicum	Saxifragaceae	Parrilla	Shrub	Native	−.70	−.10	3.80	3.07
Rosa eglanteria	Rosaceae	Rosa mosqueta	Shrub	Exotic	−.24	…[a]	9.71	2.97
Schinus patagonicus	Anacardiaceae	Laura	Understory tree	Native	.03	−.21	5.24	2.35
Tristerix corymbosus	Loranthaceae	Quintral	Parasitic shrub	Native	−.50	−.50	…[b]	…[b]
Vicia nigricans	Leguminosae	Arvejilla	Vine	Native	.08	.03	1.80	3.45

Note: Variables A_i, F_i, s_i, and p_i defined in text.

[a] Fruit set could not be measured for species.

[b] Species did not have enough visits to allow calculation of specialization and were therefore excluded from the analyses.

Table A2: Insect species included in the study

Order/species	Family	Origin	A_i	s_i	p_i
Hymenoptera:					
Heterosarus sp.	Andrenidae	Native (?)	1.00	1.82	7.63
Bombus dahlbomii	Apidae	Native	−.42	3.57	5.13
Bombus ruderatus	Apidae	Exotic	−.09	1.84	7.07
Chalepogenus caeruleus	Apidae	Native	.55	1.00	5.52
Manuelia gayi	Apidae	Native	−.46	1.36	7.56
Manuelia postica	Apidae	Native	−.46	3.82	6.60
Colletes seminitidus	Colletidae	Native	.79	2.80	4.19
Policana albopilosa	Colletidae	Native	−.27	2.00	3.33
Caenohalictus sp. 2	Halictidae	Native (?)	.16	1.57	4.78
Ruizantheda mutabilis	Halictidae	Native	.28	3.12	4.32
Megachile sp. 1	Megachilidae	Native (?)	.00	1.00	7.56
Sp. 052	Braconidae	Native (?)	−.75	1.87	3.26
Sp. 061	Formicidae	Native (?)	−.25	2.69	3.14
Sp. 078	Sphecidae	Native (?)	−.43	1.77	7.59
Sp. 073	Torymidae	Native (?)	−.13	2.61	3.27
Vespula germanica	Vespidae	Exotic	−.23	4.08	7.53
Diptera:					
Phthiria sp. 1	Bombilidae	Native (?)	−.21	1.60	7.61
Phthiria sp. 2	Bombilidae	Native (?)	.08	1.40	7.58
Sapromyza fulvicornis	Lauxaniidae	Native	−.37	2.85	8.31
Trichophthalma amoena	Nemestrinidae	Native	.04	3.03	3.89
Trichophthalma jaffueli	Nemestrinidae	Native	.07	1.09	7.58
Allograpta hortensis, Toxomerus vertebratus	Syrphidae	Native	.66	3.62	6.49
Platycherius (*Carposcalis*) sp.	Syrphidae	Native	.40	4.77	6.11
Syrphus octomaculatus	Syrphidae	Native	.00	3.04	6.89
Sp. 120	Syrphidae	Native (?)	−.16	2.92	7.95
Sp. 109	Tabanidae	Native (?)	.50	2.07	2.52
Sp. 210	Phoridae	Native (?)	−.42	1.36	7.58
Coleoptera:					
Anthaxia sp.	Buprestidae	Native (?)	−.31	1.79	7.62
Sp. 055	Nitidulidae	Native (?)	−.62	3.88	5.49
Sp. 112	Staphylinidae	Native (?)	−.44	2.23	7.95
Sp. 011	Melyridae	Native (?)	.25	1.83	7.74

Note: Variables A_i, s_i, and p_i defined in text. Numbers in the species column indicate the catalog number in the collection deposited in the Ecology Department of the Universidad del Comahue, in Bariloche, Río Negro, Argentina. A question mark in the "Origin" column indicates species that were presumably native but whose origins could not be confirmed because of incomplete identification.

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