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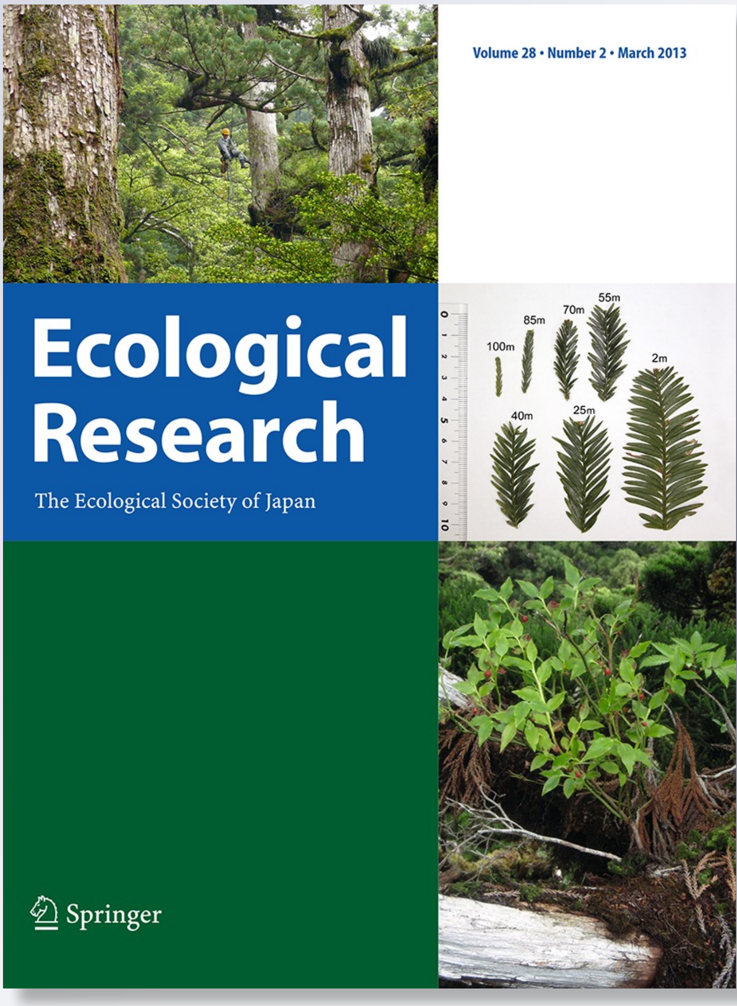

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ORIGINAL ARTICLE

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Of volcanoes and insects: the impact of the *Puyehue–Cordon Caulle* ash fall on populations of invasive social wasps, *Vespula* spp.

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Abstract Volcanic eruptions have important effects on terrestrial ecosystems. The biotic effects of volcanic ash on insect populations vary from widespread and catastrophic to subtle and localized. Volcanic eruptions may increase insect mortality through the effects of the ash plume, and these vary by taxon or specific biological features. The *Puyehue–Cordon Caulle* Volcanic Complex is the most recent eruption in Patagonia. Here we explore and describe the effects of the eruption of this volcanic complex on invasive *Vespula* spp. populations. These wasps are very abundant social hymenoptera that have recently invaded Patagonia. We placed baited traps following the gradient of deposited ash, and revisited them once a week during February to April. No wasps were caught where ash deposition levels exceeded 3.0 cm. The number of wasps caught in sites with minimal ash deposits was similar to that of previous years. In locations where ash layers are intermediate, a few wasps were observed, but only during the peak of wasp abundance. We show that *Vespula* spp. populations were severely affected by the ash deposition and plume, caused by this eruption. These results show catastrophic effects of ash deposition over a large area, even at great distances from the eruption epicenter. We conclude that wasp mortality explained by the volcanic eruption may reach distant areas, and cause local extinction. In areas where active volcanoes are common, invasive insects may encounter an additional obstacle in their invasion success.

Keywords Yellowjackets · Insects · Exotic · Ash deposition · Patagonia · Argentina

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Introduction

Volcanoes are of interest to earth scientists as subjects of study in their own right, but they have important implications for other disciplines as a result of their impact over a broad range of spatial scales. This is because active volcanoes are found in many different regions and their activity can have varied and complex consequences upon several human activities, such as airport operation, tourism, farming, beekeeping, and upon vegetation and domestic animals (del Moral and Grishin 1999).

For terrestrial ecosystems surrounding the eruption sites, volcanic activity can have immediate and devastating physical impacts due to blast waves, pyroclastic flows, lahars, and volcanic bombs (Annen and Wagner 2003). Ash fall, the >0.03-mm particles produced during and sometimes long after a major eruptive event, can have strong direct effects on the biota, such as the immediate and massive loss of habitat (Arendt et al. 1999). However, ash-derived effects are less evident and there is less information available about them. Note that the lighter fractions of volcanic ash can be dispersed more widely, affecting thousands of km^2 (Martin et al. 2009).

The biotic effects of ash from volcanoes on insect populations vary from widespread and catastrophic to subtle and localized, and ranges from the equivalent of a short-term, broad-spectrum insecticide application (Klostermeyer et al. 1981) to the long-term disruption of herbivore–predator–parasitoid equilibrium (Wille and Fuentes 1975). The main cause of insect mortality, after exposure to volcanic ash, is assigned to desiccation resulting from abrasion of the insect cuticle, spiracles occlusion, excess salivation from grooming, and the disruption of digestive activity through the accumulation of ash boli in the gut (Wille and Fuentes 1975; Brown and Hussain 1981; Edwards and Schwartz 1981). Also, insect mortality rates vary by taxon, life stage, extent of exposure to ash particles, and biological features such as the availability of shelter or assisted escape (Akre et al. 1981; Brown and Hussain 1981; Marske et al. 2007). However, volcanic ash apparently could promote the survival of other insects as has been shown for *Coccus viridi* (Hemiptera, Coccidae) and *Sipha flava* (Hemiptera, Aphididae) after the Irazú volcano eruption in Costa Rica in 1963 (Wille and Fuentes 1975).

The southern region of the Andes Mountains (36°–44°S, 72°W) has numerous volcanoes and in Patagonia, eruptions of variable magnitude are not infrequent events. Approximately 50 volcanoes show or have shown some type of eruption in recent times (Besoain 1985). The latest eruption is that beginning on June 4, 2011, of the *Puyehue–Cordon Caulle* Volcanic Complex (2,236 m a.s.l., 40°32′S–72°2′W, Chile). The eruption produced a 5-km-wide ash fall and a gas column of up to 14,000 m during the first day, shedding into the atmosphere approximately 950 million tons of ash. Due to the prevailing westerly winds, 24 million ha of Patagonia ended covered with ashes to different degrees (Gaitán et al. 2012). Lava blocks, fragments of rock carried by the plume, fell to the ground by loss of energy and sustainability affecting the immediate surroundings of the craters. Approximately 15–17 cm of coarse ash fall was received in Villa La Angostura, 54 km SE of the vent; and 3–4.5 cm of medium to coarse tephra (3–6 mm in diameter) fell in the city of San Carlos de Bariloche, located 100 km SE of the vent (Wilson et al. 2012). The volcanic dust—lighter material carried by the wind—(i.e., ash plume or plume, <0.03 mm in diameter) in turn was carried by the wind thousands of kilometers and also continued to emerge for several months.

Vespula spp. are social hymenopteran insects belonging to the Vespidae family that are native to the Palearctic region. *Vespula germanica* (Fabricius; Hymenoptera) in the last century has invaded New Zealand, Australia, South Africa, North America, Canada, Chile, and Argentina, where it was first detected in 1980. *Vespula vulgaris* (Linnaeus; Hymenoptera) has invaded Australia, Asia, New Zealand, and in 2010 Argentina (Willink 1980; Masciocchi et al. 2010). Both wasp species, when in high numbers, may negatively affect natural ecosystems and numerous economic activities such as beekeeping, horticulture, tourism, and cattle rearing. Also, the painful and occasionally fatal sting may interfere with human outdoor activities and affect residential areas where wasps are attracted to stored food and refuse (Akre and MacDonald 1986). Because of these reported problems, there has been extensive research on the ecology and control of these wasps in many invaded areas (Beggs et al. 1998; Beggs 2001; Sackmann et al. 2001).

Here we describe the effects of the eruption of the *Puyehue–Cordon Caulle* Volcanic Complex, on invasive *Vespula* spp. populations. While we do not explore mechanisms in detail here, we aim to contribute to the knowledge on the extent to which volcanic activity can affect non-native insect populations, using *Vespula* spp. as a study model. This is because *Vespula* wasps are very abundant in the affected area and were inactive during the eruption (Farji-Brener and Corley 1998; Barlow et al. 2002). We thus expect to contribute knowledge on the spatial scale and on the effects of volcanic activity on insect species. As *Vespula* spp. are pestiferous, invasive species, we also attempt to initiate studies that lead to evaluate whether the effects of this specific volcanic event contribute to effectively reducing local wasp populations. We hypothesize that the volcanic eruption, through the insecticidal effect of volcanic ash, can locally eradicate wasp colonies in areas close to the volcano, and reduce populations following a gradient of ash intensity.

Methods

Description of *Puyehue–Cordon Caulle* Volcanic Complex eruption and ash characterization

The *Puyehue–Cordon Caulle* Volcanic Complex is a cluster of Pleistocene to recent volcanic centers that are aligned in a northwest–southeast trend, oblique to the main volcanic front of the Southern Volcanic Zone of the Chilean Andes. The complex forms a transversal, 15-km-long by 4-km-wide ridge, which consists of four different volcanoes: the Cordillera Nevada (1,799 m a.s.l.), the Pliocene Mencheca volcano, the Cordon Caulle fissure vents (1,793 m a.s.l.) and the Puyehue stratovolcano (2,236 m a.s.l.) (Gerlach et al. 1988; Lara et al. 2006). The Volcanic Complex rests upon the trace of a traverse fault with the larger north–south Liquiñe–Ofqui Fault (Lavenu and Cembrano 1999). The chemical composition of the *Puyehue–Cordon Caulle* Volcanic Complex is mainly rhyodacitic to rhyolitic, with subordinated basaltic to andesitic types among the earlier lavas (Gerlach et al. 1988). The Volcanic Complex has a long record of active history spanning from 300,000 years ago to the present. The historical eruptive activity, referred as the period span after the Spanish conquest (i.e., the last ~500 years), is only partially known and the record appears poor. In the last century, eruptions were recorded during the years: 1914, 1919, 1921–1922, 1929, 1934, 1960, 1990 (Lara et al. 2006), and 2011 (Gaitán et al. 2012).

Overview of the biology of *Vespula* wasps

Two species of introduced *Vespula* wasps have established in Argentina. *Vespula* spp. colonies, like those of other social insects, have caste differentiation. Generally, there is one queen, numerous workers, and a few drones (males). Post-hibernating queens begin nest construction in dry and protected sites, usually occupying pre-existing holes dug out in the soil (Sackmann et al. 2000). Colonies are founded in spring and are annual. The first workers continue building the nest, maintain and defend it, and also provide food to the larvae and queen. Each colony can hold between 3,000 and 5,000 workers in peak season (Willink 1991; Sackmann et al. 2000). Towards the end of the summer, the queen begins to produce reproductive individuals (drones and new queens), which leave the nest to mate. While drones die, queens look for shelter to hibernate until the following spring (Harris 1996). *Vespula* spp. are opportunistic predators and scavengers, (Akre and MacDonald 1986; Barr et al. 1996; D' Adamo and Lozada 2005). In NW Patagonia, mated queens are visible from late September and most colony activity subsides by April/May.

Study area

This study was carried out in the region that received the greatest ash falls after the eruption of *Puyehue–Cordón Caulle* Volcanic Complex in June 2011 (Gaitán et al. 2012), and the surrounding non-affected areas. It comprises urban, suburban, and rural areas, nearby to San Carlos de Bariloche, Villa La Angostura, San Martín de los Andes and El Bolsón cities, in NW Patagonia, Argentina (40°–42°S, 71°–72°W, Fig. 1). In this region, the climate is temperate, dominated by a marked west-to-east decrease in precipitation (from 3,000 to 600 mm in less than 100 km). Vegetation reflects this climatic pattern, encompassing a striking shift from humid *Nothofagus*-dominated forests towards the west, to *Austrocedrus*-dominated dry forests on the border of the grass-shrub Patagonian steppe to the east (Paruelo et al. 1998).

Sampling methods

We placed wasp traps following the gradient of deposited ash as described by Gaitán et al. (2012; Fig. 1). We determined a total of 51 sampling sites within Neuquén

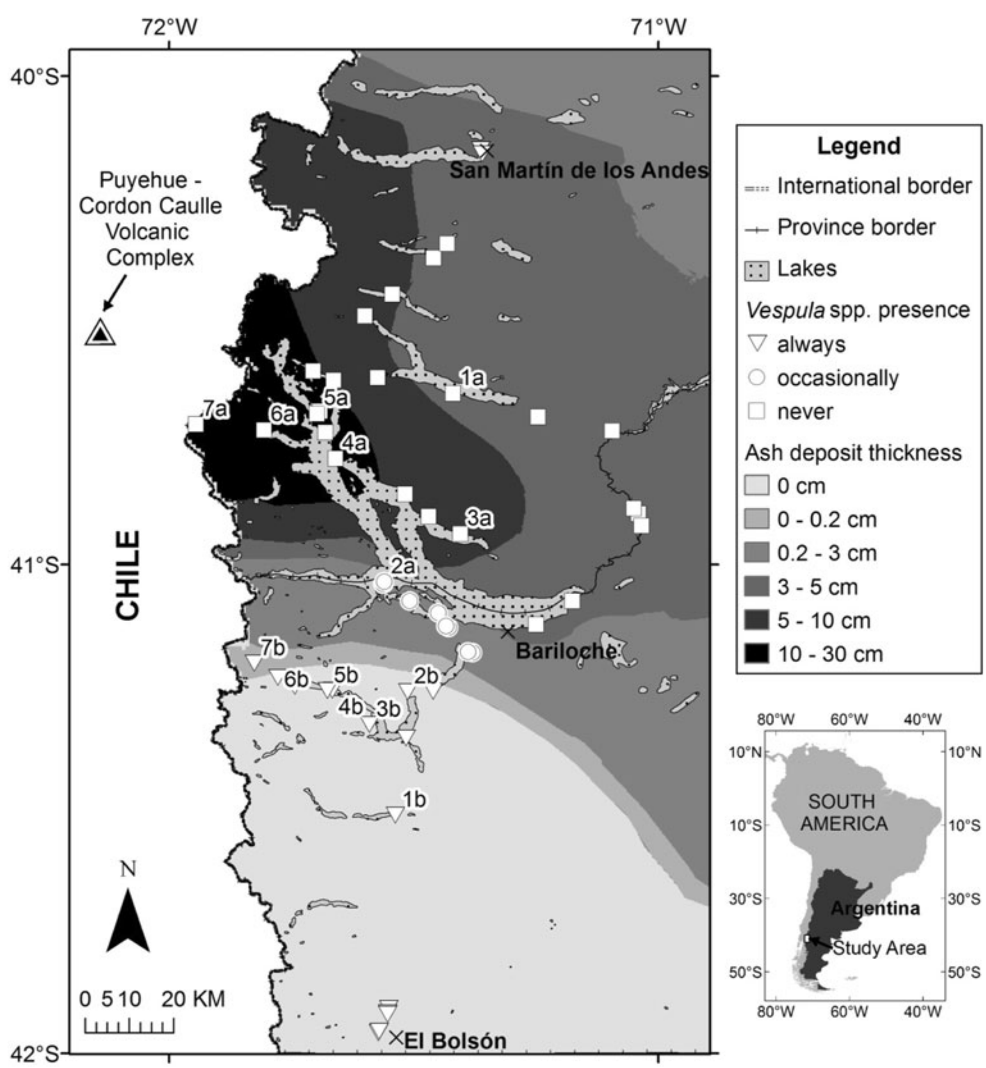

Fig. 1 Map of the study area with the location of the 51 sampling sites in NW Patagonia (Argentina). The sites chosen for the paired tests are identified with numbers from 1 to 7; *a* indicates sites with ash and *b* sites without ash

and Río Negro provinces (Fig. 1). These were separated on average by 5 km, and a minimum of 600 m from one another. Each trap consisted of a plastic bottle with a small piece of meat (approximately 10 g) half filled with water, and a few drops of detergent to reduce surface tension. We recorded the number of wasps collected in the bottles at each of the 51 sites and changed the bait every 7 days of exposure. We also selected seven pairs of sites with and without ash deposits, following a blocked design on precipitation gradient (Barros et al. 1983). Blocking allowed removing the variability related with environmental features associated with rainfall variation. Sites without ash served as controls because the changes in the abundance of many insect species throughout the years may be due to the interaction of many factors. At each site, we placed traps and manually collected the data once a week during February, March, and April (peak wasp abundance) of 2012.

Statistical analysis

To analyze effects of ash deposit on *Vespula* spp. abundance, we performed a block ANOVA, where site pairs with and without ash deposits were blocks (Zar 1996). We converted abundance data into ranges to perform the analysis, because *Vespula* spp. abundance data did not meet normal distribution. Additionally, we performed univariate logistic regression analysis to determine how ash deposit thickness determines the presence probability of *Vespula* spp. We used presence/absence of *Vespula* spp. in all sampled sites ($n = 51$) as the dependent variable, and ash thickness at each site as the independent variable. All analyses were carried out using the R statistical environment (R Development Core Team 2009).

Results

No wasps were caught where the ash deposition levels on the ground exceeded 3.0 cm. In turn, captures in sites with no ash, or where ash deposited was minimal (≤ 0.2 cm), wasps were recollected during the whole sampling period. In locations where ash layers rested between 0.2 and 3.0 cm, a few wasps were observed during the month of April only (Fig. 1). In sum, 45 % of the baited traps caught no wasps, 26 % captured wasps only at the peak of wasp abundance (ash levels between 3.0 and 0.2), and the remaining 29 % captured wasps throughout the sampling period.

A synthesis of the main features of selected sites used in the paired sampling is shown in Table 1. The sites fell in localities bearing between 1,400 and 3,000 mm of precipitation, and the farthest site from the volcano was at 122 km and the closest 26 km. The ash levels ranged between 0–0.2 and 1.5–30 cm in sites without and with ash, respectively.

Table 1 Environmental features of study sites studied in paired experiment and wasp abundance (total and per species) in these sites

Code name	Precipitation level (mm)	Distance from the volcano (km)	Ash deposition thickness (cm)	Elevation (m a.s.l.)	Latitude	Longitude	Wasp abundance (total no. of individuals)		
							V. Vulgaris	*V. germanica*	Total
1a	1,400	62.69	3.0–5.0	844	40°38′57.6″S	71°25′08.5″W	0	0	0
1b	1,400	121.16	0	547	41°30′46.3″S	71°32′15.6″W	33	66	99
2a	1,600	75.13	1.5–3.0	789	41°02′05.3″S	71°33′35.3″W	2	3	5
2b	1,600	97.58	0	854	41°15′36.5″S	71°30′44.4″W	14	55	69
3a	1,600	77.35	7.5–10.0	784	40°56′11.6″S	71°24′16.8″W	0	0	0
3b	1,600	100.75	0	1,182	41°19′39.5″S	71°35′25.3″W	0	9	9
4a	1,800	49.93	10.0–15.0	788	40°46′58.6″S	71°39′34.6″W	0	0	0
4b	1,800	90.87	0	931	41°15′25.2″S	71°39′59.6″W	118	293	411
5a	2,000	41.94	10.0–15.0	854	40°41′26.8″S	71°41′49.4″W	0	0	0
5b	2,000	90.61	0	874	41°15′29.7″S	71°40′37.3″W	95	292	387
6a	2,500	36.13	15.0–30.0	771	40°43′25.8″S	71°48′19.6″W	0	0	0
6b	2,500	84.49	0	842	41°13′52.7″S	71°46′40.4″W	3	44	47
7a	3,000	26.87	15.0–30.0	1,285	40°42′44.2″S	71°56′39.2″W	0	0	0
7b	3,000	80.04	0–0.2	1,008	41°12′07.7″S	71°49′34.9″W	5	22	27

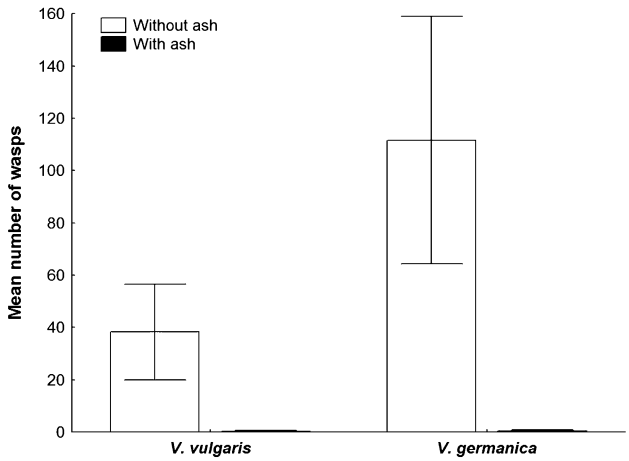

Fig. 2 Mean number of *V. vulgaris* and *V. germanica* wasps (±SE) in sites with and without ash

In all sites where the wasps were present, the abundance of *V. germanica* was greater than that of *V. vulgaris* (Fig. 2). We captured wasps only in sites not affected by ash deposition (1-7b) except for one site in which five wasps were caught (2a). Data showed significant differences in the total amount of wasps captured among sites with and without ash set in similar precipitation conditions ($F = 53.45$, $p < 0.0003$, block effects were not significant $p > 0.05$; Fig. 2).

The presence of *Vespula* spp. was negatively related with ash thickness (Nagelkerke's $R^2 = 0.820$, $n = 51$; Wald = 9.7027, $p < 0.0018$). The regression equation for the model is: Logit(p) = 2.45–1.75 ash thickness (cm).

Discussion

Invasive *Vespula* spp. populations inhabiting NW Patagonia were negatively affected by the ash emissions caused by the 2012 eruption of the *Puyehue–Cordon Caulle* Volcanic Complex. Wasp presence was negatively correlated with the amount of ash deposited in each site. In those places where ash deposits exceeded 3 cm, wasps disappeared completely. These results show catastrophic effects of ash deposition over a large area, reaching great distances from the eruption epicenter. In more remote locations, primarily affected by the ash plume, the decrease of wasp abundance was not total; and in sites with no ash, or where ash deposits were minimal (≤ 0.2 cm), wasps caught were similar to or greater than that of previous years (Masciocchi, unpublished data).

The absence of wasps in areas heavily affected by the volcano may result from the direct effect of the raining ash on overwintering sites of queens of *Vespula* spp. Given that the eruption was in winter, when queens are hibernating in protected places, they may have been physically buried under the ash. However, wasp abundance was reduced dramatically also at locations further away from the epicenter. It is likely that at these sites, queens were not killed directly but were affected by lack of appropriate nesting sites or otherwise during the early phases of colony development. Undoubtedly, ash deposition changed the soil surface making it less aggregated, covering pre-existing voids and retaining water and moisture differentially. Previous studies have suggested that the start of the colony is a critical stage of the wasp's life cycle, given that during this stage a single queen is responsible for all nest tasks, such as nest construction, egg laying, foraging, and feeding the first emerging larvae (Akre et al. 1981).

Equally important may have been the effects of airborne ash on the survival of the first workers or even their prey. Studies on the effects of volcanic eruptions on the arthropod fauna suggest that an increase in their mortality may be due to hygroscopic and abrasive properties that volcanic particles have, as well as through the intoxication caused by the direct ingestion of ash contaminated foods (Wille and Fuentes 1975; Marske et al. 2007). Food shortage, caused by ash deposition, is another important cause of insect mortality. Recent studies have shown that the visual pattern of honey bees is affect by the ash deposition on flowers *Apis mellifera* bees could not see the flowers covered in ash, implying extra energy allocated during nectar foraging (Martínez et al. 2012). For predatory insects, declining populations in some of their prey may be another indirect cause of death. Although these mechanisms have not been specifically evaluated for *Vespula* spp. here, we cannot rule out their importance in explaining current local abundance. Future studies should focus on the mechanisms involved in reducing wasp populations, whether wasp populations will recover, and how long the effect of volcanic depositions will affect *Vespula* wasps in Patagonia.

The impact of volcanic eruptions on the arthropod community is not straightforward. During the course of the eruption the effects on the populations are mostly quantitative, similar to the application of a broad spectrum insecticide (Klostermeyer et al. 1981), while later the effect is substantially qualitative. The arthropod community could suffer a drastic reduction in the number of individuals in the short term, while in the long term species composition may be affected, for example by the loss of those species most susceptible to the ash, or through an increase in the population density of more tolerant species. For non-native species that have evolved in regions with little or no exposition to volcanic activity, the effects could be devastating.

The scale of the volcanic eruption (i.e., surface area affected, duration, amount and kind of gases and other materials emitted, and periodicity) and time of the year when an eruption occurs are also important factors determining the extent of the effects on insect populations. In the case of the *Puyehue–Cordon Caulle* Volcanic Complex, the activity occurred during the austral winter, when most insects were inactive. However, as we show here, for some species, the timing of the eruptive event may be of limited importance. The rain of volcanic material in the recent event in NW Patagonia was devastating to *Vespula* spp. populations in the proximities of the eruption epicenter, but also no wasps were caught in an area of 500,000 ha, due to the effects of volcanic ash plume.

One of the most commonly accepted truisms in the field of invasion ecology is that disturbance facilitates invasion. This is because disturbances, by their nature, may create invasion windows that non-native species can occupy (Lockwood et al. 2007). For example, the success of Argentine ants (*Linepithema humile*), a major pest in nearly all continents it has invaded, is often associated with local disturbances such as fragmentation (Suarez et al. 1998). Another ant's (*Acromyrmex lobicornis*) invasion pathways into Patagonia have also been connected to the disturbance caused on native steppe habitat by road works (Farji-Brener 1996). However, the frequency and extent of disturbance in relation to the species life histories are important determinants of success of alien species in novel habitat. We show here that the eruption of the *Puyehue–Cordon Caulle* Volcanic Complex did not favor *Vespula* spp. invasive populations in NW Patagonia and in fact drove them, at some sites, to local extinction. It remains to be seen whether the strong negative effects of the volcanic ash fall on non-native wasps, may favor the recovery of the native insect communities. A worthy undertaking rests in understanding how the volcanic ash fall may re-set ecological succession in the affected areas, and may favor management and control of populations of *Vespula* spp.

We conclude that wasp mortality explained by the volcanic eruption may reach far away areas, and cause local extinction. In areas such as Patagonia, where active volcanoes are a common feature of the landscape, invasive insects may encounter an additional obstacle in their invasion success. This study increases the current knowledge regarding the effect of a volcanic eruption on invasive species.

Conclusions

- Invasive *Vespula* spp. populations inhabiting NW Patagonia were negatively affected by the ash deposition caused by the 2012 eruption of the *Puyehue–Cordon Caulle* Volcanic Complex.
- In those places where ash deposits exceeded 3 cm, wasps disappeared completely; however, in more remote locations, primarily affected by the ash plume, the decrease of wasp abundance was not total.
- The absence of wasps in areas heavily affected by the volcano may result from the direct effect of the raining ash on overwintering sites of queens of *Vespula* spp. However, at locations further away from the epicenter, wasps may have been affected by the lack of appropriate nesting sites or otherwise during the early phases of colony development.
- The effects of airborne ash on the survival of the first workers or even their prey, due to hygroscopic and abrasive properties, as well as through the intoxication caused by the direct ingestion of ash-contaminated foods, could be other causes of death.
- The strong negative effects of the volcanic ash fall on non-native wasps may favor the recovery of native communities affected by these opportunistic invaders. While exotics may make use of disturbance to aid the invasion process, less frequent events, of more extensive time and spatial scale such as volcanic eruptions may re-set succession and favor management of their populations.

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