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REPORT

Changes in interaction biodiversity induced by an introduced ungulate

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Abstract

Long-term conservation of biodiversity may depend not only on the maintenance of its component parts but also on their interactions. Here we provide strong evidence that an introduced species is able to affect the network of interactions among coexisting species. We studied plant–pollinator interactions in native forest sites with and without domestic cattle and used these data to construct plant–pollinator interaction networks. Results from nonmetric multidimensional scaling and permutation tests suggest that the presence of cattle has significantly modified the structure of the plant–pollinator interaction network. The effect of cattle on network structure was mainly because of the modification of a few highly frequent interactions, which are likely important from a functional perspective. This overwhelming influence of a few interactions on observed community patterns should serve as a caution to those studying community and ecosystem properties.

Keywords

Cattle, interaction biodiversity, introduced species, matrix dissimilarity, network structure, nonmetric multidimensional scaling, plant–pollinator interactions.

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INTRODUCTION

Human-aided species introductions stand out as a major anthropogenic modification of ecological systems (Vitousek *et al.* 1997; Wilcove *et al.* 1998). Many invasions have resulted in great changes in species composition, habitat structure and ecosystem processes (Elton 1958; Simberloff 1991; Williamson 1996; Vitousek *et al.* 1997). There is increasing concern that anthropogenic disturbances in general, and human-aided species introductions in particular, may strongly affect species interactions, including those among plants and pollinators (Sudgen 1985; Buchmann & Nabham 1996; Kearns *et al.* 1998; Kremen *et al.* 2002).

Many studies documenting anthropogenic changes, and most conservation efforts designed to mitigate them, are concerned with maintaining biodiversity at multiple levels of organization, mainly species diversity and genetic diversity of populations (Caughley 1994; Meffe & Carroll 1994; Pickett *et al.* 1997). However, the long-term conservation of biodiversity may depend not only on maintaining the 'parts' that compose such diversity but also on the way these parts are assembled – what Thompson (1997) has termed 'the conservation of interaction biodiversity.' Previous studies of anthropogenic effects on plant–pollinator interactions have considered interactions among subsets of species within a community and the fitness consequences of such interactions, particularly for plants (Sudgen 1985; Aizen & Feinsinger 1994a,b; Kearns *et al.* 1998; Renner 1998; Kremen *et al.* 2002; Vázquez & Simberloff 2002, 2004). However, to our knowledge, no previous study has considered the effect of introduced species on properties of whole networks of interacting species. Here we present results from a field study that strongly suggest that cattle introduced in a native temperate forest of the southern Andes have modified the structure of an interaction network of plants and pollinators.

MATERIALS AND METHODS

Field methods and sites

Data used in this research are from a previously published study (Vázquez & Simberloff 2002), where a full description of field methods is given. We studied plant–pollinator interactions in four grazed and four ungrazed sites in native *Nothofagus dombeyi* forest in and around Nahuel Huapi National Park, Argentina. Grazed and ungrazed sites were paired to minimize effects of environmental variability;

paired sites were chosen to be as similar as possible except for the presence of cattle (see Vázquez & Simberloff 2002). Grazed sites had been subject to moderate levels of grazing by cattle for extended periods (>20 years). Introduced ungulates, particularly cattle, are a main source of anthropogenic alteration of native forests in this region (Veblen *et al.* 1992; Veblen & Alaback 1996; Relva & Veblen 1998; Vázquez 2002b; Vázquez & Simberloff 2004). Of 15 plant species originally included in the study, 14 received visits by presumed pollinators (i.e. flower visitors that contacted floral reproductive parts and thus have the potential to be effective pollinators) and were thus included in the analysis; a total of 90 presumed pollinator species were recorded (see Supplementary Material for list of species and their interactions).

Quantification of plant–pollinator interactions

With the above data we constructed a plant–pollinator interaction network for each of the eight sites (Fig. 1). These networks can also be represented as two-dimensional matrices (see Supplementary Material) in which each column represents a plant and each row a pollinator species, and cells represent the number of times each interaction was observed (Vázquez & Aizen 2003).

We used the proportion of visits in which a particular pollinator species contacted the reproductive parts as a rough estimate of its effectiveness (Vázquez & Simberloff 2002). 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 values corresponding to each combination of plant and pollinator species as entries in the interaction matrix. Interaction matrices were standardized by sampling effort by dividing the entries of each matrix by the number of observation periods in the corresponding site. We conducted all analyses using both the standardized and the unstandardized (raw) matrices. As results with the two data formats were similar, only results for standardized data are reported.

Statistical analyses

Dissimilarity among plant–pollinator interaction matrices was estimated with Kulczynski's and Bray-Curtis' distance coefficients (Legendre & Legendre 1998) between all pairs of matrices. Both distance coefficients are semimetric, and each is an appropriate measure of dissimilarity between data matrices containing species abundances; in both cases, differences between abundant species contribute to the same degree to the coefficient as differences between rare species (Legendre & Legendre 1998).

To check whether extremely frequent interactions had a disproportionate weight in the distance coefficients, we log-transformed the data and then recalculated the distance coefficients. Results were unaffected by the choice of the coefficient or by the use of raw or log-transformed data; therefore, only results for Kulczynski's coefficient calculated on untransformed data are reported. Interaction matrices were sparse, with many cells with zero values. When calculating distances between pairs of matrices double zeros were taken into account, because they are an integral part of the structure of the interaction network that we intended to quantify (i.e. they represent absence of a particular interaction in each of the sites). The resulting pairwise distance matrix was used as input for nonmetric multidimensional scaling (MDS), an ordination technique useful for representing multivariate data in two or three dimensions (Legendre & Legendre 1998). This analysis was performed with the MDS procedure of SAS statistical software (SAS Institute 1999).

A permutation test was conducted to assess statistical significance of the dependence of pairwise site similarities on shared grazing regime and on geographical location, under the null hypothesis that distances between pairs of sites sharing the same grazing regime (i.e. grazed–grazed or ungrazed–ungrazed) and in the same geographical location do not differ from those between pairs of sites with different grazing regime (i.e. grazed–ungrazed) and/or at different geographical locations. The interaction between grazing effect and geographical location could not be tested because there was only one replicate (i.e. site) per combination of grazing regime and geographical location. To conduct this test, we constructed two additional matrices with the same dimensions as those of the similarity matrix: in one, pairs of sites sharing the same grazing regime were represented by ones and pairs of sites with different grazing regimes were represented by zeros, independently of geographical location; in the other, pairs of sites at the same location were represented by ones and pairs of sites at different locations were represented by zeros, independently of grazing regime. We then calculated two statistics, the standardized Mantel statistic (r_M) and Clarke's R (Legendre & Legendre 1998) that measure the independence of entries of one matrix from those of the other. We randomly permuted the elements of one of the matrices and recalculated the statistic 10 000 times, then calculated confidence limits enclosing the least extreme values of the statistics.

As the interaction networks were composed of many rare species with few recorded interactions, and because the presence of such species could have influenced the results, we conducted a new set of MDS and permutation analyses after excluding species with fewer than eight recorded interactions. Such exclusion reduced the total

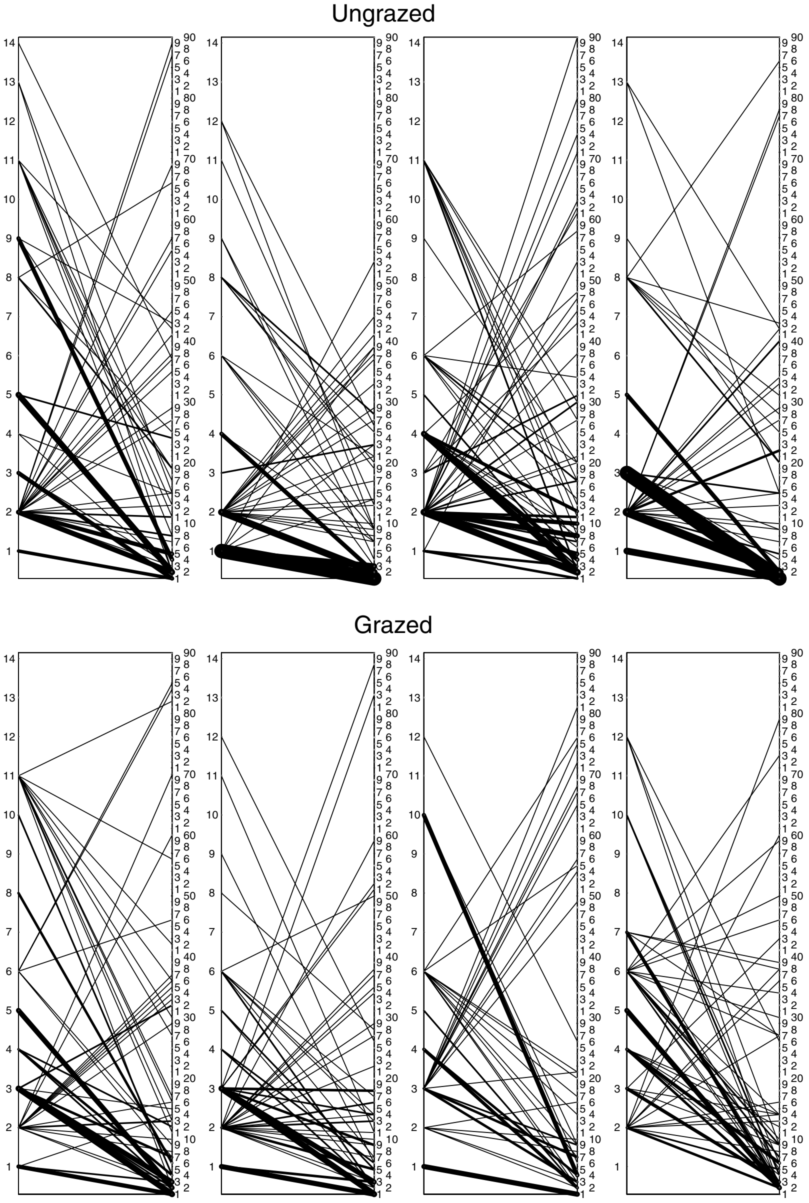

Figure 1 Plant–pollinator interaction networks in the eight sites. In each network, lines indicate pairs of interacting species; end points of lines represent plant (left) and pollinator (right) species. Species identities are indicated by numbers (see Supplementary Material for names; notice that only first digit is given for pollinator species, except for multiples of 10). Line thickness is proportional to the square root of the standardized frequency of interaction between the plant–pollinator species pair. Upper row, ungrazed sites (from left to right: Llao Llao, Safariland, Lago Mascardi, Península Quetrihué); lower row, grazed sites (from left to right: Cerro López, Arroyo Goye, Lago Mascardi, Península Quetrihué). Grazed and ungrazed sites in the same geographical location are vertically aligned.

number of species to 12 plants and 34 pollinators. Results are reported for both the complete and reduced matrices. All permutation tests were performed using an algorithm written in Matlab (MathWorks 1999) (available upon request).

A final test was conducted to assess the influence of specific interactions on the overall significance of the permutation tests. To this end, we removed each of the 1260 cells in each interaction matrix, then calculated the Mantel statistic again for each of the 1260 reduced data sets. Mantel statistics derived from each reduced data set were compared with the randomization confidence intervals described above. The interactions whose removal caused the statistic to become nonsignificant were regarded as highly influential.

RESULTS

Figure 1 shows the plant–pollinator interaction webs for the eight sites. MDS reveals that ungrazed sites are distinctly separated from grazed sites in the two-dimensional space defined by the first two coordinates resulting from this ordination (Fig. 2). These results suggest that the structure of the plant–pollinator interaction network in each site is not independent of the presence of cattle. Furthermore, results of the permutation test strongly suggest that the

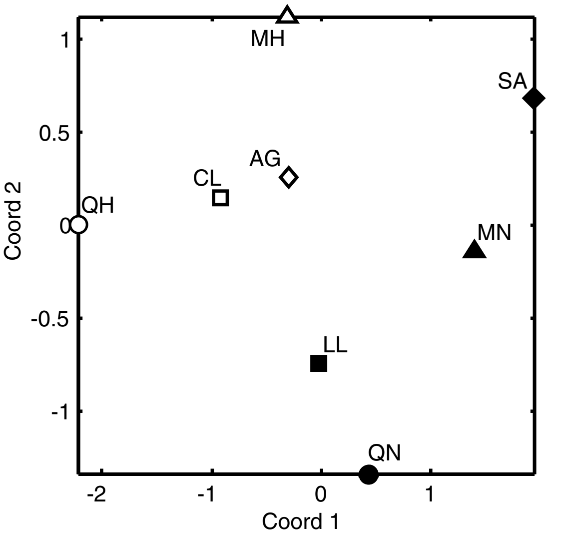

Figure 2 Reduced-space plot of first two coordinates resulting from nonmetric multidimensional scaling (MDS). White symbols: grazed sites (CL, Cerro López; AG, Arroyo Goye; MH, Mascardi; QH, Quetrihué); black symbols: ungrazed sites (LL, Llao Llao; SA, Safariland; MN, Mascardi; QN, Quetrihué). Paired sites are represented by the same symbol. The good fit of the linear regression of the distance among original descriptors (x) vs. those obtained after reduction with MDS (y) suggests that reduced-space scaling is a good representation of the data ($y = 0.2236 + 0.9037x$; $P < 0.0001$; $R^2 = 0.89$; Legendre & Legendre 1998).

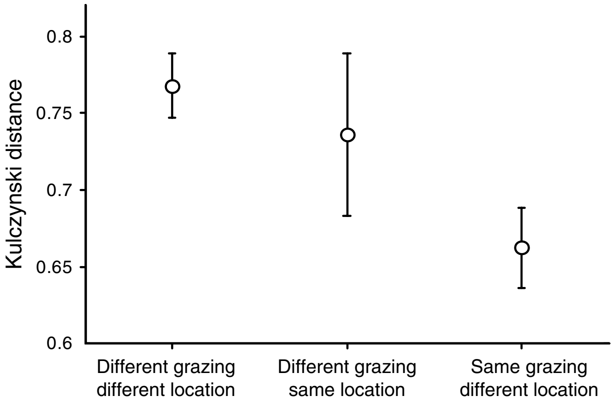

Figure 3 Mean ± SE distances between pairs of sites in three different categories: sites with different grazing regime in different geographical locations (left), sites with different grazing regime within the same geographical location (middle) and sites with the same grazing regime in different geographical locations (right).

association between similarity structure and shared grazing regime is highly significant. The exclusion of species with fewer than eight recorded interactions from the data did not change the results (Table 1).

Is the effect of cattle on intersite similarity strong enough to remove the similarity imposed by geographical proximity? Sites differing in geographical location but sharing the same grazing regime tend to be more similar to each other than sites differing in both grazing regime and geographical location, whereas sites in the same location but with different grazing regime tend to fall somewhere in between. This observation suggests a strong effect of the presence of cattle, but that this effect is attenuated by the similarity imposed by geographical location (Fig. 3). However, a permutation test did not reject the null hypothesis that sites in the same geographical location are not more similar than sites in different locations (Table 1), suggesting that the overall effect of geographical location is weak compared with that of the presence of cattle.

Although the above results suggest the existence of strong effects of cattle on the structure of the plant–pollinator interaction networks of Nahuel Huapi, the analysis is silent about the details of such effects. In particular, we ask whether all pairwise interactions contribute equally to the observed pattern in intersite dissimilarity and, if not, which interactions contribute most. The permutation tests conducted after removal of each of the 1260 cells of the matrix indicate that only a handful of pairwise interactions drive the observed dissimilarity pattern, while the influence of the remaining interactions is minimal (Table 2).

Factor	Interaction matrix	Test	Observed statistic	95% Permutation confidence limits	
Grazing	With rare species	Mantel's r_M	−0.5305	−0.3954	0.3868
		Clarke's R	−0.0212	−0.0158	0.0166
	Without rare species	Mantel's r_M	−0.5275	−0.3909	0.3829
		Clarke's R	−0.0216	−0.0162	0.0162
Location	With rare species	Mantel's r_M	0.0807	−0.4118	0.3670
		Clarke's R	0.0054	−0.0231	0.0224
	Without rare species	Mantel's r_M	0.0819	−0.4169	0.3647
		Clarke's R	0.0062	−0.0231	0.0224

Table 1 Results from permutation tests to evaluate independence of intersite dissimilarities from grazing regime and geographical location. Tests evaluate the null hypotheses that dissimilarities among interaction matrices in each site are independent of grazing regime and geographical location. Confidence limits enclose the 95% less extreme statistics

Table 2 Influence of particular interactions between pairs of species on results of Mantel permutation test. Listed below are pairs of interacting species whose removal caused the Mantel statistic to become non-significant at the 95% (**) or 99% (*) significance level (numbers to the left of species names match those of Fig. 1 and Supplementary Material). The resulting value of Mantel's statistic after removal of the selected interaction (r_M) is also given

Plant species	Pollinator species	r_M
2 *Alstroemeria aurea*	2 *Bombus dahlbomii*	−0.0029**
3 *Schinus patagonicus*	3 *Ruizantheda mutabilis*	−0.4478*
4 *Berberis darwinii*	2 *Bombus dahlbomii*	−0.4848*
9 *Ribes magellanicum*	4 *Trichophthalma amoena*	−0.4918*
2 *Alstroemeria aurea*	8 *Manuelia gayi*	−0.4996*
2 *Alstroemeria aurea*	5 *Bombus ruderatus*	−0.5015*

All influential interactions identified by the above test are among pairs of relatively abundant species whose abundances tend to covary, either negatively or positively, with the presence of cattle (Vázquez & Simberloff 2002, 2004). For example, the herb *Alstroemeria aurea* interacts very frequently with the bumblebee *Bombus dahlbomii* in ungrazed sites, but it does so less frequently in grazed sites, where both species are relatively rare; conversely, the interaction between the understorey tree *Schinus patagonicus* and the halictid bee *Ruizantheda mutabilis* is frequent in grazed sites but virtually absent from ungrazed sites (Fig. 1, Table 2). Thus, the observed effect of cattle on site dissimilarity is brought about by the change in the frequency of a few 'dominant' interactions.

DISCUSSION

The results presented here suggest that the structure of plant–pollinator interaction networks in Nahuel Huapi is strongly affected by the presence of cattle. Our work adds to a growing literature showing that introduced species can, and often do, alter the properties of communities they invade in multiple ways (Simberloff 1991; Williamson 1996; Mooney & Hobbs 2000). Together with recent reports by Vander Zanden *et al.* (1999) and Henneman & Memmott (2001), our study demonstrates the potential of introduced species to modify the structure of entire networks of interacting species. Our study also adds to the long list of documented effects of introduced mammalian herbivores (de Vos *et al.* 1956; Ebenhard 1988; Dennis 1997; Smit *et al.* 2001; Wardle 2001; Vázquez 2002b), thus supporting the notion that introduced consumers in general and herbivores in particular tend to have disproportionately strong impacts on the ecosystems they invade (Duffy 2003).

In a broader context, our results should serve as a caution to those studying community and ecosystem properties and how they change as a result of species invasions and other anthropogenic alterations of ecosystems. Rather than being a consequence of an overall change in the structure of the interaction web, these results are the product of the overwhelming influence of a few frequent interactions among relatively abundant species. Thus, although our multivariate tests suggest strong effects of cattle on an emergent property of plant–pollinator interaction webs, that effect boils down to changes in a few 'dominant' interactions.

Of course, the fact that the above changes in species interactions occur does not mean they are ecologically relevant. Plant–pollinator interactions are known to be, in most cases, highly resilient, and changes of the sort we have documented may have few consequences for the interacting species (Ollerton 1996; Waser *et al.* 1996). Thus, although the demonstration of an effect of an introduced species on the structure of the plant–pollinator interaction network is itself significant, it should be interpreted with caution.

The above caveat notwithstanding, it is likely that the few interactions found to drive the observed patterns in network structure are in fact important for at least one of the two interaction partners involved. For example, in the highly influential interaction between the herb *A. aurea* and the bumblebee *B. dahlbomii* (see Table 2), the bumblebee is in fact the most important pollinator of the herb (Aizen 2001), while the herb is in turn the most important flower resource for the bumblebee during the summer (Vázquez 2002a; Vázquez & Simberloff 2004). A similar situation occurs with other interactions listed in Table 2: they represent the most frequent interactions for the participating species. Although visitation frequency is not necessarily synonymous with interaction strength (Schemske & Horvitz 1984), it seems likely that the few statistically influential interactions are in fact also biologically important for the participating species.

The maintenance of the few dominant interactions may also be important for other species in the system. Some of the species involved in these interactions are extremely generalized, interacting with many rare specialists. Thus, the degree of specialization and of mutual dependence is likely to be highly asymmetric. For example, *B. dahlbomii* and *A. aurea* are the most generalized pollinator and plant species, respectively, in our study system (Morales & Aizen 2002; Vázquez & Simberloff 2002), interacting with a large number of species, many of them rare species that interact almost exclusively with these super-abundant generalists (Fig. 1). Although the vast majority of these interactions may be virtually irrelevant for *B. dahlbomii* and *A. aurea*, they are likely to be important for the rare specialists involved in them. Thus, these dominant interactions potentially represent 'keystone interactions' (in analogy with the keystone species concept; Paine 1969; Power *et al.* 1996), and their persistence may be important for the maintenance of a much larger set of interactions.

Although our analysis has identified clear changes in the interactions among plants and pollinators that are likely the result of the presence of cattle, it does not provide an answer to the more fundamental question of how those changes were brought about. As in most ecological studies, the complex nature of the study system requires the consideration of multiple, non-exclusive mechanisms. Some of the observed changes may be attributed to the change in the population abundance of individual species in response to cattle. For example, the abundances of two of the plant species involved in the influential interactions listed in Table 2, *A. aurea* and *R. magellanicum*, sharply decrease in grazed sites (Vázquez & Simberloff 2004). Thus, the lower frequencies of some of their interactions in grazed sites may simply reflect their increased rarity. However, the abundance of other species is not strongly affected by cattle (Vázquez & Simberloff 2002, 2004), and therefore changes in their interactions probably involve more complex mechanisms, including changes in the relative visitation frequency of pollinators to the different plant species.

We have attempted to characterize the effects of an introduced species on the structure of an entire network of interacting species. We have found strong evidence of such effects and have demonstrated that they mainly result from changes in a few selected interactions. Whether these results are general or just a peculiarity of our study system is an open question; we hope our work will motivate others to seek an answer.

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SUPPLEMENTARY MATERIAL

The following material is available from http://www.blackwellpublishing.com/products/journals/suppmat/ELE/ELE534/ELE534sm.htm

Table S1 Plant species included in the study.
Table S2 Flower visitor species recorded visiting flowers of plants.
Table S3 Pollinator effectiveness matrix.
Tables S4–S11 Plant-pollinator interaction matrices.

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