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

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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, extirping 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 invaders (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 dombeyoi (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. Alsplach, 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; Rykkén 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, © 2008 The Authors
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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 × 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
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>
<thead>
<tr>
<th>Taxon</th>
<th>Treatment Mean (SD)</th>
<th>Time</th>
<th>Interaction</th>
<th>Pre-poisoning abundance Controls</th>
<th>Poisoned</th>
<th>Post-poisoning abundance† Controls</th>
<th>Poisoned</th>
</tr>
</thead>
<tbody>
<tr>
<td>General (305, 24,643)</td>
<td>0.05 (0.84)</td>
<td>13.09</td>
<td>&lt;0.001</td>
<td>295.4 (153.3)</td>
<td>462.0 (316.5)</td>
<td>238.5 (160.5)</td>
<td>302.9 (250.9)</td>
</tr>
<tr>
<td>Coleoptera (175, 7865)</td>
<td>3.71 (0.09)</td>
<td>6.79</td>
<td>&lt;0.001</td>
<td>47.9 (45.1)</td>
<td>157.9 (190.9)</td>
<td>45.5 (47.6)</td>
<td>138.7 (129.2)</td>
</tr>
<tr>
<td>Formicidae (14, 7064)</td>
<td>1.31 (0.28)</td>
<td>5.18</td>
<td>&lt;0.001</td>
<td>100.4 (86.5)</td>
<td>82.1 (67.3)</td>
<td>82.5 (110.2)</td>
<td>70.2 (96.6)</td>
</tr>
<tr>
<td>Araneae (78, 1400)</td>
<td>8.23 (0.02)</td>
<td>16.86</td>
<td>&lt;0.001</td>
<td>29.2 (10.9)</td>
<td>12.5 (5.6)</td>
<td>26.2 (14.5)</td>
<td>10.0 (6.4)</td>
</tr>
<tr>
<td>Apiformes (16, 202)</td>
<td>5.16 (0.05)</td>
<td>6.71</td>
<td>&lt;0.001</td>
<td>2.6 (2.7)</td>
<td>5.25 (5.3)</td>
<td>0.4 (0.6)</td>
<td>2.1 (3.9)</td>
</tr>
<tr>
<td>Lepidoptera (*, 4116)</td>
<td>2.97 (0.12)</td>
<td>8.86</td>
<td>&lt;0.001</td>
<td>75.0 (59.7)</td>
<td>67.2 (142.0)</td>
<td>63.8 (77.4)</td>
<td>33.5 (26.3)</td>
</tr>
<tr>
<td>Blattaria (1, 645)</td>
<td>11.00 (0.01)</td>
<td>8.76</td>
<td>&lt;0.001</td>
<td>0.4 (0.9)</td>
<td>28.6 (41.8)</td>
<td>1.6 (3.3)</td>
<td>12.2 (16.4)</td>
</tr>
<tr>
<td>Hemiptera (9, 795)</td>
<td>1.71 (0.22)</td>
<td>11.68</td>
<td>&lt;0.001</td>
<td>20.0 (26.6)</td>
<td>3.7 (3.8)</td>
<td>16.9 (28.7)</td>
<td>2.8 (5.9)</td>
</tr>
<tr>
<td>Homoptera (1, 1047)</td>
<td>15.19 (0.004)</td>
<td>2.06</td>
<td>0.03</td>
<td>4.7 (7.1)</td>
<td>5.3 (10.0)</td>
<td>1.4 (1.7)</td>
<td>0.9 (2.0)</td>
</tr>
<tr>
<td>Orthoptera (7, 185)</td>
<td>1.56 (0.24)</td>
<td>4.16</td>
<td>&lt;0.001</td>
<td>6.4 (8.0)</td>
<td>27.1 (36.3)</td>
<td>7.2 (14.2)</td>
<td>11.1 (17.7)</td>
</tr>
<tr>
<td>Dermaptera (3, 1324)</td>
<td>17.14 (0.003)</td>
<td>20.10</td>
<td>&lt;0.001</td>
<td>8.8 (8.0)</td>
<td>66.5 (41.0)</td>
<td>2.7 (3.9)</td>
<td>21.2 (23.8)</td>
</tr>
</tbody>
</table>

*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.

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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 during the 3 years (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).
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
arthropods are highly sensitive to environmental changes at small spatial scales (e.g. m²) (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

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.
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 of pests can have different outcomes in different ecosystems. This highlights the importance of considering the specific characteristics of each community when evaluating the impacts of invasive species.

For instance, in the present study, the abundance of wasp species in Patagonia was compared to that in New Zealand. The results showed that wasp populations in Patagonia were lower than in New Zealand. This suggests that the presence of the invasive species, *V. germanica*, may not yet cause significant effects on the native arthropods. However, further research is needed to understand the long-term effects of these invasions on the native arthropod community.

The table below presents the mean (SD) abundance of species in control and poisoned sites, as well as the results of the repeated measures ANOVA for the community, Coleoptera, Araneae, and Formicidae.

### Table 3. Mean (SD) abundance in control and poisoned sites of discriminating species for the community, Coleoptera, Araneae, and Formicidae

<table>
<thead>
<tr>
<th>Group</th>
<th>Species</th>
<th>Control (mean ± 1SE)</th>
<th>Exclusion (mean ± 1SE)</th>
<th>Treatment (wasp exclusion)</th>
<th>Interaction (wasp exclusion × time)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coleoptera</td>
<td>Atheta chilensis</td>
<td>0.5 ± 0.2</td>
<td>0.5 ± 0.2</td>
<td>0.131 (0.8)</td>
<td>0.72</td>
</tr>
<tr>
<td>Chilotiis sp.</td>
<td></td>
<td>3.5 ± 1.2</td>
<td>7.6 ± 2.8</td>
<td>0.03</td>
<td>0.89</td>
</tr>
<tr>
<td>Cenmalopus araucanus</td>
<td>1.2 ± 0.3</td>
<td>0.7 ± 0.2</td>
<td>0.68</td>
<td>0.43</td>
<td>1.06</td>
</tr>
<tr>
<td>Eumenas chilensis</td>
<td>1.1 ± 0.4</td>
<td>0.7 ± 0.2</td>
<td>0.17</td>
<td>0.69</td>
<td>2.19</td>
</tr>
<tr>
<td>Loncovilius discoides</td>
<td>1 ± 0.3</td>
<td>0.7 ± 0.2</td>
<td>2.12</td>
<td>0.18</td>
<td>2.37</td>
</tr>
<tr>
<td>Metius malachiticus</td>
<td>2.1 ± 1.1</td>
<td>0 ± 0.0</td>
<td>2.41</td>
<td>0.16</td>
<td>1.15</td>
</tr>
<tr>
<td>Mimosanotes nigronevulaceae</td>
<td>3.9 ± 2.1</td>
<td>34.5 ± 10.8</td>
<td>7.59</td>
<td>0.02</td>
<td>2.57</td>
</tr>
<tr>
<td>Periplophora flavida</td>
<td>0.8 ± 0.7</td>
<td>0.9 ± 0.7</td>
<td>1.83</td>
<td>0.68</td>
<td>0.71</td>
</tr>
<tr>
<td>Sericoides sp.</td>
<td>18 ± 0.4</td>
<td>5.3 ± 1.5</td>
<td>0.83</td>
<td>0.39</td>
<td>1.55</td>
</tr>
<tr>
<td>Systolosoma breve</td>
<td>0.1 ± 0.1</td>
<td>8.2 ± 2.2</td>
<td>30.4</td>
<td>&lt;0.001</td>
<td>7.03</td>
</tr>
<tr>
<td>Tetragononoevirids</td>
<td>1.8 ± 0.9</td>
<td>0.1 ± 0.0</td>
<td>0.06</td>
<td>1.54</td>
<td>0.13</td>
</tr>
<tr>
<td>Trigroomatus unistriatus</td>
<td>2.9 ± 0.9</td>
<td>0.4 ± 1.1</td>
<td>1.99</td>
<td>0.12</td>
<td></td>
</tr>
<tr>
<td>Araneae</td>
<td>Amaurobidae juveniles</td>
<td>0 ± 0.0</td>
<td>0.88</td>
<td>0.38</td>
<td>0.54</td>
</tr>
<tr>
<td>Anaphilectidae juveniles</td>
<td>0.5 ± 0.3</td>
<td>0 ± 0.0</td>
<td>0.07</td>
<td>0.80</td>
<td>1.99</td>
</tr>
<tr>
<td>Anystinae juveniles</td>
<td>0.5 ± 0.1</td>
<td>0.6 ± 0.2</td>
<td>11.47</td>
<td>0.01</td>
<td>1.41</td>
</tr>
<tr>
<td>Cybalius juveniles</td>
<td>0.6 ± 0.2</td>
<td>0 ± 0.0</td>
<td>3.09</td>
<td>0.11</td>
<td>2.93</td>
</tr>
<tr>
<td>Eurypus camis</td>
<td>0.1 ± 0.0</td>
<td>0.4 ± 0.2</td>
<td>0.058</td>
<td>0.82</td>
<td>0.59</td>
</tr>
<tr>
<td>Eurypus spinifera</td>
<td>0.2 ± 0.1</td>
<td>0 ± 0.0</td>
<td>2.01</td>
<td>0.20</td>
<td>0.52</td>
</tr>
<tr>
<td>Lycosa sp.</td>
<td>0.8 ± 0.2</td>
<td>0.2 ± 0.1</td>
<td>0.01</td>
<td>1.01</td>
<td>1.89</td>
</tr>
<tr>
<td>Lycosidae juveniles</td>
<td>1.1 ± 0.3</td>
<td>0 ± 0.0</td>
<td>11.74</td>
<td>0.01</td>
<td>2.05</td>
</tr>
<tr>
<td>Meriola foraminosa</td>
<td>0.1 ± 0.0</td>
<td>0 ± 0.0</td>
<td>3.77</td>
<td>0.09</td>
<td>0.75</td>
</tr>
<tr>
<td>Meriola penai</td>
<td>0.1 ± 0.0</td>
<td>0.9 ± 0.3</td>
<td>1.86</td>
<td>0.21</td>
<td>2.3</td>
</tr>
<tr>
<td>Metallata rurulenta</td>
<td>1.7 ± 0.3</td>
<td>2.6 ± 0.3</td>
<td>5.5</td>
<td>0.05</td>
<td>0.82</td>
</tr>
<tr>
<td>Formicidae</td>
<td>Camponotus chilensis</td>
<td>7.8 ± 1.8</td>
<td>1.4 ± 0.6</td>
<td>11.03</td>
<td>0.01</td>
</tr>
<tr>
<td>Camponotus distinctus</td>
<td>3.1 ± 1.0</td>
<td>0.2 ± 0.1</td>
<td>7.85</td>
<td>0.02</td>
<td>1.22</td>
</tr>
<tr>
<td>Doromyrmex minutus</td>
<td>0.3 ± 0.1</td>
<td>0 ± 0.0</td>
<td>0.46</td>
<td>0.51</td>
<td>1.4</td>
</tr>
<tr>
<td>Doromyrmex tener</td>
<td>0.4 ± 0.2</td>
<td>0 ± 0.0</td>
<td>1.87</td>
<td>0.21</td>
<td>1.15</td>
</tr>
<tr>
<td>Lasiopeates atriventris</td>
<td>2.1 ± 1.3</td>
<td>1.0 ± 0.7</td>
<td>0.1</td>
<td>0.76</td>
<td>0.30</td>
</tr>
<tr>
<td>Lasiopeates piceus</td>
<td>31 ± 4.1</td>
<td>54.3 ± 11.3</td>
<td>0.014</td>
<td>0.91</td>
<td>1.05</td>
</tr>
<tr>
<td>Pogononyrmex angustus</td>
<td>14 ± 2.6</td>
<td>0.1 ± 0.0</td>
<td>277.1</td>
<td>&lt;0.001</td>
<td>7.26</td>
</tr>
<tr>
<td>Pogononyrmex × odoratus</td>
<td>0.1 ± 0.1</td>
<td>0 ± 0.0</td>
<td>1.28</td>
<td>0.29</td>
<td>1.16</td>
</tr>
</tbody>
</table>

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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.

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References


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