ORIGINAL PAPER

Competition for food between the exotic wasp *Vespula germanica* and the native ant assemblage of NW Patagonia: evidence of biotic resistance?

Maité Masciocchi · Alejandro G. Farji-Brener · Paula Sackmann

Abstract The success of a biological invasion may depend on the interactions between the invader and the native biota. However, little experimental evidence demonstrates whether local species can successfully compete with exotics. We experimentally determined the existence of competition for food between the exotic wasp *Vespula germanica*, one of the most recent Patagonian invaders, and the native ant assemblage. Both wasps and ants are generalist predators and scavengers, sharing habitat and food resources. We selected 30 sites within scrubland habitats where both ants and wasps were present. At each site, we placed containers with protein baits under three treatments: wasp exclusion, ant exclusion, and control (i.e., free access for wasps and ants). Ant exclusion increased the number of wasps (with regard to a control), but wasp exclusion did not affect ant abundance. This result suggests that native ants affect the foraging activity of exotic wasps but not vice versa. Aggressive behaviors and worker aggregation may explain the competitive advantage of ants. Ants bite wasp legs and massively aggregate on food sources, physically limiting the landing of wasps on baits. If the outcome of interactions at baits reported here influence wasp population-level parameters, this competitive interaction could be one of the factors explaining the low abundance of this exotic wasp in NW Patagonia in comparison with other invaded regions.

Keywords Agonistic behavior · Biological invasions · *Dorymyrmex tener* · Yellowjackets

Introduction

There are many possible reasons why a species may or may not become invasive after its arrival to a new area outside its native distribution range. Some authors propose that the invaders attributes, such as their dispersion mode or level of ecological plasticity, are key factors determining their success (DiVittorio et al. 2007; Richards et al. 2006). Other studies suggest that the cause of invasion success is the climatic matching between the invaded and native areas of distribution (Holway et al. 2002a), high resource availability (Davis et al. 2000), and/or the absence of natural enemies (Keane and Crawley 2002). Nevertheless, the composition of the invaded community has been proposed as one of the most important causes of the success or failure of an invasion (Kennedy et al. 2002; Fridley et al. 2007). Local species can outcompete the exotics and thus reduce the success of the invader (Maron and Vila 2001; Levine et al. 2004; de Rivera et al. 2005).

M. Masciocchi · A. G. Farji-Brener (✉) · P. Sackmann
Lab. Ecotono. CRUB-UNComa, INIBIOMA-CONICET,
8400 Bariloche, Argentina
e-mail: alefarji@crub.uncoma.edu.ar

Although this hypothesis (i.e., a form of biotic resistance) has been largely proposed as a key factor explaining the success of an invasion (Elton 1958; Simberloff 1989), little experimental evidence exists demonstrating competitive dominance of native over exotic species (Levine et al. 2004; Vilá and Weiner 2004; Von Holle 2005; Von Holle and Simberloff 2005; Fridley et al. 2007). Furthermore, insects are among the most important invaders and components of native assemblages (Simberloff 1989; Williamson 1996), but most of the studies on biological invasions were focused on other taxonomic groups. In the current study, we experimentally assess the existence of competition for food between the exotic wasp *Vespula germanica* (Fabricius) and the native ant assemblage of NW Patagonia.

The German wasp *V. germanica* (yellowjacket) is a social vespid native to Eurasia and Northern Africa that has invaded NW Patagonia 30 years ago (Farji-Brener and Corley 1998; Willink 1980). It has also invaded and become established in New Zealand, Tasmania, Australia, South Africa, the USA, Canada, and Chile (Archer 1998). This species is an opportunistic predator and scavenger (Akre and Mac Donald 1986; Harris 1991; Barr et al. 1996; Sackmann et al. 2000), and preys on and competes with native insects, having the potential to restructure hosting communities (Beggs and Rees 1999; Beggs 2001). Although *V. germanica* inhabits several habitats of Patagonia, its local abundance at present is lower than in other invaded countries, such as New Zealand (Sackmann et al. 2008).

Native ants of NW Patagonia are good candidates to compete with *V. germanica*. Competition is considered one of the key factors structuring ant assemblages (Hölldobler and Wilson 1990). Dominant ants often show aggressive behavior, territoriality, and recruitment of nest mates (Parr 2008). Particularly, the ant assemblage of Patagonian scrubland is dominated by species of the genus *Dorymyrmex* Mayr, which show high colony densities, large number of workers, and strong agonistic behaviors (Kusnesov 1953; Farji-Brener et al. 2002; Sackmann and Farji-Brener 2006). Additionally, these ants inhabit the same habitats as *V. germanica*. Finally, native ants are opportunistic predators and scavengers, consuming the same prey items as *V. germanica* (Sackmann et al. 2000; Farji-Brener et al. 2002). In sum, several characteristics of Patagonian native ants

such as their food preferences, high abundance, and aggressive and mass-recruitment behaviors make them a potential competitor for *V. germanica*.

We assessed, using experimental baits and selective exclusions for wasps and ants, the existence of competition between these two groups. We expect that, if exotic wasps are competitively superior to native ants, then ant abundance will increase (with regard to a control) in wasp exclusions, and in turn, wasp abundance will not be affected by ant exclusion. Conversely, if native ants are competitively superior to exotic wasps, then ant exclusion will increase wasp abundance (with regard to a control), but ant abundance will remain unaffected by wasp exclusion. If wasps outcompete native ants, then the low population densities of *V. germanica* in NW Patagonia could not be explained by competition with local ants. Moreover, this could be an example of how an exotic insect can impact the native fauna. Conversely, if native ants appear to be competitively superior over *V. germanica*, then this work could be an example of how native species negatively affect the success of exotics (e.g., biotic resistance).

Methods

Study area and species

The study was conducted in the Nahuel Huapi National Park, Patagonia, Argentina (41°S, 72°W). The climate of this area is dominated by an abrupt west-to-east decrease in precipitation. Mean annual precipitation varies from 3,500 mm per year in the western zone of the park to 500 mm in the eastern zone over the course of 150 km due to the rain shadow effect of the Andes on the passage of moist Pacific air masses. Vegetation types reflect this climatic pattern, forming three major habitats along the west-to-east gradient: forest, scrubland, and steppe. The experiments were carried out in the scrubland habitat, where semi-arid shrub vegetation and forests of *Austrocedrus chilensis* and *Nothofagus antarctica* grow along the foothill zone, in sites of 1,800–1,400 mm of mean annual precipitation (Correa 1969–1998). Both wasps and ants are conspicuous components of this habitat type.

Vespula germanica (Fabricius) is a social wasp that has a wide diet. Carbohydrate sources are often

flower nectars, bee honey, and homoptera excretions. Protein sources come from a wide range of alive and death arthropods, and carrion (Sackmann et al. 2000). Although *V. germanica* searches for food individually, it shows an aggregative behavior after discovery of food sources (local enhancement, see D'Adamo et al. 2000). This foraging behavior allows wasps to compete for and exploit food more efficiently. Wasps usually build underground nests and show a flying foraging ratio from their colonies of 200 m (Edwards 1980). *V. germanica* tolerates low temperatures, showing a wide daily and seasonal foraging activity (Akre et al. 1989). Ants of the genus *Dorymyrmex* are the dominant species of the ant assemblage in the Patagonian scrubland (Farji-Brener et al. 2002; Sackmann and Farji-Brener 2006); *Dorymyrmex tener* Mayr is the most abundant ant species at this habitat. This species is a generalist predator and an opportunistic scavenger (Kusnesov 1953, 1959). *D. tener* consumes flower nectars, homoptera excretions, and alive and dead arthropods, and shows mass recruitment behavior (AG Farji-Brener, pers. obs. Farji-Brener et al. 2009). Like *V. germanica*, this ant species can forage under extreme temperature conditions (Farji-Brener et al. 2002; Sackmann and Farji-Brener 2006).

Experimental design

Field experiments were carried out between 10 a.m. and 5 p.m. during February, March, and April (late austral summer) of 2006 and 2007, when both *V. germanica* and ants foraging activity shows its peak. Earlier in the summer, wasp activity is low and workers are not much attracted to protein baits (Sackmann and Corley 2007; Sackmann et al. 2008). Given that the aim of this study was to assess the existence of competitive interactions, after doing a

preliminary sampling, we selected 30 scrubland sites in which wasp and ants were simultaneously present. To get independent data from each replicate, the minimum distance between sampling sites was 500 m. This distance minimizes the chance that ants or wasps of the same nest appear in two different sample sites. In each sampling site, three baits were presented simultaneously in plastic containers of 7 cm diameter and 2 cm depth. The baits contained fresh raw minced beef and tuna fish (1:1) (hereafter, protein). Earlier works and field observations demonstrated that this food baits were attractive to ants and wasps (Spurr 1995; Sackmann et al. 2000; Sackmann and Corley 2007). Baits were offered under three treatments: wasp exclusion (−W), ant exclusion (−A), and control (C). In the wasp exclusion treatment the baits were beneath a metallic mesh, with cells of 0.3 cm sides, avoiding the access of wasp but allowing the access of ants. The containers were buried into the ground with their rims leveled with the soil surface. In the ant exclusion treatment the rim of the plastic containers were coated with solid Vaseline and placed on the soil (i.e., not buried), avoiding ant access but allowing the access of wasp flying to the baits. Control baits were placed in plastic containers without a mesh and Vaseline, but buried into the soil with the rims leveled with the surface. Thus both ants and wasps were able to reach control baits (Fig. 1).

Treatments within each site were randomly located in an imaginary triangle of 1 × 1 × 1 m to minimize potential position effects. Between 1 and 2 h after baits were placed in the field, we counted the number of wasp removing bait in each plastic container (i.e., in all kind of treatments) and then we took all the baits to the laboratory to count and identify the ants. The plastic containers with their corresponding bait were individually bagged and preserved in

Fig. 1 Details on the sampling design. (−A) ant exclusion treatment, (−W) wasp exclusion treatment, and (C) control treatment. See text for further explanations. Photo credit: M. Masciocchi

alcohol 70%. We used keys by Kusnesov (1959) and compared the collected individuals with material deposited in the Laboratorio Ecotono collection to identify species.

Data analysis

To analyze the effect of ant and wasp exclusions we employed a one-way analysis of variance (ANOVA) block design. Exclusion (three levels: −W, −A, and C) was considered as a fixed factor. The sampling site (i.e., the block) was considered as a random factor. Response variables were the number of wasp and the number of ants removing bait in a plastic container. These variables were examined to meet the ANOVA assumptions and transformed when necessary as follows: $x' = \log(x + 1)$. Fisher post hoc comparisons of means were employed when ANOVA results were statistically significant ($P < 0.05$).

Results

We captured a total of 12,957 ants corresponding to six species. *D. tener* Mayr was the dominant species (97.5% of all captures). *Camponotus chilensis* Spinola represented only the 1.5% of the captures, while *Dorymyrmex antarcticus* Forel, *Camponotus distinguendus* Spinola, *Lasiophanes picinus* Roger, and *L. valdiviensis* Forel represented the remaining 1%.

Both exclusion treatments were successful (see Table 1 for ANOVA results). Wasp exclusions (−W) reduced wasp abundance by 90%, and ant exclusions (−A) reduced ant numbers by 99% with regard to control treatments (Fisher LSD, $P < 0.001$; Fig. 2). However, the effect of these exclusions was asymmetric. Whereas a decrease in the number of ants positively affected wasp abundance, a decrease in the

Table 1 Results of the one-way, block analysis of variance for the number of wasps and ants at food baits

	Wasps			Ants		
	F	df	P	F	df	P
Exclusion	20.2	2	<0.001	16	2	<0.0001
Site (block)	1.5	29	0.1	2.8	29	<0.0004
Error		58			58	
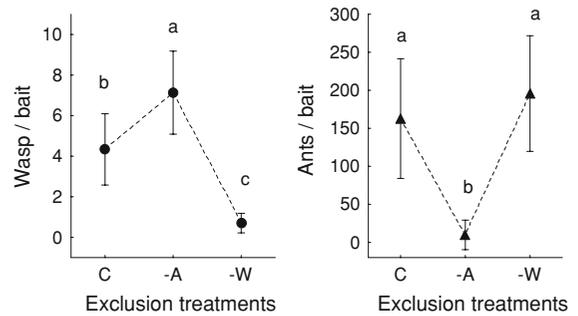
Fig. 2 Mean number (±1 SD) of wasps (left) and ants (right) per bait. Treatments are wasp exclusion (−W), ant exclusion (−A), and control (C). See further explanation in the text. Different lowercase letters imply statistically significant differences ($P < 0.01$, Fisher post hoc test). See Table 1 for ANOVA results
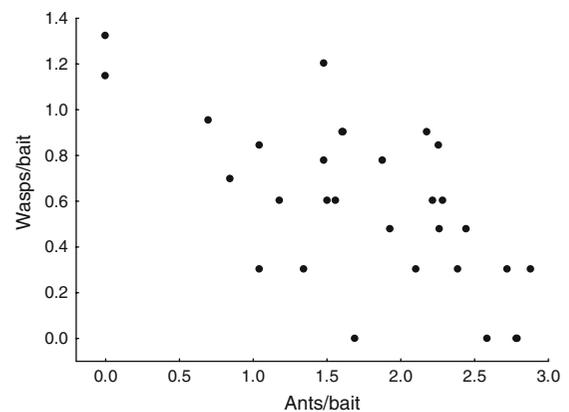
Fig. 3 Relationship between the number of wasps and ants per bait in control treatments. Each point represents a food bait. Data were transformed as $x' = \log(1 + x)$

number of wasp did not affect ant abundance. Mean number of wasps/bait in ant-excluded treatments was 74% higher than in the control treatment, but the mean number of ants/bait in wasp exclusions did not change with regard to controls (Fig. 2). Accordingly, the abundance of wasps and ants at control baits were negatively correlated ($r = -0.67$, $n = 30$ baits, $P < 0.001$, Fig. 3).

Since ant exclusion increased wasp abundance (but not vice versa), we analyzed whether this effect depended on ant abundance. We calculated the wasp-reduction effect (WRE) as the difference between the mean number of wasps in ant-excluded treatments and controls, i.e., WRE = (−A) − C. Then we used a simple regression model to determine whether ant

abundance affects WRE. Ant abundance only explained 23% of WRE ($F_{(1, 31)} = 9.5$, $R^2 = 0.23$, $P < 0.05$).

Discussion

We found experimental and correlative evidence supporting the hypothesis that native ants successfully compete with exotic wasps. First, an increase in ant abundance was associated with a decrease in wasp number at control baits, suggesting the existence of competition between these two groups. Second, ant exclusion increased wasp abundance by 74%, but wasp exclusion did not affect ant abundance. Overall, these results strongly suggest that, whereas native ants negatively affect the foraging activity of the exotic wasp *V. germanica*, this invader does not affect the ant's foraging activity.

Native ants, especially *D. tener*, appear to be superior competitor for food than *V. germanica*. At least two ant behaviors may explain this pattern: aggression and aggregation on food sources. First, ants showed strong physical aggressions against wasps when they foraged on baits. When wasps landed on baits, ants rapidly and massively bit wasp legs. Second, *D. tener* shows massive recruitment of nest mates to food sources. This aggregation of workers at baits makes it difficult or prevents access to food sources by other insects. This is especially true for *V. germanica*, a species that needs to land on the food source to cut it into transportable fragments (Sackmann et al. 2000). Accordingly, the reduction of wasp abundance due to the presence of ants (i.e., the WRE) was stronger at high ant abundance. A high density of ants on baits might thus deter wasp landing by displaying an aggressive behavior and/or acting as a physical barrier. Whatever was exactly the mechanism, wasps rarely collected food at baits colonized by this dominant ant species.

The experimental approach is considered one of the more powerful tools to recognize the mechanisms that generate patterns in nature. However, manipulations might generate undesirable effects and unrealistic results (Underwood 1997). For example, experimental baits may inadequately represent how food sources can be found in nature. However, the use of experimental food baits for insects is widely accepted in ecological studies because they offer advantages compared with the use of natural preys (Agosti et al. 2000). This procedure reduces the likelihood that variations in relative abundance, quality, odor, and form of the food source affect the foraging behavior of consumers. These variables are almost impossible to control if natural preys, such as dead insects, carrion, flower nectar or homopteran excretions are employed in an experiment. In addition, and supporting our experimental results, we had observed aggressive interactions between wasps and ants in natural conditions (i.e., fights for insect preys), suggesting that the observed competition for baits might reflect what happens in nature. The amount of bait employed might also cause another undesirable effect, stimulating high wasp and ant densities that rarely occur in nature. However, field observations and other nonmanipulative studies showed similar ant and wasp abundances to those reported here (Farji-Brener et al. 2002; Sackmann et al. 2001). Overall, we believe that the results found in this study were not merely a consequence of the use of artificial baits, and adequately reflect what happens in natural conditions.

Ants seem to be better competitors for food than wasps in scrublands of NW Patagonia. However, this result is ecologically relevant only if food availability is limited for wasps. At the late summer, the demand for food of ants and wasp colonies is high because sexual individuals are being produced (Kusnesov 1953, 1959; Sackmann et al. 2008). Simultaneously the abundance of preys becomes to decrease (Sackmann 2006; Sackmann et al. 2008). Considered together, these facts suggest that food is a limiting factor for ants and wasps during this time of the year and thus, competitive interactions more intense. Under this scenario, native ants may restrict the population growth of *V. germanica* in this habitat by constraining the access of wasp to preys.

Interspecific competition is thought to be one of the most important mechanism structuring ant assemblages (Hölldobler and Wilson 1990; Parr 2008), so ants probably evolve in highly competitive environments. This selective pressure confers some characteristics to ants, such as strong territoriality, agonistic behaviors, and massive recruitment to food sources, making ants impact native arthropod assemblages when they invade other systems (Holway et al. 2002b). This work suggests that, for the same reasons, native dominant ants may be good

candidates to outcompete exotic insects and thus resist insect invasions.

Biotic resistance has been proposed as a key factor determining the failure of biological invasions and/or regulating exotic populations (Simberloff 1989; Levine et al. 2004; de Rivera et al. 2005; Von Holle 2005). Although NW Patagonia is an adequate area for the establishment and population growth of *V. germanica* (D'Adamo et al. 2002), wasp abundance in this region is up to eight times lower than in similar habitats of New Zealand (Sackmann et al. 2008). Several hypotheses have been postulated to explain this pattern. One is the absence of *Ultracoelostoma* homopterans in Patagonia, which are key food sources for wasps in New Zealand beech forests (Beggs 2001; Sackmann et al. 2008). It has been also postulated that the colonization of *V. germanica* in the Patagonian region ($\sim$ 30 years) is more recent than the wasp establishment in New Zealand ($\sim$ 60 years). We propose that the competitive superiority of native ants over exotic wasps found in this study could be another cause that limits the abundance and/or geographical expansion of *V. germanica* in Patagonia. However, the importance of native ants controlling the populations of exotic wasp deserves more study because we still do not know whether the competitive superiority of ants reported here affects population-level parameters of wasps. Our results, although promising, are not conclusive, but are the essential first step to study this topic in the near future.

References

Agosti D, Majer L, Alonso I, Schultz T (2000) Ants. Standard methods of measure and monitoring biodiversity. Smithsonian, Washington

Akre R, Mac Donald P (1986) Biology, economic importance and control of yellow jackets. In: Vinson S (ed) Economic impact and control of social insects. Pergamon Press, New York, pp 353–412

Akre R, Ramsay C, Gable A, Baird C, Standford A (1989) Additional range extension by the German yellow jacket *Paravespula germanica* (Fabricius), in North America (Hymenoptera: Vespidae). Pan-Pacific Entomol 65:79–88

Archer ME (1998) The world distribution of the euro-asian species of *Paravespula* (Hymenoptera: Vespidae). Entomol Mon Mag 134:279–284

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

Beggs JR (2001) The ecological consequences of social wasp (*Vespula* sp.) invading an ecosystem that has an abundant carbohydrate resource. Biol Conserv 99:17–28. doi:10.1016/S0006-3207(00)00185-3

Beggs JR, Rees J (1999) Restructuring of lepidoptera communities by introduced *Vespula* wasps in a New Zealand beech forest. Oecologia 119:565–571. doi:10.1007/s004420050820

Correa M (1969–1998) Flora Patagónica, Vol 7. INTA, Buenos Aires

D'Adamo P, Sackmann P, Lozada M, Corley J (2000) Local enhancement in the wasp *Vespula germanica*. Are visual cues all that matter? Insectes Soc 4:289–291. doi:10.1007/PL00001717

D'Adamo P, Sackmann P, Corley JC, Rabinovich M (2002) The potential distribution of German wasps (*Vespula germanica*) in Argentina. NZ J Zool 29:79–85

Davis M, Grime J, Thompson K (2000) Fluctuating resource in plant communities: a general theory of invasibility. J Ecol 88:528–534. doi:10.1046/j.1365-2745.2000.00473.x

de Rivera CE, Ruiz G, Hine A, Jivoff P (2005) Biotic resistance to invasion: native predator limits abundance and distribution of an introduced crab. Ecology 86:3364–3376. doi:10.1890/05-0479

DiVittorio C, Corbin J, D'Antonio C (2007) Spatial and temporal patterns of seed dispersal: an important determinant of grassland invasion. Ecol Appl 17:311–316. doi:10.1890/06-0610

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

Elton CS (1958) The ecology of invasions by animals and plants. Methuen, London

Farji-Brener AG, Corley J (1998) Successful invasions of hymenopterans insects into NW Patagonia. Ecologia Aust 8:237–249

Farji-Brener AG, Corley J, Bettinelli J (2002) The effect of fire on ant communities in northwestern Patagonia: the importance of habitat structure and regional context. Div Dist 8:235–243. doi:10.1046/j.1472-4642.2002.00133.x

Farji-Brener AG, Gianoli E, Molina-Montenegro M (2009) Small-scale disturbances spread along trophic chains: leaf-cutting ant nests, plants, aphids, and tending ants. Ecol Res 24:139–145. doi:10.1007/s11284-008-0491-3

Fridley JD, Stachowitcz JJ, Naeem S, Saex DF, Seabloom EW, Smith MD, Stohlgreb TJ, Tilman D, Von Holle B (2007) The invasion paradox: reconciling patter and process in species invasions. Ecology 88:3–17. doi:10.1890/0012-9658(2007)88[3:TIPRPA]2.0.CO;2

Harris RJ (1991) Diet of the wasps *Vespula vulgaris* and *Vespula germanica* in honeydew beech forest of the South Island. NZ J Zool 8:159–169

Hölldobler B, Wilson EO (1990) The ants. Harvard University Press, Cambridge

Holway D, Suarez A, Case T (2002a) Role of abiotic factors in governing susceptibility to invasion: a test with Argentine ants. Ecology 83:1610–1619

Holway D, Lach L, Suarez A, Tsutsui N, Case T (2002b) The causes and consequences of ant invasions. Annu Rev Ecol Syst 33:181–233. doi:10.1146/annurev.ecolsys.33.010802.150444

Keane R, Crawley M (2002) Exotic plant invasions and the enemy release hypothesis. Trends Ecol Evol 17:164–170. doi:10.1016/S0169-5347(02)02499-0

Kennedy T, Naeem S, Howe M, Knops J, Tilman D, Reich P (2002) Biodiversity as a barrier to ecological invasions. Nature 417:636–638. doi:10.1038/nature00776

Kusnesov 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

Kusnesov N (1959) La fauna de hormigas en el oeste de la Patagonia y Tierra del Fuego. Acta Zool Lilloana 17:321–401

Levine MJ, Adler B, Yelenik G (2004) A meta-analysis of biotic resistance to exotic plant invasions. Ecol Lett 7:975–989. doi:10.1111/j.1461-0248.2004.00657.x

Maron J, Vila M (2001) When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. Oikos 95:361–373. doi:10.1034/j.1600-0706.2001.950301.x

Parr C (2008) Dominant ants can control assemblage species richness in a South African savanna. J Anim Ecol 77:1191–1198. doi:10.1111/j.1365-2656.2008.01450.x

Richards C, Bossdorf O, Muth N, Gurevitch J, Pigliucci M (2006) Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. Ecol Lett 9:981–993. doi:10.1111/j.1461-0248.2006.00950.x

Sackmann P (2006) Efectos de la variación temporal y los métodos de captura en la eficiencia de un muestreo de coleópteros en la reserva natural Loma del Medio, El Bolsón, Río Negro. Rev Soc Entom Arg 65:35–50

Sackmann P, Corley JC (2007) Control of Vespula germanica (Hymenoptera: Vespidae) populations using toxic baits: bait attractiveness and pesticide efficacy. J Appl Entomol 131:630–636. doi:10.1111/j.1439-0418.2007.01132.x

Sackmann P, Farji-Brener AG (2006) Effect of fire on ground beetles and ant assemblages along an environmental gradient in NW Patagonia: does habitat type matter? Ecoscience 13:360–371. doi:10.2980/i1195-6860-13-3-360.1

Sackmann P, D'Adamo P, Rabinovich M, Corley J (2000) Arthropod prey foraged by the German wasp (Vespula germanica) in NW Patagonia, Argentina. NZ Entomol 23:55–59

Sackmann P, Rabinovich M, Corley J (2001) Successful removal of German yellow jackets (Hymenoptera Vespidae) by toxic baiting. J Econ Entomol 94:811–816

Sackmann P, Farji-Brener AG, Corley J (2008) The impact of an exotic social wasp (Vespula germanica) on the native arthropod community of north-west Patagonia, Argentina: an experimental study. Ecol Entomol 33:213–224. doi:10.1111/j.1365-2311.2007.00952.x

Simberloff D (1989) Which insect introductions succeed and which fail? In: Drake J, Mooney H (eds) Biological invasions: a global perspective. Scope 37. Willey, Chichester, pp 61–72

Spurr E (1995) Protein bait preferences of wasps (Vespula vulgaris and V. germanica) at Mt Thomas, Canterbury, New Zealand. NZ J Zool 22:281–289

Underwood J (1997) Experiments in ecology. University Press, Cambridge

Vilá M, Weiner J (2004) Are invasive plant species better competitors than native plant species?–Evidence from pair-wise experiments. Oikos 105:229–238. doi:10.1111/j.0030-1299.2004.12682.x

Von Holle B (2005) Biotic resistance to invader establishment of a southern Appalachian plant community is determined by environmental conditions. J Ecol 93:16–26. doi:10.1111/j.0022-0477.2004.00946.x

Von Holle B, Simberloff D (2005) Ecological resistance to biological invasions overwhelmed by propagule pressure. Ecology 86:3212–3218. doi:10.1890/05-0427

Williamson M (1996) Biological invasions. Chapman and Hall, London

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