

Successful invasions of hymenopteran insects into NW Patagonia

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Abstract. *We describe the successful invasion of hymenopteran insects into NW Patagonia. We analyse the importance of the invading species and the characteristics of the invaded community, as well as the role of disturbance on the invasion process, by presenting the most conspicuous of the best documented case studies: the wasps *Vespula germanica* and *Sirex noctilio*, the bumblebee *Bombus ruderatus*, and the leaf cutting ant *Acromyrmex lobicornis*. In their native habitats, these insects are common and have a wide geographical range. In turn, ecological plasticity appears to be the most important demographic trait related to invasion success shared by these species. We believe that climatic matching between the community invaded and the invader's native range together with the absence of natural enemies are the community characteristics better related to invasion success. The role played by biotic resistance remains unclear. The successful establishment of the studied cases is related to some extent to resource liberation due to exogenous disturbance, or competitive displacement of a native species. This might suggest that the native hymenoptera community of NW Patagonia is species saturated, which in turn, could imply that species interactions are important in the community structure in environments where physical variables have been regarded as key factors.*

Introduction

The study of biological invasions is central to both theoretical and applied ecology. Invasions may allow us to identify parameters related to the dispersal, establishment, and persistence of the invading populations. Furthermore, the role invaders play in their new habitat, and their consequences on the ecosystem, may shed light on the characteristics of the invaded community. In addition, because many invaders may become pests (Williamson 1996), or affect conservation practices (Pimm and Gilpin 1989, Caughley 1994), their study can provide useful information for management and control.

There is some debate on the role played by the invaders themselves, the invaded community and disturbance in the process of invasion (Lodge 1993). Some authors have emphasised the importance of community structure, proposing that species composition and richness as well as food web structure determines habitat invasibility (Fox and Fox 1986, Pimm 1989, 1991). Others, instead, suggest that all communities may be equally invaded and that the invading species characteristics, such as reproductive rates, dispersal abilities, native habitat range and ecological plasticity are more powerful predictors of the patterns of invasions (Crawley 1989, Hengved 1989). In addition, human disturbance and mobility have been considered by many as central events promoting successful biological invasions (Fox and Fox 1986, Hobbs and Huenneke 1992, D'Antonio and Dudley 1995).

As it has occurred, for instance, in biodiversity studies, the analysis of invasions has been the subject of a biased perspective: most work has been done on conspicuous plants and vertebrates setting aside other groups such as the insects. For example, of the 22 chapters on biological

invasions covered by SCOPE (Scientific Committee on Problems of the Environment), only one is devoted specifically to the insects (Simberloff 1989). Furthermore, of the few works tackling insect invasions, most are the product of studies on deliberate introductions for biological control and not on natural invasions (Lawton and Brown 1986, Crawley 1987, Simberloff 1989). However, insects are among the most important invaders. For instance, it has been estimated that more than half of the invaders into the USA are insects (Williamson 1996). Among the insects, the hymenoptera are one of the most important orders, in both abundance and ecological importance. There are an estimated 300.000 species, adopting as diverse roles as scavengers, pollinators, parasitoids, predators, seed dispersers or herbivores. These characteristics, coupled with their high dispersal capacities and highly developed sociality, point to them as potentially very successful invaders responsible for considerable impact on the systems invaded (Simberloff 1989). A spectacular example is the African honey bee invasion in the Americas (Smith 1991). Since the introduction of 47 queens by geneticist Warwick Kerr into Brazil in 1956, through amazing dispersal attributes and hybridisation with other domestic bees, it took them less than 35 years to reach southern USA. Indeed, they are now the dominant bee species in most tropical and subtropical areas in the continent (Smith 1991). Wasps and ants, in turn, are also good invaders. Well known examples are the fire ant, *Solenopsis invicta* and the Argentine ant *Linepithema humile* into the USA, and *Vespula* spp. in several parts of the world (Gambino et al. 1987, 1990; Porter and Savignano 1990, Spradbery and Maywald 1992, Allen et al. 1994, Fowler et al. 1994, Vinson 1994, Barr et al. 1996, Human and Gordon 1996, Archer 1998).

Despite geographical isolation and a rigorous climate, Patagonia is no exception for both invasions and the bias to study plant (Rapoport 1991, 1993, Richardson et al. 1994, Gobbi et al. 1995) and vertebrate introductions (Christie 1984, Chehebar and Ramilo 1992, Veblen et al. 1992, Grigera et al. 1994). Despite the fact that invasions by hymenoptera into NW Patagonia are a common event in recent years (Willink 1980, Farji-Brener 1996, Roig-Alsina and Aizen 1996, D'Adamo et al. 1997, Klasmer et al. 1998), there is little and disperse information. Our aim is to describe the natural history and the ecological consequences of some recent invasions of hymenopteran insects into NW Patagonia. We will then explore whether they can tell us something about the invaded community.

We shall consider as invaders, following Drake and Mooney (1989), those organisms colonising and persisting in a community in which they have never been before. We will therefore present the most conspicuous hymenopteran invasion cases: the wasps *Sirex noctilio*, and *Vespula germanica*, the bumblebee *Bombus ruderatus*, and the leaf-cutting ant *Acromyrmex lobicornis*.

Because baseline information on insect diversity and insect invasions (including failures) is rare, we do not expect to test existing hypotheses on biological invasions with these few cases. Notwithstanding this, we believe the information provided here will contribute to the current discussion on the role played by introduced species, native communities and disturbances on the process of invasion. In this sense we concur with the view that, only through detailed studies on the natural history of invaders and on the specific communities which are the subject of invasions we may understand how species colonise new areas. This will lead to more precise and general predictions (Ehrlich 1989, Simberloff 1989, Lodge 1993).

Case study 1: the wasp *Vespula germanica*

The European wasp *Vespula* (*Paravespula*) *germanica*, also known as yellowjackets, is a truly social vespid native to Eurasia and Northern Africa with a wide geographical range (Archer 1998). This hymenopteran is a well know invader as shown by its successful establishment in South Africa, Australia, New Zealand, and the Americas (Spradbery and Maywald 1992, Tribe and Richardson 1994, Archer 1998). Range expansion is generally associated with human settlements (Akre et al. 1989) and their dispersal rates have been estimated at about 70 km/year (D'Adamo et al. 1997). Throughout the world, most ecosystems invaded are temperate and seasonal areas, ranging from forests to deserts (see Archer 1998). In 1974, this wasp was introduced in Chile (Peña et al. 1975).

By 1980, a few individuals were observed across the Andes in the province of Neuquen, Argentina (Willink 1980). Since then, *Vespula germanica* has rapidly spread reaching steppe and coastal areas, and is now a dominant predatory insect of NW Patagonia (Willink 1991, D'Adamo et al. 1997).

In NW Patagonia, as in other parts of the world, *Vespula germanica*, builds annual nests above or below the ground, in some cases making use of protected sites such as barns, houses and gardens, where the progeny is raised (Spradbery and Maywald 1992). These nests are initiated by overwintering mated queens at the beginning of the Spring. The first workers emerging, rapidly give the nest its final structure which will bear about 3,000 individuals (Willink 1991). With the exception of egg laying, workers are in charge of most colony activities such as tending larvae, and foraging. At the end of the summer the queen's production shifts towards reproductive individuals (between 100-600 virgin queens per colony) which mate in nuptial flights. After mating, queens search for refuges, such as the bark of trees or stored lumber where they remain until the next Spring. Exceptionally, nests may overwinter and reach outstanding population numbers (Harris 1996).

Vespula germanica is an opportunistic predator and scavenger. Foraging is carried out individually by workers within a limited range from the nest, but there is a remarkable aggregative response to resource concentration probably due to social facilitation (Akre and MacDonald 1986). However, it has been shown that there may also be worker recruitment, at least to carbohydrate-rich food sources (Overmeyer and Jeanne 1998). Yellowjackets feed on a diversity of insects, but may also forage for nectar and honeydew and scavenge on dead mammals, birds and garbage (Akre and MacDonald 1986, Barr et al. 1996). Because these wasps can tolerate low temperatures, foraging activity is prolonged within the day and throughout the season (Akre et al. 1989, J. Corley, pers. obs.).

Yellowjackets can have an important impact on the native arthropod biota (Akre and MacDonald 1986, Gambino et al. 1987, Harris 1996). In NW Patagonia, wasps are common in *Nothofagus* dominated forests, ecotonal scrub and steppe areas and have been observed preying upon domestic honeybees as well as on the native insect fauna (Farji-Brener and Corley 1998, D'Adamo et al. 1997). However there are so far no systematic data on their potential impact in this region.

Case study 2: the leaf-cutting ant *Acromyrmex lobicornis*

In the early 50's, the leaf-cutting ant *Acromyrmex lobicornis* had not reached the valley of the Alumine river, and had not been reported in the National Parks of Patagonia (Kusnezov 1951, 1953). By 1980, ant nests were common further south, in the valley of the Limay River (E. Rapoport, pers. comm.). At present, this leafcutter is found in the Nahuel Huapi National Park, some 15 km to the East of the city of Bariloche (41° S, 72° W), and could be still in expansion (Farji-Brener 1996).

As all species of *Atta* and *Acromyrmex*, *A. lobicornis* is endemic of the Americas, and cuts leaves and flowers to cultivate the fungus on which they feed (Hölldobler and Wilson 1990). This leaf-cutting ant species has one of the largest geographical ranges in the New World, and the largest in Argentina (Farji-Brener and Ruggiero 1994). Its distribution includes mountains, subtropical rain forests, and deserts showing great ecological plasticity (Kusnezov 1953, 1978). Such plasticity is also shown by its capacity to (1) adjust to temperature variations as they can forage during either day and night hours (Pilatti and Quirndn 1996), (2) harvest on both mono and dicot leaves, (3) modify nest structure to minimize the effects of the ambient temperature for fungus culture (Zolessi and González 1974, Farji-Brener 1998), and (4) move to a new nest after disturbance (Claver 1990, Farji-Brener 1998).

Dispersal by this species is limited to winged adults. Once every year, at the beginning of the summer, each colony produces 100-1000 reproductive individuals (males and females) which mate with individuals from other nests during the nuptial flight (Bonetto 1959, Hölldobler and Wilson

1990). Mated queens travel up to 11 km from the nest and found a new colony (Fowler et al. 1986). The geographical expansion of *A. lobicornis* in NW Patagonia may have been promoted by the disturbances generated by road building and maintenance, which may be acting as corridors for range expansion (Farji-Brener 1996, 1998). Although the reasons why these ants choose such disturbed sites where to nest are yet unknown, they could be related to the physical character of the soils and/or the abundance of palatable plants found at these sites.

These ants have both direct and indirect effects on the native community. The most obvious direct effect is their role as primary consumers. *A. lobicornis* harvests an average 8.5 kg/year/nest of plant material, more than other species of the same genus (Fowler et al. 1990, Pilatti et al. 1997). This species is one of the most important herbivores in steppe areas. Considering, for instance, the high nest densities found in some places in Patagonia, a total of about 450 kg of plant material may be harvested per year in only one hectare. However, as leaf cutters are common in disturbed sites, the affected vegetation is mostly exotic. In fact, almost 70% of the diet of *A. lobicornis* in such environments is composed of exotic species such as *Erodium cicutarium*, *Bromus tectorum*, *Carduus nutans* and *Marrubium vulgare* (Farji-Brener and Franzel, unpublished data).

Case study 3: the woodwasp *Sirex noctilio*

The wood wasp *Sirex noctilio* is probably the least illustrative example of a natural invasion. Native to Mediterranean Europe, a few dormant individuals were accidentally introduced with lumber into NW Patagonia in 1993 (Klasmer et al. 1998). *S. noctilio* is, with the exception of the also exotic *Urocerus gigas*, the only siricid wasp present in Patagonia (P. Klasmer, pers. comm.). It is a primitive phytophagous insect, that in its natural environment attacks pine trees with a prior pathological condition and hence has little economic importance. However, it has become a major pest of softwood forestations in the Southern Hemisphere (Madden 1988). Successful invasions by this wasp have been reported in Australia and New Zealand, South Africa and South America (Madden 1988). Each female, after copulating during flight, may lay up to about 250 eggs during her short -a fortnight long- life span (Ipinza Carmona and Molina 1991). Eggs are laid individually or in groups of 2 to 3, about 1.5 cm within the wood of the trees. An outstanding ecological feature of this group, is that larvae cannot feed or grow on wood, but they rely on its prior alteration which is achieved by a symbiont, species-specific, basidiomycetous fungus (Madden 1988). Generally, the life cycle of *S. noctilio* takes 12 months, but, for some individuals, may actually last up to 36 months (Corley et al. 1998). This, probably reflects high ecological plasticity as it is a means of dealing with unpredictable environments. In Western Patagonia, adult emergence begins in late December and may extend until early June, with a peak in March (Klasmer et al. 1998).

In NW Patagonia, the distribution of this wasp is tied to the distribution of pine plantations, which is restricted to an intermediate rain regime (between 500 and 900 mm/year). Populations are, however, well established, seeming to be at low densities (tree attack rates less than 3%) with a somewhat stabilised 50:50 sex ratio (Corley, unpublished data). The native conifer, *Austrocedrus chilensis*, the only tree which grows in the same areas where pine forestations are common, induces oviposition behaviour in *S. noctilio* females, but eggs, if laid, are not successful (P. Klasmer, pers. comm.)

One of its parasitoids used in biological control, the exotic hymenopteran *Ibalia leucospoides* was detected together with *S. noctilio* in the Patagonian plantations. This natural enemy may cause an average 20% mortality but is probably of little regulatory importance (Taylor 1978, Corley, unpublished data).

Case (that needs further) study 4: the bumblebee *Bombus ruderatus*

In 1982, the European bumblebee *Bombus ruderatus* was introduced into Chile to improve pollination of white clover (*Trifolium repens*) (Arretz and Macfarlane 1986). Four years later, due to remarkable dispersal and abundance, this species was listed as one of the common bees of Chile (Toro 1986). In 1992, this exotic bumblebee was common in Southern Chile, but it was not recorded in NW Patagonia (Asperen de Boer 1992). By 1993, Roig-Alsina and Aizen (1996) reported *B. ruderatus* at several sites in the West of the Province of Río Negro, Argentina. At present, its geographical range in NW Patagonia includes rural, scrub, and Nothofagus and Austrocedrus forests (Roig-Alsina and Aizen 1996).

Several hundred species of *Bombus* are known worldwide. Most are typical of temperate habitats of the Northern Hemisphere. Bumblebees have a primitive social structure. They build annual colonies in subterranean nests, in many cases using abandoned mice and bird nests. By the end of spring, virgin queens abandon the maternal nests (which finally disappears), mate and disperse in search of appropriate refugia where to spend the winter. Foraging for nectar and pollen, as well as scouting for a site where to nest, will begin the following spring (Michener 1974). *B. ruderatus* is known for its pollination abilities in temperate environments, and builds one of the most numerous colonies of the genus (Michener 1974).

A long-term study of the pollination dynamics of *Alstroemeria aurea* (amancay) indicates that populations of this bumblebee in NW Patagonia have increased in the last years. Furthermore, they might be displacing the only native bumblebee of the region, *Bombus dahlbomii*. In the last five years, *B. ruderatus* has increased its relative rate of visit to this native plant species in the upper Challhuaco valley from 1 % to 30% (M. Aizen, pers. comm.). In addition, this study suggests that disturbance may favour its presence (Roig-Alsina and Aizen 1996). While populations of amancay in forests with little disturbance are almost exclusively visited by *B. dahlbomii*, populations located only 600 m away, in sites with high levels of disturbance, have visitation rates by the exotic *B. ruderatus* above 60% (Aizen and Feinsinger 1998). Given that the native bumblebee plays an important role in native plant pollination, its competitive exclusion by its exotic counterpart could affect short and long-term plant dynamics in the region.

Discussion: why have these invaders been successful?

The insects described here arrived in NW Patagonia through different ways. These include direct human introduction (*S. noctilio*), human transportation into a neighbouring region and then naturally expanding into Patagonia (*B. ruderatus* and *V. germanica*), and through the natural expansion of their distribution (*A. lobicornis*). It is interesting to note that two of the four species described arrived from Chile, suggesting that the Andes at these latitudes and at this time are not a barrier for the dispersion of the hymenoptera.

All these invasions are characterised by their remarkable success. All species have established stable populations and rapidly became part of the insect fauna of NW Patagonia. Why have they been successful? In this section we explore the relative importance of the demography of the invader species, the characteristics of the invaded community, and the role of disturbance on the process of their successful invasion. Finally, we discuss the possibility of inferring local community characteristics through the invasion of these hymenoptera.

The invaders

The species described in this study have all a wide native range and have been successful in other parts of the world where they have invaded (Table 1). This probably indicates that the demographic aspects they share and make them common species in their native habitats could be related to their invasion success (Crawley 1989, Williamson 1996). Among these, ecological plasticity appears to be common for the hymenoptera that invaded NW Patagonia. With the obvious exception of *S.*

Table 1. Classification of the hymenoptera which successfully invaded NW Patagonia according to organism characteristics cited as central for the success of a biological invasion.

Characteristic	<i>Sirex noctilio</i>	<i>Vespula germanica</i>	<i>Bombus ruderatus</i>	<i>Acromyrmex lobicornis</i>
Native range size	small	large	?	large
Previous invasion success	high	high	high	high
Dispersal rate	low	high	high	intermediate
Ecological plasticity?				
Foraging niche breadth	narrow	broad	broad	broad
Foraging strategy	selective	solitary, partially recruiting, opportunistic	solitary, opportunistic	recruiting, selective opportunistic
Activity season length (month/year)	5-6	9-10	5-6	11
Sociality	none	high	primitive	high
Other	prolonged quiescence	nest location	?	nest location
R-selected traits				
# generations/yr	≤1	1	1	1
# reproductive ♀/♀/yr	100	100-600	150 (*)	300-2000(*)
Reproductive ♀ longevity	16 d	1 yr	1 yr	10 yr
Larvae tending	no	yes	yes	yes
Density dependency	probable	yes	yes(*)	yes(*)
Dependency on environment	high	low	high	low
Main ecological role	phytophagous	predator/scavenger	pollen, nectar feeder	herbivore

Sources. *Bombus ruderatus*: Michener 1974, Heindrich 1981, Roig-Alsina and Aizen 1996, M. Aizen pers. comm.; *Sirex noctilio*: Corley et al. 1998, Corley unpublished data; *Vespula germanica*: Akre et al. 1980, Willink 1980, 1991; Akre and Mac Donald 1986, Fordham et al. 1991, Spradbery and Maywald 1992, Tribe and Richardson 1994, Overmeyer and Jeanne 1998 and pers. obs.; *Acromyrmex lobicornis*: Kusnezov 1978, Weber 1982, Fowler et al. 1986, Fowler 1987, Hölldobler and Wilson 1990, Diehl-Fleig 1993, Farji-Brener and Ruggiero 1994, Farji-Brener 1996, 1998, Pilatti et al. 1997, pers. obs. (*) data characteristic of taxon or of similar species of the same genus.

noctilio, whose survival is strictly dependent on the existence of exotic pine trees, the rest of the species are characterised by having several indicators of high plasticity: (1) Tolerance to a wide range of physical conditions, adjusting their activity to deal with unfavourable circumstances. For instance, both *V. germanica* and *A. lobicornis*, can be active in early winter if the weather is good. (2) The ability to shift their diet according to resource availability. *V. germanica* actively preys upon live insects but aggregates strongly to carrion or garbage as a protein source as soon as this becomes available, whereas *A. lobicornis* can harvest in both a selective or opportunistic frequency-dependent manner, and *B. ruderatus* modifies its rate of flower visits according to resource patch quality. (3) Flexible nesting habits. For example, yellowjackets can build subterranean or hanging nests according to inundation regime or other site characteristics; bumblebees can use abandoned mice and bird nests, and the leaf-cutting ant species can respond rapidly to disturbance by abandoning their affected nests and building a new one. In NW Patagonia, ecological flexibility could be an important trait as resource availability is affected by short term, unpredictable weather changes. Even the woodwasp, *S. noctilio* and its hymenopteran parasitoid *I. leucospoides*, despite their host specificity, show attributes, such as the delayed adult emergence that may be related to habitat unpredictability (Corley et al. 1998).

Winter survival, is probably another ecological feature common to these species which could affect invasion success in the rigorous conditions of NW Patagonia. Hymenopteran insects are ectothermic animals whose survival and activity patterns are, in many cases, temperature dependent. There are several ways in which these organisms overcome the winter. For instance, yellowjacket

and bumblebee mated queens hibern in protected refugia until spring begins. *S. noctilio*, in turn, remain as quiescent larvae within the sapwood throughout the winter and spring (Corley et al. 1998). Finally, leaf-cutting ants can modify their mound-nest structure to regulate the internal temperature, which allows the fungal development required for colony feeding (Farji-Brener 1998). Several authors have suggested that successful invaders typically have r-selected traits (Lawton and Brown 1986, Lodge 1993). However, it is hard for us to say if this is the case for the insects here studied (Table 1). Population growth rates of these organisms (number of reproductive females per female) are high but are probably not significantly higher than for other comparable hymenoptera (Akre et al. 1980, Hölldobler and Wilson 1990, Gambino 1991). Other, r-selected characters such as the absence of density-dependence, low parental care of the offspring, a high dependency of environmental factors, and a low longevity show great variation among the case studies analysed (Table 1). For these insects, some of these attributes are typically associated with social development (e.g.: lack of offspring tending in *S. noctilio* versus the rest), but in some cases may even vary within comparable social behaviour (e.g.: queen longevity in *A. lobicornis* and *V. germanica*).

The community

The community characteristics that better relate to the invasion success in NW Patagonia are the climatic matching with native range and the absence of natural enemies (Table 2). Pre-adaptation to a given climate coupled with the absence of predators, parasites or pathogens of regulatory importance can determine the success of any invasion (Lawton and Brown 1986, Crawley 1987, Simberloff 1989).

Both wasp species and the bumblebee described are native to temperate seasonal environments or else have wide geographical ranges. The current distribution of both wasp species in the Southern Hemisphere is generally related to such seasonal conditions (i.e., both have successfully invaded Australia, Tasmania, southern South Africa and New Zealand). However, the leaf-cutting ant *A. lobicornis*, endemic of the Americas, is a different case. Despite the fact that its distribution covers almost all Argentina (Kusnezov 1978), the populations inhabiting the southern areas are more abundant in desert landscapes (Kusnezov 1953, Claver 1990, Farji-Brener 1996, 1998; Pilatti et al. 1997). Such adaptation to dry habitats may help explain their restricted distribution in NW Patagonia, which is currently limited to the steppe region.

Although there is little information on these case studies to substantiate conclusions on the role played by "biotic resistance" and local food web structure on invasion success, it seems that for populations of *V. germanica* and *A. lobicornis* interspecific competition has had little importance. Although there is a native bumblebee with a similar ecological role as *B. ruderatus*, the establishment of populations of the exotic species has been remarkably successful. In addition, the species we have described here have diverse ecological roles, and have established at different levels of the local food web structure. Past work has suggested that the structure of the local assemblages can be central in determining where in the food web will alien species have a better chance of becoming established (Pimm 1991). However, *Vespula germanica* has found little resistance in establishing as a dominant predator and scavenger while *Acromyrmex lobicornis* became a primary consumer in the same trophic chain.

The role of disturbance

All of the cases studied here have been associated to some degree on disturbance for colonisation or establishment. Among the several ways in which disturbance can modify the resource base of a community (creating or amplifying resources, see Fox and Fox 1986), the creation of new resources seems to have been central to the invaders in NW Patagonia. The abundance of *Vespula germanica* is related to human activity as shown by the fact that yellowjackets can forage for garbage and use human constructions to nest. *Acromyrmex lobicornis*, in turn, builds nests in steppe roadborders and selectively harvests exotic plants related to such disturbance (Farji-Brener 1996, 1998). Probably the most remarkable example is *Sirex noctilio* whose eggs are only viable in exotic pine trees, and thus strictly depend on habitat replacement by an exotic species.

Table 2. Characteristics of the process of invasion and of invaded community related to the invasion success of Hymenoptera in NW Patagonia.

Characteristic	<i>Sirex noctilio</i>	<i>Vespula germanica</i>	<i>Bombus ruderatus</i>	<i>Acromyrmex lobicornis</i>
Human transportation	yes	indirect	indirect	no
Habitat invaded	pine plantation	urban, steppe, scrubland, forest	urban areas, scrubland, forest	steppe, river banks
Climatic matching	high	high	high	high
Dependence on disturb.	high	high/intermediate	high/intermediate	high
Natural enemies	yes	no	no	no
Abundance control	bottom-up	bottom-up	bottom-up	bottom-up
Similar species	no	no?	yes	no?
Competition	no	no?	yes	no
Community or ecosystem effect	none	impoverishment of local insect fauna?	displacement of local bumblebees	nests act as a weed source

Sources. *Sirex noctilio*: Taylor 1978, Madden 1988, Klasmer et al. 1998, Corley, unpublished data and pers. obs.; *Vespula germanica*: Willink 1980, 1991, P. D'Adamo and P. Sackmann, pers. comm., and pers. obs.; *Bombus ruderatus*: Roig-Alsina and Aizen 1996, Aizen and Feinsinger 1998, M. Aizen, pers. comm.; *Acromyrmex lobicornis*: Kusnesov 1978, Farji-Brener 1996, 1998, Farji-Brener and Margutti 1997 and pers. obs.

The influence of disturbance on invasibility depends however on the attributes of each system. For example, it is important to distinguish what resources are limiting success and on what sort of disturbance will have the most powerful effect in increasing the chance of success. The case studies we have looked at here have been related to disturbances that increased food availability or nesting sites, suggesting that food and refuge (this could be more related to the harsh climate rather than to predatory pressure) are important constraints in NW Patagonia.

Effects on the community

There is little information on the effects that these exotic insects have on the native community. The best known case is that of the leaf cutting ant species on soil and vegetation, which shows how their nests can act as dispersal sources for weeds, thus increasing plant diversity. *Acromyrmex lobicornis* dumps organic waste of fungal growth on the soil surface close to the nest. These "refuse" contain organic matter and nutrients up to 9 times higher than those found in the adjacent soil. In this refuse, two exotic plants *Carduus nutans* and *Onopordum acanthium* have higher densities than elsewhere. Some laboratory experiments have shown that individuals growing on these refuges have higher growth rates and seed production than those growing away from the nests (Farji-Brener and Ghermandi 1997). Furthermore, small-scale disturbances due to nest construction and maintenance can increase plant species diversity (Lewis et al. 1991, Farji-Brener and Ghermandi 1996). The role of leaf-cutting ants on plant communities of NW Patagonia is complex, especially in relation to exotic vegetation. While they can negatively affect some species through selective foraging, they can favour others by the disturbance related to the nests. However, it should be noted that nests are found in the highly disturbed steppe sites such as road banks, thus many of their effects are diluted by practices such as road maintenance, which suggests an overall low impact at the ecosystem level (Farji-Brener and Margutti 1997).

Despite a lack of local information, potential impact by the other species can be inferred from reports for other regions. For instance, *Vespula spp* are important predators that affect the activity of an array of arthropods in Hawaii (Gambino et al. 1987, 1990, Gambino 1991) and New Zealand (Harris 1996). *Vespula germanica* preys on other insects such as ants, spiders and bees in Patagonia (Farji-Brener and Corley 1998). It is worth noting that the region lacks native social vespids and leaf cutting ants. An interesting hypothesis to put to test is whether the ecological similarity between

invaders and local species affects invasion success (Pimm 1989), as for instance, there is a native counterpart for the alien bumblebee.

Can we infer community characteristics from these invasions? A speculation

Can the invasions described suggest how the community is structured and which are the ecological processes responsible for it? We believe that the manner in which invasions have occurred may be informative on, for example, whether the community is species saturated (see Price 1991). The traditional way of looking into this issue is through the analysis of the effects that an increase of the regional species pool has on the local species richness (Cornell 1985). If local richness rises consistently with the regional pool, the community is not species saturated and species richness is a function of meso-scale process such as dispersal. In other words, there would be "room" for more species, but these simply cannot reach the site. In contrast, local communities would be species saturated if an increase in the regional pool is not reflected in the local pool. Following the same reasoning as above, species would be able to reach the site (dispersal is no constraint) but simply do not "fit" and so cannot establish successfully. This pattern suggests that local processes such as species interactions are responsible for the maintenance of the number of species in the assemblage (Price 1991). If a community is not species saturated, then there are vacant niches whereas if it is species saturated these would not exist. There is some debate on the vacant niche concept, because the definition of the niche includes species characteristics (Crawley 1989). However, if we regard an empty niche as a synonym of available resources of some kind, then there are examples of empty niches in natural systems (Williamson 1996).

In theory, a simple way of looking through invasion history, for evidences of empty niches (hence of community species saturation) is by determining if invaders are playing some new role in the assemblage or are using some "new" resource. This, simple in words, is difficult to put into practice. One of the main drawbacks is that one must possess a full knowledge of the studied community and this is usually far from achieving as such information is virtually non-existing. Alternatively, invasion failure analysis can also provide an insight of community structure. But, usually information on invasion failure is scarce. In turn, how invaders established in their new habitat can offer a shortcut, albeit limited, to understanding community species packing. Should local species be using all available resources, we would expect that the invader, to be successful, must either outcompete native dwellers or depend on some exogenous disturbing event, responsible for liberating resources (see Fox and Fox 1986). On the contrary, should dispersal or other larger scale process be limiting local richness, we would expect invaders having the highest dispersal rates (or carried by humans) to become established with success, irrespective from disturbance or competitive abilities.

The species analysed here all have either displaced a native organism with a similar ecological role (*Bombus ruderatus*), relied on disturbance for successful establishment of their populations (*Vespa germanica* and *Acroinyrmex lobicornis*) or else depends on a new resource exclusively used by it (*Sirex noctilio*). This suggests that the native assemblage of the Hymenoptera in NW Patagonia could be species saturated. The exotic and the native bumblebees share common resources but avoid each other, suggesting a competitive interaction. The other examples are instead related to disturbance. For instance, the leaf cutting ant species selectively forages on exotic plants associated with exogenous disturbance whereas yellowjacket success can be related to garbage, orchards and bee hives for food and human buildings as protected nesting sites (Fordham et al. 1991, Farji-Brener 1996).

In natural systems, there is evidence of empty niches in insect assemblages, suggesting that these communities are unsaturated of species (Simberloff 1981, Lawton 1984). However, there is also evidence for saturated insect communities which suggest that local interactions are important in maintaining species diversity (Fowler and Claver 1991). In NW Patagonia, the invasions by hymenoptera support the view that the local processes could be maintaining current species

diversity. Additional support in favour of a tight species packing in this region comes from plant invasion. The successful establishment of most exotic vegetation is closely related to exogenous disturbances (Rapport 1991, 1993, Margutti et al. 1996).

Given that, this interpretation of community structure is based on a relationship between exogenous disturbance and invasion success, we must take into account the null hypothesis that invaders are associated with disturbance irrespective of the community invaded. If this were the case, disturbance-dependence for successful establishment is more related to the invaders life history, and then there would be little to infer about the invaded community structure. This however deserves further study.

Our hypothesis that local processes are important for the maintenance species number in NW Patagonia, does not rule out the central role of historical and abiotic events in determining community structure. However, it is interesting to analyse the importance of species interactions in temperate communities (see also Price 1991 and Aizen and Ezcurra 1998), where past work has emphasised the role played by abiotic factors.

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