The impact of an exotic social wasp (*Vespula germanica*) on the native arthropod community of north-west Patagonia, Argentina: an experimental study

PAULA SACKMANN[1], ALEJANDRO FARJI-BRENER[1] and
JUAN CORLEY[2]   [1]Laboratorio Ecotono, INIBIOMA, CRUB-Universidad Nacional del Comahue/CONICET,
Pasaje Gutiérrez 1125, Bariloche, Río Negro, Argentina and [2]Laboratorio de Ecología de Insectos
EEA INTA Bariloche, Río Negro, Argentina

Abstract. 1. Biological invasions are usually thought to have a negative impact on native communities. However, data supporting this idea are often based on comparative studies between invaded and non-invaded areas, and are spatially and temporally limited.

2. The present study experimentally assessed the impact of an exotic wasp, *Vespula germanica*, on the native arthropod community of north-west Patagonia during 3 years in an area of 80 ha. *Vespula germanica* is an exotic social vespid that invaded north-west Patagonia 20 years ago. It has been suggested that its populations affect native arthropods because of its broad diet and also because Patagonia lacks natural enemies and potential competitors for these wasps.

3. Using wasp-specific toxic baits, *V. germanica* abundance was reduced in five sites of native woodlands during 3 consecutive years. The abundance, species richness, and composition of arthropods between non-poisoned (control) and poisoned sites was then compared, both before and after the wasps were poisoned.

4. Wasp abundance represented 6% of the total arthropod catches in non-poisoned sites and was reduced, on average, by 50% in the treated areas. The abundance, species richness, and composition of the arthropod community (305 species, 24 600 individuals) did not differ between control areas and areas where the abundance of *V. germanica* was reduced. Significant differences in response variables were found only before wasp poisoning had begun and were related to variations among sites.

5. These results suggest that *V. germanica* is not affecting the local arthropod assemblages, contradicting past work in other regions. The low relative abundance of wasps in Patagonia, when compared with other invaded regions, might explain the findings.

6. The present study provides further evidence for the importance of large-scale experimental work with before/after comparisons to fully understand the impact of invaders on natural communities.

Key words. Biological invasions, German wasps, impact of exotic species, social wasps, Yellowjackets.

Introduction

Biological invasions are often proposed as one of the leading causes of biodiversity loss (Diamond, 1989; Pimm & Gilpin,

1989; Caughley, 1994). Several studies have linked invasions of predatory species to the local extinction of native species. Well known examples are the introduction of the brown tree snake (*Boiga irregularis*) causing the disappearance of reptiles, birds, and mammals in Guam (Fritts & Rodda, 1998) or the effects of introducing Nile perch (*Lates niloticus*) into Lake Victoria, extirpating several native cichlids (Worthington *et al.*, 1994). Predation may be the major mechanism that affects

communities after an invasion, but competition may also modify the structure of invaded assemblages, as has been shown for invasive ants (Pimm, 1991; Lodge, 1993; Williamson, 1996; Holway, 1998; Vanderwoude *et al.*, 2000; Cook, 2003; Sanders *et al.*, 2003).

Although biological invasions are usually thought to be responsible for diversity loss, data supporting this hypothesis are usually limited, mostly based upon a number of observations and also spatially and temporally limited (see Gurevitch & Padilla, 2004). Of course, obtaining quantitative data on the impact of invasive species is sometimes impossible, but it is equally true that correlation has too often been assumed to imply causation. For instance, the decline of native species and the occurrence of invasions by alien species that co-occur in space and time may not imply a causal relationship as other environmental disturbances (e.g. habitat alteration) might promote both extinction and invasion (Didham *et al.*, 2005). Hence, it has been suggested that ideal studies of the impact of an alien species should incorporate both before/after and control/impact comparisons, bolstered by experimental manipulations (additions and removals of the invader). Also, it would be desirable that the scale of the study should control natural variation in the response variable over space and time (Parker *et al.*, 1999).

Besides methodological issues, the analysis of the impact of biological invasions has been subject to a biased perspective: most work has been carried out on plants and vertebrates, overlooking other groups like insects. This is despite the fact that insects are among the most important invaders known (Simberloff, 1989; Williamson, 1996) and many, such as social insects, especially wasps and ants, are particularly effective invaders (Simberloff, 1990; Moller, 1996).

Despite geographical isolation and rigorous climate, Patagonia is no exception for both the occurrence of invasions and the bias to study plant (Rapoport, 1991, 1993; Richardson *et al.*, 1994; Gobbi *et al.*, 1995) and vertebrate introductions (Christie, 1984; Chehebar & Ramilo, 1992; Veblen *et al.*, 1992; Grigera *et al.*, 1994; Vázquez, 2002; Vázquez & Aragón, 2002). Despite the fact that invasions by Hymenoptera into Patagonia have occurred in recent years (Farji Brener & Corley, 1998), there are so far no systematic data on their potential impact in this region (Willink, 1980; Farji-Brener, 1996; Roig-Alsina & Aizen, 1996; Sackmann *et al.*, 2003).

The German wasp (*Vespula germanica*) is a social vespid native to Eurasia and Northern Africa that has successfully invaded and established in Patagonia, Argentina, as well as among other regions such as New Zealand, Tasmania, Australia, South Africa, USA, Canada, and Chile (Archer, 1998). This species preys on and competes with native insects, having the potential to restructure hosting communities (Beggs, 2001). Experimental work has shown that wasp predation rates on some caterpillars, mealworms, and orb-web spiders are so high that certain species are likely to become locally extinct (Barr *et al.*, 1996; Toft & Rees, 1998; Beggs & Rees, 1999). In addition, wasps can compete with native bird and invertebrate species by heavily feeding on important common food resources (Moller & Tilley, 1989; Moller *et al.*, 1991; Beggs, 2001).

Since its invasion in the early 1980s, *V. germanica* has become a common insect in north-west Patagonia (Farji-Brener &

Corley, 1998; D'Adamo *et al.*, 2002). In this region, *V. germanica* preys on at least nine orders of arthropods, which make up the 80% of its diet (Sackmann *et al.*, 2000). Because of its broad diet, its tolerance to diverse climatic conditions, and the absence of natural enemies, this species has the potential to impact strongly on the native arthropod communities (Farji-Brener & Corley, 1998).

The aim of this study was to assess experimentally whether *V. germanica* impacts on the native arthropod community of north-west Patagonia. This was done by reducing wasp abundance with toxic baits in 80 ha (poisoned sites) during 3 years and comparing the abundance, richness, and species composition of native arthropod communities before and after wasp abundance reduction in those sites and in nearby non-poisoned sites.

Materials and methods

Study area

The study was carried out in the nature reserve *Loma del Medio*, located in El Bolsón, Argentina (41°40′–42°10′S and 71°42′–71°20′W). The area is dominated by mixed forests of *Nothofagus dombeyii* (Fagaceae) and *Austrocedrus chilensis* (Cupresaceae). Mean annual precipitation is 900 mm, but 65% of the rain falls between May and August (autumn–winter). Mean annual temperature is 9 °C. Ten sites were selected within the reserve. In five of those sites, the abundance of *V. germanica* was reduced during 3 consecutive years (poisoned sites) while the others were kept as controls (non-poisoned sites, Fig. 1). Because wasps travel on average 200 m from the nest during foraging (Edwards, 1980), non-poisoned and poisoned sites were separated by at least 1 km (see Sackmann *et al.*, 2001). Because inseminated females may fly more than 1 km to find a site to nest (H. Moller, J. R. Beggs, J. A. V. Tilley, R. J. Toft, N. J. Wilson & P. A. Alspach, unpublished data) and thus re-invade poisoned plots, all treatment plots were poisoned every year (see below). The distance between non-poisoned and poisoned sites within the different groups was 0.4–6.4 km (Fig. 1). This separation is within the range of those reported in previous studies (e.g. Porter & Savignano, 1990; Rykken *et al.*, 1997; Koivula *et al.*, 1999; Eubanks, 2001; Cook, 2003), and can be assumed to provide independent information for ecological analyses (e.g. Moretti *et al.*, 2004). Non-poisoned and poisoned sites were not completely scattered because the effectiveness of toxic baiting in reducing wasp abundance largely increases at larger areas (Sackmann *et al.*, 2001). So, partially grouping the poisoned sites ensures the effectiveness of toxic baiting.

Wasp and arthropod sampling

In order to estimate wasp and arthropod abundance, nine pitfall traps and one malaise trap were placed at each site, during 1 week per month from January to April in 2002, 2003, and 2004. Before and after that period of time wasp abundance is almost zero in the region (Sackmann *et al.*, 2001; and P. Sackmann,
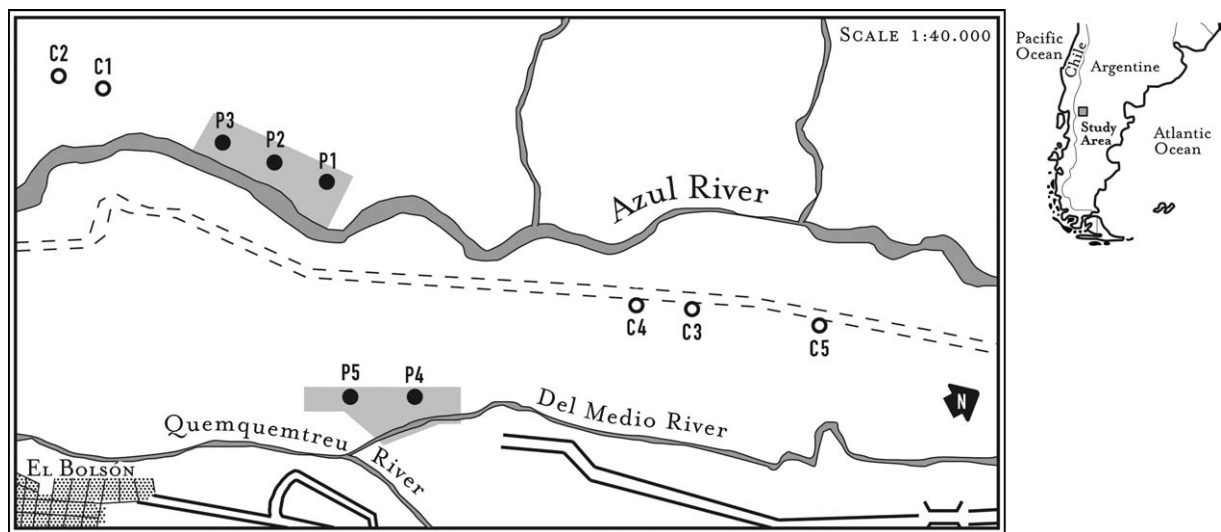
Fig. 1. Study area and relative position of sampling sites (P, poisoned sites; C, control sites). The shaded area corresponds to the surface where toxic baits were placed.

field observations at the study area). To determine wasp abundance, in particular the effectiveness of toxic baiting, additional malaise trap sampling dates were added (February and December 2002, December 2003 and March 2004). Malaise traps were placed in the centre of each site and pitfall traps were spread at an intensity of 9 traps $\times$ 100 m²/site. Pitfall traps were plastic cups (9 cm diameter, 12 cm depth) partly filled with water, ethylene glycol, and detergent. The contents from the nine traps at each site were pooled to one sample. The following taxonomic groups were separated from the malaise traps catches: *V. germanica*, Coleoptera, Lepidoptera, Araneae, Apiformes, and Formicidae, while Coleoptera, Homoptera, Dermaptera, Blattaria, Hemiptera, Araneae, and Formicidae were separated from pitfall catches.

Specimens were firstly identified to family level and, within each family, sorted to species (40%) or morphospecies (60%). The use of morphospecies or recognisable taxonomic units (RTUs) as the basis for the analysis of diversity patterns in hyper-diverse or poorly known invertebrate taxa has been critically evaluated in previous studies. In general, the evidence suggests that careful use of morphospecies allows reliable assessments of insect species diversity (Oliver & Beattie, 1993, 1996a,b; Beattie & Oliver, 1994; Pik *et al.*, 1999; see also Friend & Williams, 1996; Lawton *et al.*, 1998; Anderson & Ashe, 2000; Bolger *et al.*, 2000; Werner & Raffa, 2000). In the present analysis, the identification of species and morphospecies was based on the analysis of morphological characters. Identification keys published by Kusnezov (1953), Peña Guzmán (1987), Borror *et al.* (1992), and Goulet and Huber (1993) were used. All material was sent out to specialists for definitive identification (see Acknowledgements). In the case of Lepidoptera, all captured individuals were counted but were not determined to the species/morphospecies level. Then, only the variation of the total abundance between control and poisoned areas was analysed. Henceforth both species and morphospecies will be referred to as species.

Wasp abundance control

Following Sackmann *et al.* (2001), wasp abundance was reduced using toxic baits in 5 out of 10 sites during 3 years. Toxic baiting was carried out immediately after the February samplings in 2002, 2003, and 2004. In 2002, two samplings were carried out before toxic baiting began, therefore catches from those months allowed before–after treatment comparisons to be made. It was assumed that this pre-poisoning sampling was sufficient to reflect the community history. Toxic baits were prepared the same day of baiting with 0.1% fipronil® mixed with raw minced beef. The bait was placed in feeding stations on an approximately 20×50 m grid that covered 80 ha in total. Feeding stations were made of 500 ml plastic bottles with both ends cut off. This design avoids carrion feeding birds reaching toxic baits. Feeding stations were hung approximately 1.5 m from the ground in trees and shrubs to avoid ground-foraging ants reaching toxic baits. Occasionally flies can reach the baits, however given that flies are solitary foragers and that bait exposure was limited to 10 h, it was assumed that this had a very low impact at the population level within this group.

Data analysis

Wasp and arthropod abundance variation was analysed with repeated measures ANOVA, using wasp abundance reduction as the fixed factor (non-poisoned vs poisoned sites) and time (16 months for *V. germanica* and 12 months for the arthropods) as the repeated measures factor. Because multiple tests were performed on the same data set, the α level was corrected with the Benjamini–Hochberg method (Verhoeven *et al.*, 2005). Fisher LSD test was used for *a posteriori* comparisons.

Because estimates of species richness can be influenced by differences in sample size (e.g. number of beetles captured in each collecting station), expected richness was calculated and

compared by sample-based rarefaction curves (Gotelli & Colwell, 2001). This method re-samples a pool of *N* individuals repeatedly at random (Gotelli & Colwell, 2001). Rarefaction curves were re-scaled to the number of individuals captured (see Gotelli & Colwell, 2001) and different curves were compared (e.g. expected Coleoptera richness in non-poisoned and poisoned sites for year 2003) at the highest value shared among curves (e.g. $n = 325$ to compare expected Coleoptera richness in non-poisoned and poisoned sites). The differences between expected richness in non-poisoned and poisoned sites were compared by eye, which is the usual way of comparing such estimates (e.g. Gotelli & Colwell, 2001). Rarefaction was used to estimate the whole community richness (all groups taken together), and to estimate the richness of Coleoptera, Araneae, and Formicidae in non-poisoned and poisoned sites. Only samples of January and February were used for those calculations because abundance and richness of the different groups was too low in March and April. Therefore, expected richness for 2002 corresponded to the *before wasp abundance reduction* situation. Calculations were made using ESTIMATES 6.1 (Colwell, 2000). Additionally, to do a more complete analysis and to include all groups (e.g. those with low abundance and/or species richness), we analysed whether the difference between the mean observed richness in non-poisoned and poisoned sites changed in the 12 months of sampling (e.g. if the difference between non-poisoned and poisoned sites increased with time). Spearman rank correlations were performed for the above-mentioned groups and for Apiformes, Hemiptera, and Orthoptera.

The analyses on species composition changes was performed for the whole community, Coleoptera, Araneae, and Formicidae, however only results for the community are completely reported since the results for the other groups were much alike. For Coleoptera, Araneae, and Formicidae we only report the abundance of discriminating species in control and poisoned sites, and the corresponding repeated measures ANOVA results (see below). Multivariate community analyses were undertaken using PRIMER v.5.0 (Clarke & Gorley, 2001). To display the relationships between different sites (both poisoned and control sites) non-metric multidimensional scaling (MDS) with the Bray–Curtis similarity coefficient was used. The MDS algorithm attempts to place data points in a coordinate system such that the ranked distances are preserved. This method makes no assumptions, so is well suited for non-normal data and does not assume linear relationships among variables. Ordinations were iterated several times from 10 different starting values to ensure that a global optimum was achieved (indicated by no decline in the stress value). To analyse if species composition changed along the years the RELATE procedure of PRIMER was used. This procedure determines if there is any concordance between similarity matrices. Kendall's coefficient of concordance was used to test the agreement between similarity matrices (the same matrices that gave rise to the MDS plots) corresponding to 2002, 2003, and 2004. To reduce the weight of highly abundant species, data were fourth-root transformed. Data collected in January and February 2002 were used, therefore the similarity matrix for 2002 corresponded to the *before wasp abundance reduction* situation. Species were selected that contributed to average dissimilarity between groups (control vs poisoned sites) using the SIMPER procedure of PRIMER. With this procedure discriminating species can be detected. For example, species that contribute much to the dissimilarity between groups (i.e. large average contribution to dissimilarity) but also do so consistently in inter-comparisons of all samples in the two groups (i.e. SD of the contribution to dissimilarity is small). Again, to reduce the weight of highly abundant species, data were fourth-root transformed. For those species or groups (e.g. orders or families depending on the level of determination reached), the variation of their abundance between poisoned and control sites was analysed with repeated measures ANOVA [fixed factor: wasp poisoned (control vs treatment) and repeated measure
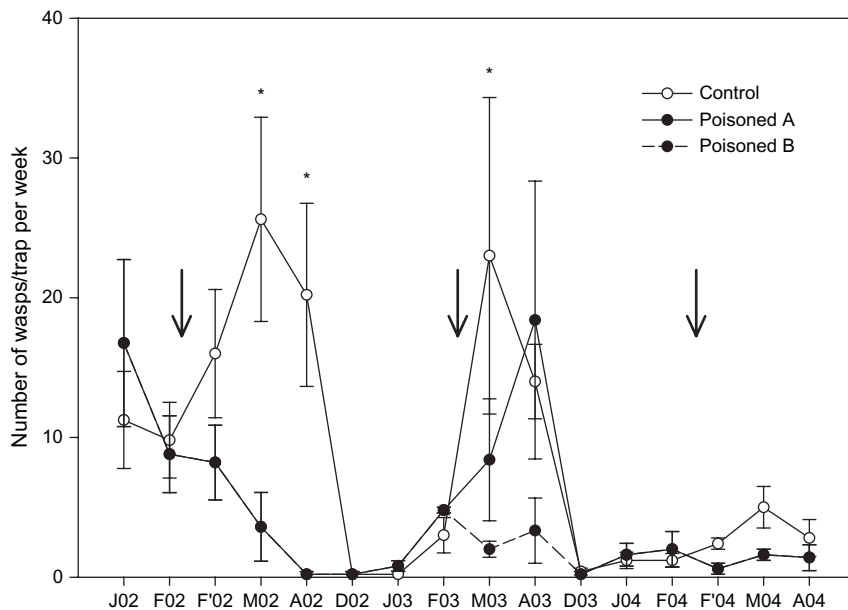

Fig. 2. *Vespula germanica* abundance during the 3 years of sampling. Poisoned A: complete data and Poisoned B: data for sites P4 and P5 were excluded after March 2003. Arrows show toxic baiting events, asterisks indicate significant differences ($P < 0.05$). Means $\pm$ 1 SE are shown. J, January; F, February; M, March; A, April; D, December.

factor: time (12 months)]. Once more, the Benjamini–Hochberg method was applied to correct the α level.

Results

Control of Vespula germanica *abundance*

The abundance of *V. germanica* was significantly reduced in the poisoned sites ($F_{(1,6)} = 7.81$, $P = 0.03$; Fig. 2). On average, the reduction in malaise trap catches at poisoned sites throughout the 3 years was 44.6%. The variation of wasp abundance during the 3 years also differed between poisoned and control sites ($F_{(15,90)} = 3.87$, $P < 0.001$, Fig. 2). Wasp abundance was the same in poisoned and control sites before toxic baiting began (January 2002: $P = 0.5$ and February 2002: $P = 0.6$, Fig. 2). During the sampling period of 2002, wasp abundance was reduced by 80% in the poisoned sites compared with control plots. After placing the toxic baits (March and April), wasp abundance was significantly higher in control than in poisoned sites (for both months: $P = 0.01$).

During 2003, toxic baiting effectiveness was low in two out of five poisoned sites (P4 and P5, Fig. 1), with an average wasp reduction of 30% (Fig. 2). If P4 and P5 sites are excluded from calculations, the level of reduction reaches 85% and the overall (average for the 3 years of sampling) reduction in poisoned sites reaches 54% (Fig. 2, compare poisoned A and poisoned B). Notwithstanding this, if all sites are considered, wasp abundance was higher in control than in poisoned sites during March ($P = 0.03$, Fig. 2). Because the low effectiveness of poison baiting in two sites, all following analyses (e.g. differences in arthropod communities between poisoned and control sites) were performed both including and excluding P4 and P5 sites. However because no differences arose between analyses (P4 and P5 included and not included) only results for the complete data set are reported.

In summer 2004, wasp abundance was naturally low in the study area. Wasp reduction in the poisoned sites reached 56%

but wasp abundance did not differ between poisoned and control sites during the wasp flight season ($P > 0.26$, Fig. 2).

Impact of Vespula germanica *on the arthropod community*

After 3 years sampling, a total of 24 643 individuals belonging to 305 species/morphospecies were captured (Table 1). The observed richness represented between 86 and 96% of the expected richness for the study area (Sackmann, 2006). *Vespula germanica* was the third most abundant species in control sites along the 3 years of sampling (670 individuals captured) after two ant species (*Lasiophanes picinus*: 1837 individuals and *Pogonomyrmex angustus*: 830 individuals). However, wasp abundance represented only 5.9% of the total arthropod abundance. In poisoned sites, wasp abundance dropped to 2.3% (370 individuals) of the total. The most abundant species at poisoned sites were *Lasiophanes picinus* (3260 individuals) and *Mimodromites nigrotestaceus* (Carabidae, 2069 individuals).

Abundance variation between poisoned and control sites

The abundance of the arthropod community (all groups considered together) and its variation during the 3 years of sampling did not differ between sites where *V. germanica* abundance was reduced and control sites (Table 1, Fig. 3). Likewise, the abundance and its variation of the Coleoptera, Formicidae, Araneae, Apiformes, Lepidoptera, Hemiptera, Homoptera, and Orthoptera were similar between poisoned and control sites (Table 1, Fig. 3 for Coleoptera, Formicidae, Araneae, and Lepidoptera).

Before wasp abundance reduction, Blattaria and Dermaptera were, respectively, 98.6% ($P = 0.03$) and 86.8% ($P = 0.02$) more abundant in poisoned than in control sites. Throughout the study, these groups were always more abundant in poisoned

Table 1. Mean (SD) abundance of analysed groups in control and poisoned sites and results of the repeated measures ANOVA [fixed factor: wasps abundance reduction (poisoned vs control sites) and repeated measure factor: time (12 months)]. Significant *P*-values are given in bold [critical *P*-values for ANOVA were calculated using the Benjamini–Hochberg method (Verhoeven *et al.*, 2005)]. The number of species/morphospecies for each group, followed by total number of individuals captured, is given in parentheses after each group name.

Taxon	Treatment $F_{(1,8)}$	P	Time $F_{(11,88)}$	P	Interaction $F_{(11,88)}$	P	Pre-poisoning abundance Control	Poisoned	Post-poisoning abundance† Control	Poisoned
General (305, 24 643)	0.05	0.84	13.09	**<0.001**	1.41	0.18	295.4 (153.3)	462.0 (316.5)	238.5 (160.5)	302.9 (250.9)
Coleoptera (175, 7865)	3.71	0.09	6.79	**<0.001**	2.18	0.02	47.9 (45.1)	157.9 (190.9)	45.5 (47.6)	138.7 (129.2)
Formicidae (14, 7064)	1.31	0.28	5.18	**<0.001**	1.26	0.25	100.4 (86.5)	82.1 (67.3)	82.5 (110.2)	70.2 (96.6)
Araneae (78, 1400)	8.23	0.02	16.86	**<0.001**	0.58	0.84	29.2 (10.9)	12.5 (5.6)	26.2 (14.5)	10.0 (6.4)
Apiformes (16, 202)	5.16	0.05	6.71	**<0.001**	1.72	0.08	2.6 (2.7)	5.25 (5.3)	0.4 (0.6)	2.1 (3.9)
Lepidoptera (*, 4116)	2.97	0.12	8.86	**<0.001**	1.05	0.40	75.0 (59.7)	67.2 (142.0)	63.8 (77.4)	33.5 (26.3)
Blattaria (1, 645)	11.00	0.01	8.76	**<0.001**	3.94	**<0.001**	0.4 (0.9)	28.6 (41.8)	1.6 (3.3)	12.2 (16.4)
Hemiptera (9, 795)	1.71	0.22	11.68	**<0.001**	1.96	0.04	20.0 (26.6)	3.7 (3.8)	16.9 (28.7)	2.8 (5.9)
Homoptera (1, 1047)	15.19	0.004	2.06	**0.03**	0.51	0.88	4.7 (7.1)	5.3 (10.0)	1.4 (1.7)	0.9 (2.0)
Orthoptera (7, 185)	1.56	0.24	4.16	**<0.001**	1.03	0.42	6.4 (8.0)	27.1 (36.3)	7.2 (14.2)	11.1 (17.7)
Dermaptera (3, 1324)	17.14	**0.003**	20.10	**<0.001**	3.70	**<0.001**	8.8 (8.0)	66.5 (41.0)	2.7 (3.9)	21.2 (23.8)

*All the Lepidoptera were considered as one morphospecies.

†Means are for January and February data in order to make comparisons possible with pre-poisoning abundance means.
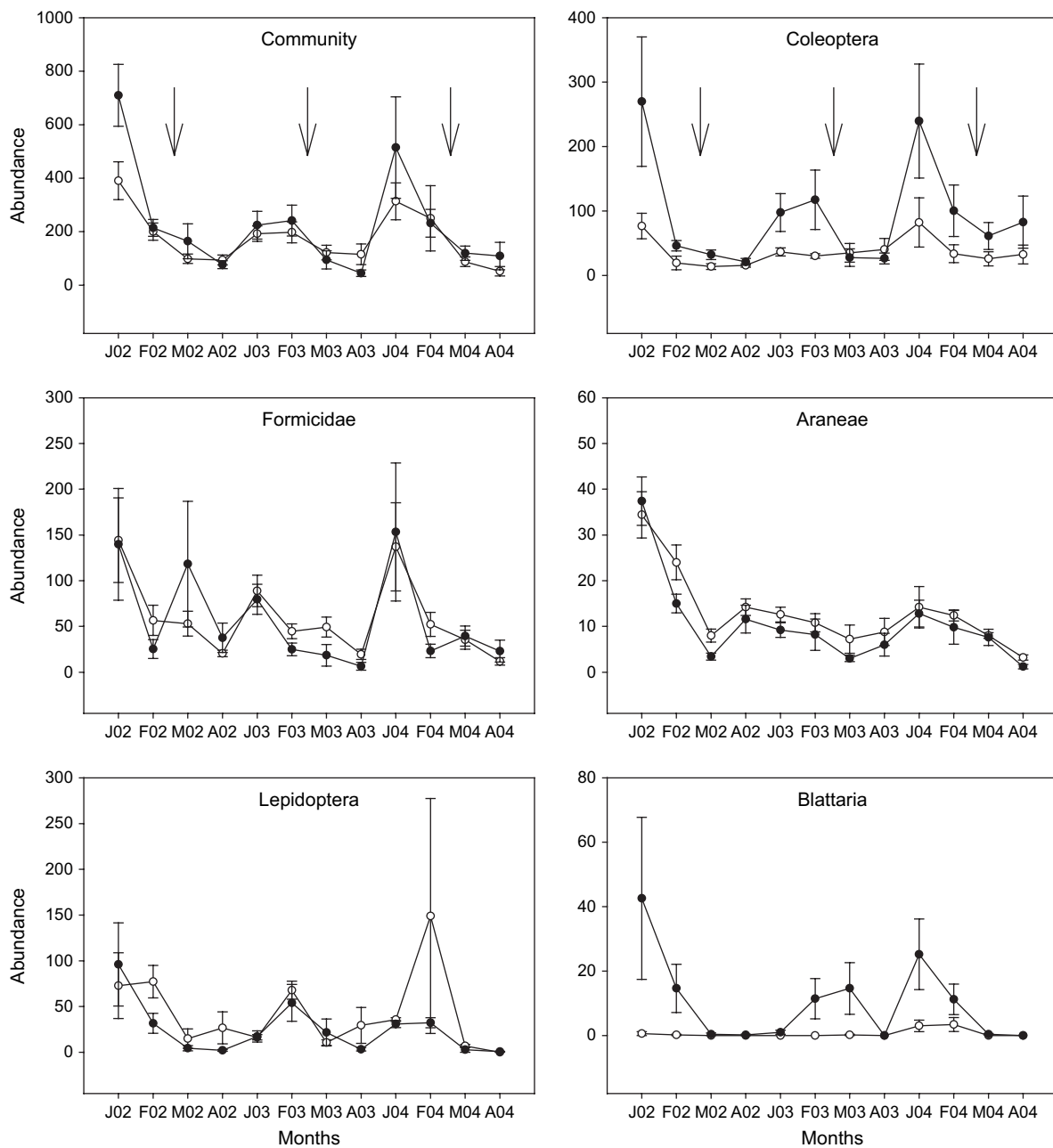
Fig. 3. Abundance variation for the whole arthropod community, Coleoptera, Araneae, Formicidae, Lepidoptera, and Blattaria through the 12 months of sampling. Means ± 1 SE are shown. ●, Poisoned; ○, Control; J, January; F, February; M, March; A, April.

than in control sites. Furthermore the abundance of these groups varied in different ways in control and poisoned sites during the 3 years (Table 1, Fig. 3 for Blattaria as example).

Richness variation between poisoned and control sites

Before toxic baiting, the estimated species richness for the whole community was higher in control than poisoned sites (Fig. 4). Similar results were obtained for some taxa such as Coleoptera and Formicidae. Conversely, estimated species richness for the order Araneae was similar between poisoned and control sites before the wasps were poisoned (Fig. 4).

Species richness for the whole community varied differently between poisoned and control sites throughout the 3 years of sampling (Fig. 4). While estimated species richness remained the same through time in control sites, it was higher in poisoned sites in 2003 than in 2002 and 2004. However, species richness in 2004 was the same as in 2002, indicating that the increase in 2003 was not sustained in time (Fig. 4).
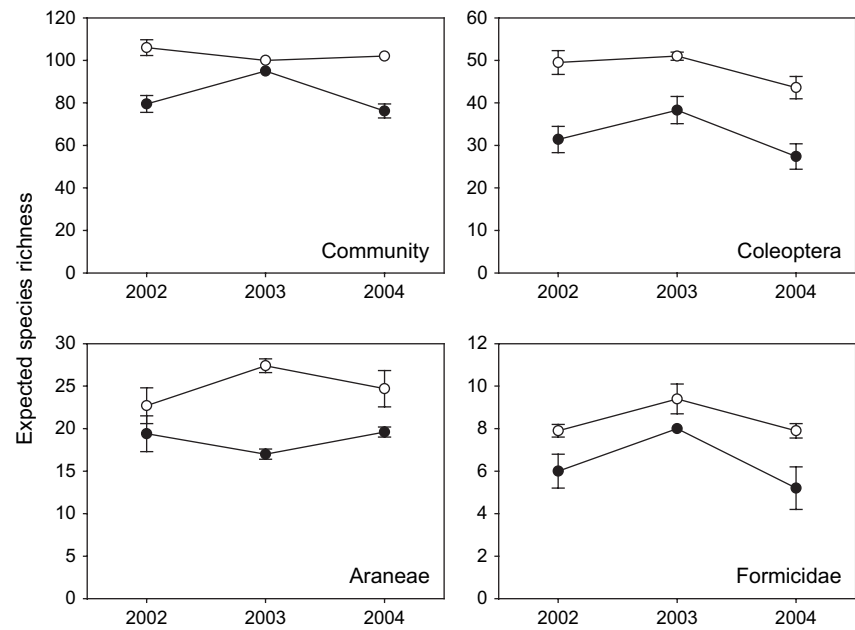
Fig. 4. Expected richness of the whole community, and of the groups Coleoptera, Formicidae, and Araneae. For each group the expected richness is compared for the same number of individuals captured (whole community = 1800, Coleoptera = 325, Formicidae = 500, and Araneae = 110). Only samples from January and February of each year were used, meaning that numbers for 2002 correspond to pre-poisoned data. Error bars correspond to one standard deviation of the mean after randomisation. ●, Exclusion; ○, Control.

The estimated richness of Coleoptera and Formicidae had a similar variation between poisoned and control sites (Fig. 4). During the 3 years of sampling, species richness was higher in control than poisoned sites.

The variation of the estimated species richness of Araneae was different in control and poisoned sites (Fig. 4); however, estimated richness at the third year of sampling (2004) was the same as richness estimated before wasp poisoning began (2002).

Finally, for the above-mentioned groups as for Apiformes, Orthoptera, and Hemiptera, the differences between the mean observed richness between control and poisoned sites remained the same for the study period (Table 2).

Changes in community composition between poisoned and control sites

The ordination of sites based on their species composition was similar during the 3 years of sampling (Fig. 5). In the 3 years, before and after the reduction of wasp abundance, poisoned and

control site groups were more similar within than between them. As a result, the underlying similarity matrices based on the whole community composition were concordant along the 3 years of sampling (2002 vs 2003: rho = 0.42, P = 0.001; 2003 vs 2004: rho = 0.43, P = 0.001 and 2003 vs 2004: rho = 0.40, P = 0.001).

Accordingly the abundance and its variation of discriminating species and orders for the community, Coleoptera, Araneae, and Formicidae were similar in poisoned and control sites, except for *Systolosoma breve* and *Pogonomyrmex angustus* and Blattaria and Dermaptera (Table 3 for species and Table 1 for Lepidoptera, Blattaria, Homoptera, and Dermaptera). These species and orders were more abundant both pre- and post-wasp abundance reduction in poisoned (*Systolosoma breve*, Blattaria, and Dermaptera) or control sites (*Pogonomyrmex angustus*, see Tables 1 and 3).

Discussion

The reduction of *V. germanica* abundance in experimental areas had no effect on the abundance, species richness, and composition of the analysed arthropod community. Although different taxonomic levels were considered (orders, families and species), no evidence was found that the exotic social wasp is causing significant negative impact on the natural communities of arthropods of north-west Patagonia.

However there were differences between poisoned and control areas, which were due to site effects, existing *before* wasp poisoning. Although poisoned and control sites were in the same habitat and within an area of 17 km², differences in abundance, richness, and species composition between poisoned and control sites were in general very pronounced before the beginning of wasp abundance reduction. These results confirm that

Table 2. Variation of the difference in mean observed richness between poisoned and control sites through the 12 months of sampling; results of Spearman correlations are shown.

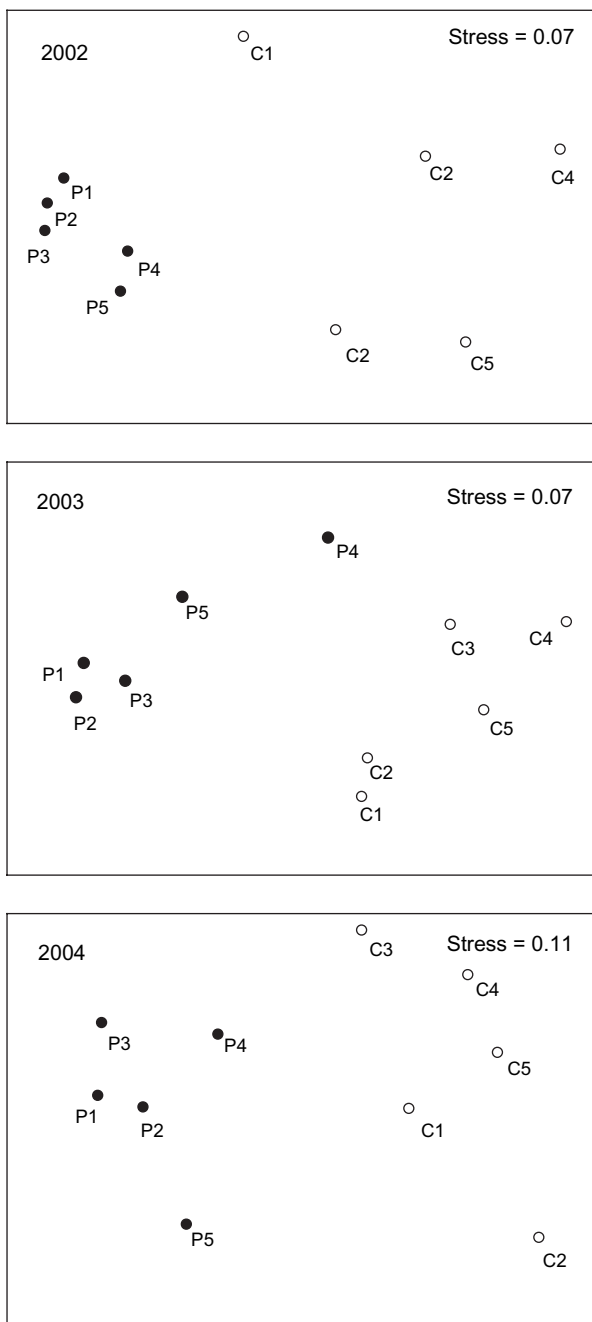| Taxon	R_s	P
General	−0.30	0.33
Coleoptera	−0.49	0.10
Araneae	0.27	0.39
Formicidae	0.26	0.41
Apiformes	0.38	0.21
Orthoptera	−0.1	0.78
Hemiptera	−0.17	0.58

Fig. 5. MDS based on species composition of the native arthropod community. Only samples from January and February of each year were used, meaning that the 2002 plot corresponds to pre-poisoned data. P, poisoned sites; C, control sites.

arthropods are highly sensitive to environmental changes at small spatial scales (e.g. m^2) (e.g. Andersen, 1997; Niemelä *et al.*, 2000; Ribera *et al.*, 2001; Moretti *et al.*, 2004). Moreover, these results enhance the importance of doing before/after comparisons in poisoned experiments. The lack of this kind of control may lead to incorrect conclusions because differences

between study units could be attributed to treatment effects when it is not so.

Evidence coming from other invaded regions suggests that *Vespula* wasps impact native communities once they are established. Some experiments carried out in New Zealand showed that the abundance of some caterpillar and spider species is reduced by wasp predation (Toft & Rees, 1998; Beggs & Rees, 1999). However, these results may not be generalised to the whole community. The evidence that *Vespula* wasps have a negative impact on the native communities in New Zealand beech forest via honeydew consumption is speculative because it is based on the wasp's consumption rate and not on variables measured on the different components of the system (e.g. birds and insect population parameters). Although the evidence is not conclusive, there are many elements that indicate that *Vespula* wasps are likely to have an impact on native communities, at least under certain conditions (see Beggs, 2001). If this is the case, why was no evidence found of wasp impact in the studied community?

There are several possible explanations for the lack of impact of *V. germanica* on the arthropod communities studied. In particular, we focus on the following ideas: (i) time span of wasp poisoning, (ii) level of wasp abundance reduction, and (iii) relative abundance and inter-annual fluctuations of wasps.

Firstly, it may be possible that a 3 year period of wasp abundance reduction may be short in terms of measuring impact; this time span may not be enough to allow for the native community to respond to the wasp poisoning treatment. However, this explanation is unlikely given the short generation time of most arthropods in relation to the length of the study and the opportunistic foraging behaviour of *V. germanica*. In a previous study that involved an exotic social insect (*Solenopsis invicta*, 13–23 years after invasion), the diversity of the native ant community increased after 3 years of poisoning of the invasive ant (Cook, 2003). Besides, *V. germanica* can switch to other prey species when the abundance of a prey becomes low, meaning that some prey species may be kept at low density by wasps, but not become locally extinct (Beggs, 2001). This means that if wasps are removed from a community, the depressed prey species may recover in a few years.

Another possible cause of the observed lack of impact is that the level of wasp reduction (50% on average) may not have been high enough to reduce the impact of *V. germanica* on the arthropod community. The experiments carried out in other regions indicate that wasp abundance needs to be reduced by 80–90% to protect vulnerable arthropod species, in particular mealworm caterpillars and orb-web spiders (Toft & Rees, 1998; Beggs & Rees, 1999). But not all species are equally vulnerable to wasp predation, so these estimates provide conservative levels of control required to conserve some species. Achieving a lower level of control is likely to be beneficial to less vulnerable species (Beggs, 2001).

However, a relative reduction of wasps *per se* does not give information on overall wasp abundance, which is the most important selective pressure to native prey or competitors. For example, in New Zealand beech (*Nothofagus* sp.) forests, an 80–90% reduction means, in practice, that the number of wasps per trap/day is lowered to five individuals. The maximum number of wasps in the control sites over the 3 years was 2.6

Table 3. Mean (SD) abundance in control and and poisoned sites of discriminating species for the community, Coleoptera, Araneae, and Formicidae analyses and results of the repeated measures ANOVA. Significant *P*-values are given in bold [critical *P*-values for ANOVA were calculated using the Benjamini–Hochberg method (Verhoeven *et al.*, 2005)].

Group	Species	Abundance (mean ± 1 SE) Control	Exclusion	Treatment (wasp exclusion) $F_{(1,8)}$	*P*	Interaction (treatment × time) $F_{(11,88)}$	*P*
Coleoptera	*Atheta chilensis*	0.5 ± 0.2	0.5 ± 0.2	0.131	0.72	0.85	0.59
	Chiliotis sp.	3.5 ± 1.2	7.6 ± 2.8	0.03	0.89	0.18	0.06
	Cnemalobus araucanus	1.2 ± 0.3	0.7 ± 0.2	0.68	0.43	1.06	0.40
	Eunemadus chilensis	1.1 ± 0.4	0.7 ± 0.2	0.17	0.69	2.19	0.02
	Loncovilius discoideus	1 ± 0.3	0.7 ± 0.2	2.12	0.18	2.37	0.01
	Metius malachiticus	2.1 ± 1.1	0 ± 0	2.41	0.16	1.15	0.16
	Mimodromites nigrotestaceus	3.9 ± 2.1	34.5 ± 10.8	7.59	0.02	2.57	0.01
	Perilopsis flava	0.8 ± 0.7	0.9 ± 0.7	1.83	0.68	0.71	0.72
	Sericoides sp. 3	18 ± 0.4	5.3 ± 1.5	0.83	0.39	1.55	0.13
	Systolosoma breve	0.1 ± 0.1	8.2 ± 2.2	30.4	**<0.001**	7.03	**<0.001**
	Tetragonoderes viridis	1.8 ± 0.9	0.1 ± 0	4.56	0.06	1.54	0.13
	Trirammatus unistriatus	2.9 ± 0.9	0.4 ± 1.1	2.06	0.19	1.59	0.12
Araneae	Amaurobiidae juveniles	0.2 ± 0.1	0.2 ± 0.1	0.88	0.38	0.54	0.87
	Anphinectidae juveniles	0.5 ± 0.3	0.1 ± 0	0.07	0.80	1.99	0.04
	Anyphaenidae juveniles	0.5 ± 0.1	0.6 ± 0.2	11.47	0.01	1.41	0.18
	Cybaeodamus enigmaticus	0.6 ± 0.2	0 ± 0	3.09	0.11	2.93	0.002
	Euryopis camis	0.1 ± 0	0.4 ± 0.2	0.058	0.82	0.59	0.82
	Euryopis spinifera	0.2 ± 0.1	0 ± 0	2.01	0.20	0.52	0.88
	Lycosa sp. 2	0.8 ± 0.2	0.2 ± 0.1	0.01	0.91	0.99	0.45
	Lycosidae juveniles	1.1 ± 0.3	0.1 ± 0	11.74	0.01	2.05	0.03
	Meriola foraminosa	0.1 ± 0	0 ± 0	3.77	0.09	0.75	0.70
	Meriola penai	0.1 ± 0	0.9 ± 0.3	1.86	0.21	2.3	0.02
	Metaltella rorulenta	1.7 ± 0.3	2.6 ± 0.3	5.5	0.05	0.82	0.62
Formicidae	*Camponotus chilensis*	7.8 ± 1.8	1.4 ± 0.6	11.03	0.01	1.7	0.08
	Camponotus distinguendus	3.1 ± 1	0.2 ± 0.1	7.85	0.02	1.22	0.28
	Dorymyrmex minutus	0.3 ± 0.1	0 ± 0	0.46	0.51	1.4	0.18
	Dorymyrmex tener	0.4 ± 0.2	0 ± 0	1.87	0.21	1.15	0.335
	Lasiophanes atriventris	2 ± 1.3	1 ± 0.7	0.1	0.76	0.30	0.98
	Lasiophanes picinus	31 ± 4.1	54.3 ± 11.3	0.014	0.91	1.05	0.41
	Pogonomyrmex angustus	14 ± 2.6	0.1 ± 0	277.1	**<0.001**	7.26	**<0.001**
	Pogonomyrmex × odoratus	0.1 ± 0.1	0 ± 0	1.28	0.29	1.16	0.32

trap day^{-1}. This means that wasp abundance in the present study is much lower than in similar New Zealand forests. Moreover, results of previous studies in Patagonia showed that wasp numbers in north western Patagonia may be three to eight times lower than in New Zealand (Sackmann *et al.*, 2001).

Whatever the reason for the lower level of wasp abundance in invaded areas of Patagonia compared with New Zealand, a naturally low wasp abundance could be the reason why *V. germanica* does not have an impact on the native arthropod community. Current wasp populations are low, and at these densities they may not yet cause significant effects on the native arthropods. Other studies of biological invasions showed that when an invader (i.e. ants) has an impact on the invaded community, its abundance represents more than 90% of the total catches (Porter & Savignano, 1990; Holway, 1998; Vanderwoude *et al.*, 2000). In the present study, the abundance of *V. germanica* in control sites represented only 6% of the total catches, 20% of Formicidae catches, 30% of Coleoptera catches, 45% of Lepidoptera catches, and 85% of Araneae catches. These numbers suggest that even

the highest wasp abundance recorded in the present study may not be high enough to have an effect on the native community.

Another factor that may be coupled to the relative low wasp abundance is the pronounced inter-annual fluctuations of *V. germanica* populations. Indeed, in the present study wasp abundance in 2004 was around 80% lower than in 2002 and 2003. Such dramatic fluctuations in population densities have been previously reported for wasp populations in New Zealand and England, and have been related to both endogenous density-dependent factors and weather (Archer, 2001; Barlow *et al.*, 2002). In north-west Patagonia wasp populations show seasonal fluctuations (P. Sackmann, pers. obs.). We propose that species whose populations are regulated by other factors than those regulating wasp abundance may temporally escape from the wasp impact. It would be interesting to study the long-term population dynamics of wasps together with the population cycles of their potential native prey.

The consequences of biotic invasions may vary to a great extent. The same invasive species can have different impacts in different communities. For example, introductions for biological

control range in effectiveness depending on the biotic conditions, biotic interactions, and genetic structure of the target species (Van Driesche & Bellows, 1996). The present study suggests that the impact of a given species may also vary according to the abundance of the invader. While no wasp effect was found in the present study, in New Zealand the introduction of *V. germanica* seems to be affecting several arthropod and vertebrate species, as well as having broader consequences that may affect the whole ecosystem. In the present study, the highest wasp abundance recorded in control sites was even lower than in comparable sites of New Zealand beech forest where wasps were removed using toxic baits (Beggs, 2001).

The fact that biological invasions have a generally negative impact on native communities is one of those ideas that is usually taken as an axiom (reification *sensu* Slobodkin, 2001). Testing and eventually rejecting those generally accepted ideas keeps science in a vital condition (Graham & Dayton, 2002). The present study experimentally assessed the impact of *V. germanica* on a native arthropod community. After reducing *V. germanica* abundance from 80 ha during 3 years, no evidence was found that this exotic wasp had an impact on native arthropod assemblages in at least one kind of forest system in northwest Patagonia. The results suggest that invaders may not always have a negative effect on the invaded communities and that their impact may eventually depend on their relative abundance.

Acknowledgements

References

Andersen, A. (1997) Using ants as bioindicators: multiscale issues in ant community ecology. *Conservation Ecology* (online) [WWW document]. URL http://www.ecologyandsociety.org/vol1/iss1/art8, accessed April 2002.

Anderson, R.S. & Ashe, J.S. (2000) Leaf litter beetles as surrogates for establishing priorities for conservation of selected tropical montane cloud forests in Honduras, Central America (Coleoptera, Staphylinidae, Curculionidae). *Biodiversity and Conservation*, **9**, 617–653.

Archer, M.E. (1998) The world distribution of the Euro-Asian species of *Paravespula* (Hym., Vespinae). *Entomologist's Monthly Magazine*, **134**, 279–284.

Archer, M.E. (2001) Changes in abundance of *Vespula germanica* and *V. vulgaris* in England. *Ecological Entomology*, **26**, 1–7.

Barlow, N.D., Beggs, R.J. & Barron, M.C. (2002) Dynamics of common wasps in New Zealand beech forests: a model with density dependence and weather. *Journal of Animal Ecology*, **71**, 663–671.

Barr, K., Moller, H., Christmas, E., Lyer, P. & Beggs, J. (1996) Impact of introduced common wasps (*Vespula vulgaris*) on experimentally placed mealworms in a New Zealand beech forest. *Oecologia*, **105**, 266–270.

Beattie, A.J. & Oliver, I. (1994) Taxonomic minimalism. *Trends in Ecology and Evolution*, **9**, 488–490.

Beggs, J. (2001) The ecological consequences of social wasps (*Vespula* spp.) invading an ecosystem that has an abundant carbohydrate resource. *Biological Conservation*, **99**, 17–28.

Beggs, J.R. & Rees, J.S. (1999) Restructuring of Lepidoptera communities by introduced *Vespula* wasps in a New Zealand beech forest. *Oecologia*, **119**, 565–571.

Bolger, D.T., Suarez, A.V., Crooks, K.R., Morrison, S.A. & Case, T.J. (2000) Arthropods in urban habitat fragments in southern California: area, age, and edge effects. *Ecological Applications*, **10**, 1230–1248.

Borror, D.J., Triplehorn, C.A. & Johnson, N.F. (1992) *An Introduction to the Study of Insects*. Saunders College, Orlando, Florida.

Caughley, G. (1994) Directions in conservation biology. *Journal of Animal Ecology*, **63**, 215–244.

Chehebar, C. & Ramilo, E. (1992) *Fauna del Parque Nacional Nahuel Huapi*. Administración de Parques Nacionales y Asociación Amigos del Museo de la Patagonia F. Moreno, Bariloche.

Christie, M. (1984) *Relevamineto de la fauna de los Parque Nacionales Lanín y Nahuel Huapi*. Vol. I, II y II. Administración de Parques Nacionales, Bariloche.

Clarke, K.R. & Gorley, R.N. (2001) *PRIMER v5: User Manual Tutorial, Primer-e*. Plymouth Marine Laboratory, Plymouth, U.K.

Colwell, R.K. (2000) *EstimateS: Statistical Estimation of Species Richness and Shared Species from Samples (Software and User's Guide)*, Version 6 [WWW document]. URL http://viceroy.eeb.uconn.edu/estimates, accessed April 2002.

Cook, J.L. (2003) Conservation of biodiversity in an area impacted by the red fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae). *Biodiversity and Conservation*, **12**, 187–195.

D'Adamo, P., Sackmann, P., Rabinovich, M. & Corley, J.C. (2002) The potential distribution of the German wasps (*Vespula germanica*) in Argentina. *New Zealand Journal of Zoology*, **29**, 79–85.

Diamond, J. (1989) The present, past and future of human caused extinction. *Philosophical Transactions of the Royal Society of London B*, **325**, 469–477.

Didham, R.K., Tylianakis, J.M., Hutchison, M.A. Ewers, R.M. & Gemmel, N.J. (2005) Are invasive species the drivers of ecological change? *Trends in Ecology and Evolution*, **20**, 470–474.

Edwards, R. (1980) Social wasps, their biology and control. Rentokil Limited, East Grinstead, U.K.

Eubanks, M.D. (2001) Estimates of direct and indirect effects of red imported fire ants on biological control in field crops. *Biological Control*, **21**, 35–43.

Farji-Brener, A.G. (1996) Posibles vías de expansión de la hormiga cortadora de hojas *Acromyrmex lobicornis* hacia la Patagonia. *Ecología Austral*, **6**, 144–150.

Farji-Brener, A.G. & Corley, J.C. (1998) Successful invasions of hymenopteran insects into NW Patagonia. *Ecología Austral*, **8**, 237–249.

Friend, G.R. & Williams, M.R. (1996) Impact of fire on invertebrate communities in mallee-heath shrublands of southwestern Australia. *Pacific Conservation Biology*, **2**, 244–267.

Fritts, T.H. & Rodda, G.H. (1998) The role of introduced species in the degradation of island ecosystems: a case history of Guam. *Annual Review of Ecology and Systematics*, **29**, 113–140.

Gobbi, M., Puntieri, J. & Calvello, S. (1995) Post-fire recovery and invasion by alien plant species in a South American woodland-steppe ecotone. *Plant Invasions: General Aspects and Special Problems* (ed. by P. Pysek, M. Rajmanek and M. Wade), pp. 105–115. Academic Publishing, Amsterdam.

Gotelli, N.J. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**, 379–391.

Goulet, H. & Huber, J. (1993) *Hymenoptera of the World: An Identification Guide to Families.* Centre for Land and Biological Resources Research Ottawa, Canada.

Graham, M.H. & Dayton, P.K. (2002) On the evolution of ecological ideas: paradigms and scientific progress. *Ecology*, **83**, 1481–1489.

Grigera, D., Ubeda, C. & Cali, S. (1994) Caracterización de la asamblea de tetrápodos del Parque Nacional Nahuel Huapi, Argentina. *Revista Cilena de Historia Natural*, **67**, 273–298.

Gurevitch, J. & Padilla, D.K. (2004) Are invasive species a major cause of extinctions? *Trends in Ecology and Evolution*, **19**, 470–474.

Holway, D.A. (1998) Effect of Argentine ant invasions on ground-dwelling arthropods in northern California riparian woodlands. *Oecologia*, **116**, 252–258.

Koivula, M., Punttila, P., Haila, Y. & Niemelä, J.K. (1999) Leaf litter and small-scale distribution of carabid beetles (Coleoptera, Carabidae) in the boreal forest. *Ecography*, **22**, 424–435.

Kusnezov, N. (1953) *Las hormigas en los Parques Nacionales de la Patagonia y los problemas relacionados. Anales del Museo Nahuel Huapi, Perito Francisco P. Moreno*, Tomo III. Ministerio de Agricultura y Ganadería de la Nación, Administración de Parques Nacionales, Buenos Aires.

Lawton, J.H., Bignell, D.E., Bolton, B., Bloemers, G.F., Eggleton, P., Hammond, P.M. *et al.* (1998) Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature*, **391**, 72–76.

Lodge, D.M. (1993) Biological invasions: lesson for ecology. *Trends in Ecology and Evolution*, **8**, 133–135.

Moller, H. (1996) Lessons for invasion theory from social insects. *Biological Conservation*, **78**, 125–142.

Moller, H. & Tilley, J.A.V. (1989) Beech honeydew: seasonal variation and use by wasps, honeybees and other insects. *New Zealand Journal of Zoology*, **16**, 289–302.

Moller, H., Tilley, J.A.V., Thomas, B.W. & Gaze, P.D. (1991) Effect of introduced social wasps on the standing crop of honeydew in New Zealand beech forests. *New Zealand Journal of Zoology*, **18**, 171–179.

Moretti, M., Obrist, M.K. & Duelli, P. (2004) Arthropod biodiversity after forest fires: winners and losers in the winter fire regime of the southern Alps. *Ecography*, **27**, 173–186.

Niemelä, J., Kotz, J., Ashworth, A., Brandmayr, P., Desender, K., New, T. *et al.* (2000) The search for common anthropogenic impacts on biodiversity: a global network. *Journal of Insect Conservation*, **4**, 3–9.

Oliver, I. & Beattie, A.J. (1993) A possible method for the rapid assessment of biodiversity. *Conservation Biology*, **7**, 562–568.

Olivier, I. & Beattie, A.J. (1996a) Designing a cost-effective invertebrate survey: a test of methods for rapid assessment of biodiversity. *Ecological Applications*, **6**, 594–607.

Oliver, I. & Beattie, A.J. (1996b) Invertebrate morphospecies as surrogates for species: a case study. *Conservation Biology*, **10**, 99–109.

Parker, I.M., Simberloff, D., Lonsdale, W.M., Goodell, K., Wonham, M., Kareiva, O.M. *et al.* (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions*, **1**, 3–19.

Peña Guzmán, L.E. (1987) *Introducción al estudio de los insectos de Chile.* Editorial Universitaria, Santiago de Chile.

Pik, A.J., Oliver, I. & Beattie, A.J. (1999) Taxonomic sufficiency in ecological studies of terrestrial invertebrates. *Australian Journal of Ecology*, **24**, 555–562.

Pimm, S.D. (1991) *The Balance of Nature? Ecological Issues in the Conservation of Species and Communities.* University of Chicago Press, Chicago, Illinois.

Pimm, S. & Gilpin, M. (1989) Theoretical issues in conservation biology. *Perspectives in Ecological Theory* (ed. by J. Roughgarden, R. M. May and S. A. Levin), pp. 287–305. Princeton University Press, Princeton, New Jersey.

Porter, S.D. & Savignano, D.A. (1990) Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. *Ecology*, **71**, 2095–2106.

Rapoport, E.H. (1991) Tropical versus temperate weeds: a glance into the present and future. *Ecology of Biological Invasions in the Tropics, National Institute of Ecology* (ed. by P. S. Ramakrishnan), pp. 11–51. ISF, New Delhi.

Rapoport, E.H. (1993) The process of plant colonization in small settlements and large cities. *Humans as Components of Ecosystems* (ed. by M. J. MacDonell and S. Pickett), pp. 190–207. Springer, New York.

Ribera, I., Doledec, S., Downie, I.S. & Foster, G.N. (2001) Effect of land disturbance and stress on species traits of ground beetles assemblages. *Ecology*, **82**, 1112–1129.

Richardson, D.M., Williams, P. & Hobbs, R. (1994) Pine invasions in the southern hemisphere: determinants of spread and invadability. *Journal of Biogeography*, **21**, 511–527.

Roig-Alsina, A. & Aizen, M. (1996) *Bombus ruderatus* Fabricius, un nuevo *Bombus* para la Argentina (Hymenoptera: Apidae). *Physis*, Secc. C, **51**, 49–50.

Rykken, J.J., Capen, D.E. & Mahabir, S.P. (1997) Ground beetles as indicators of land type diversity in the Green Mountains of Vermont. *Conservation Biology*, **11**, 522–530.

Sackmann, P. (2006) Efectos de la variación temporal y métodos de captura en la eficiencia de un muestreo de coleópteros en la Reserva Natural Loma del Medio, El Bolsón, Río Negro. *Revista de la Sociedad Entomológica Argentina*, **65**, 35–51.

Sackmann, P., D'Adamo, P., Rabinovich, M. & Corley, J.C. (2000) Arthropod prey foraged by the European Wasp (*Vespula germanica*) in NW Patagonia, Argentina. *New Zealand Entomologist*, **23**, 55–59.

Sackmann, P., Rabinovich M. & Corley, J.C. (2001) Successful removal of the European wasp by toxic baiting in NW Patagonia. *Journal of Economic Entomology*, **94**, 811–816.

Sackmann, P., Villacide, J.M. & Corley, J.C. (2003) Presencia de una nueva avispa social exótica, *Polistes dominulus* (Hymenoptera: Vespidae) en la Patagonia argentina. *Revista de la Sociedad Entomológica Argentina – RSEA*, **62**, 68–70.

Sanders, N.J., Gotelli, N.J., Séller, N.E. & Gordeon, D.M. (2003) Community disassembly by an invasive species. *Proceedings of the National Academy of Sciences*, **100**. URL www.pnas.org/cgi/doi/10.1073/pnas.0437913100, accessed January 2004.

Simberloff, D. (1989) Which insect introductions succeed and which fail? *Biological Invasions: A Global Perspective, SCOPE 37* (ed. by J. Drake and H. Mooney), pp. 61–72. John Wiley and Sons, Chichester.

Simberloff, D. (1990) Community effects of biological introductions and their implications for restoration. *Ecological Restoration of New Zealand Islands, 1990* (ed. by D. R. Towns, C. H. Daugerthy and I. A. E. Atkinson), pp. 128–136. New Zealand Conservation Science Publications, No. 2, Wellington, New Zealand.

Slobodkin, L.B. (2001) The good, the bad and the reified. *Evolutionary Ecology Research*, **3**, 1–13.

Toft, R.J. & Rees, J.S. (1998) Reducing predation of orb-web spiders by controlling common wasps (*Vespula vulgaris*) in a New Zealand beech forest. *Ecological Entomology*, **23**, 90–95.

Vanderwoude, C., Lobry de Bruyn, L.A. & House, A.P.N. (2000) Response of an open-forest ant community to invasion by introduced ant, *Pheidole megacephala*. *Austral Ecology*, **25**, 253–259.

Van Driesche, R.G. & Bellows, T.S. (1996) *Biological Control*. Chapman & Hall, New York.

Vázquez D.P. (2002) Multiple effects of introduced mammalian herbivores in a temperate forest. *Biological Invasions*, **4**, 175–191.

Vázquez, D.P. & Aragón, R. (2002) Introduction of the special issue: biological invasions in southern South America: a first step towards a synthesis. *Biological Invasions*, **4**, 1–5.

Veblen, T., Mermoz, M., Martín, C. & Kitzberger, T. (1992) Ecological impacts of introduced animals in Nahuel Huapi National Park, Argentina. *Conservation Biology*, **6**, 71–83.

Verhoeven, K.J.F., Simonsen, K.L. & McIntyre, L.M. (2005) Implementing false discovery rate control: increasing your power. *Oikos*, **108**, 643–647.

Werner, S.M. & Raffa, K.F. (2000) Effects of forest management practices on the diversity of ground-occurring beetles in mixed northern hardwood forests of the Great Lakes Region. *Forest Ecology and Management*, **139**, 135–155.

Williamson, M. (1996) *Biological Invasions*. Chapman &Hall, London.

Willink, A. (1980) Sobre la presencia de *Vespula germanica* (Fabricius) en la Argentina (Hymenoptera: Vespidae). *Neotropica*, **26**, 205–206.

Worthington, E.B. & Lowe, M.C. & McConnell, R. (1994) African lakes reviewed – creation and destruction of biodiversity. *Environmental Conservation*, **21**, 199–213.