



Long-term coexistence of two invasive vespid wasps in NW Patagonia (Argentina)

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Abstract

In Patagonia (Argentina) two non-native vespid wasps became established in the last decades. *Vespula germanica* was first detected in 1980, while *V. vulgaris* arrived some 30 years later. Both species can have a strong negative impact on agro-industrial economic activities, the natural environment, and outdoor human activities. Biological invasions may be influenced negatively by the degree of interaction with the resident native community and alien species already present. The sequential arrival and coexistence of *Vespula* wasps in Argentina for several years allows us to understand key questions of invasion ecology. Additionally, recognizing the outcome of the invasion by vespids in Patagonia, a region lacking native social wasps, may help plan species-focused mitigation and control strategies. We explored the role of competition in terms of invasion success, and the strategies that promote coexistence. Two possible scenarios, using niche overlap indices and isocline equations, were proposed to determine competition coefficients. Using a simple mathematical modeling framework, based on field collected data, we show that food resources do not play a central role in competitive interaction. The competition coefficients obtained from the equations were different from those inferred from the overlap indices (0.53 and 0.54–0.076 and 0.197, respectively). Together, these findings suggest that no matter the arrival order, *V. vulgaris*, always reaches higher densities than *V. germanica* when both species invade new regions. Our work contributes to further our understanding on the worldwide invasion processes deployed by these two eusocial insects.

Keywords *Vespula germanica* · *Vespula vulgaris* · Biotic resistance · Biological invasion · Lotka-Volterra

Introduction

Competition is considered as one of the major forces responsible for shaping the distribution of species in space and time (Tilman 1982; Connor and Simberloff 1983; Begon et al. 2006). For more than a century, questions about species competition continue to fascinate researchers. This is largely

because understanding competition can help not only understand how species in communities are organized but also address management problems, including the conservation of rare species (DeCesare et al. 2010), forecasting climate change impacts (Chu et al. 2016), and the management of biological invasions (MacDougall et al. 2009).

It is widely accepted that competition plays a key role in invasion processes (Mack et al. 2000; Vilà et al. 2011; Pyšek et al. 2012). Competitive interactions can contribute to biotic resistance, the reduction of invasion success, as it may hinder the establishment and spread of an invasive species in the new environment (Elton 1958). It is claimed that the presence of resident competitors in the arrival area may affect invasion of new species by reducing their access to resources due to exploitation or interference. Also, competition may negatively affect reproduction and population growth rates of non-native species in the new areas with exclusion as a final outcome (Davis 2009). However, resource partitioning in an ecological niche, such as by consuming different foods or using different areas of the environment, may help

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minimize overlap and therefore reduce competition (Shea and Chesson 2002).

Competitive interactions occur not only between native and invasive species but also between naturalized alien species and new alien species. For example, it has been shown that *Linepithema humile*, an invasive ant native to South America, competes with other species in the invaded range (i.e., California, USA), reducing foraging success and survival, as well as the establishment of new ant colonies (Holway and Case 2001; Kabashima et al. 2007). According to the principle of competitive exclusion, the coexistence of two species is not possible if they compete for at least one resource that is limiting for both, so that the superior competitor tends to eliminate the inferior species by competition (Gause 1934; Begon et al. 2006). However, if resources are not limiting, as may often occur in invaded areas, arriving species may also be negatively affected by resident natives or non-native competitors, if the efficiency in resource exploitation is different, and best foods are monopolized by the best competitor. For instance, the behaviors displayed by some native ants (i.e., aggression and aggregation to food sources) in NW Patagonia allowed them to forage on foods better and faster than an invasive social wasps that fed on similar items (Masciocchi et al. 2010b).

Studies of interspecific competition were disputed for the difficulty in demonstrating that competitive interspecific interactions had occurred or continued to occur other than under simplified field or laboratory conditions. However, competition may be inferred through an understanding of species behaviors and the identification of overlapped niche requirements, such as similar feeding habits (Grangier and Lester 2012; Pereira et al. 2013). Otherwise, the performance of exclusion experiments (Fox et al. 1985) or the use of mathematical modeling may allow us to infer the existence and consequences of competition (Kaplan et al. 2010; Vet et al. 2018).

The “Lotka-Volterra Model” is an example of a simple equation system approach to resource competition elaborated by Albert Lotka and Vito Volterra in the 1920s (Wangersky 1978). This classical approach has been generalized to multiple species engaging in all types of ecological interactions (Solé and Bascompte 2012). The generalized simple Lotka-Volterra equation is frequently employed to model communities due to its ease of parameterization and well-established mathematical properties (Gamarra et al. 2005; Warren et al. 2019). Theory supporting the Lotka-Volterra model rests on the assumption that species interactions play a major role in structuring a community. According to Wilson et al. (2003), taking a mean field approximation of those interactions across the community enables us to calculate a distribution of target species densities that determines, to a large degree, the temporal development of the ecological community, including the success of biological invasions.

Several species of social wasps (Hymenoptera: Vespidae) have shown to be remarkably successful invaders of new territories around the world (Spradbery and Richards 1973; Clapperton et al. 1989; Wilson and Holway 2010; Masciocchi and Corley 2013; Lester and Beggs 2019). In the last decades, *Vespula germanica* and *V. vulgaris*, native to Europe and North Africa (Delmotte and Marchal 1982; Dvorak and Landolt 2006), have invaded Australia, New Zealand, and South America, rapidly becoming very common insects within the new range (Beggs et al. 2011). Throughout the invaded range, both these wasps are recognized as having strong negative impacts on agro-industrial economic activities, the natural environment, and outdoor human events, due to their venomous sting, aggressive behavior and efficient, opportunistic foraging abilities (Clapperton 1989; Yeruham et al. 2002; Beggs et al. 2011; MacIntyre and Hellstrom 2015).

Both, *V. germanica* and *V. vulgaris*, are defined as opportunistic predators and scavengers, with food preferences influenced by the development of their colonies and the availability of resources in the environment (Akre and MacDonald 1986; Barr et al. 1996; Spurr 1995; Pereira et al. 2013). Even though both species are generalists, their diet and phenology are very similar, suggesting an overlap in food preferences and foraging behavior. Moreover, feeding activities observed for both wasp species may be disrupted by each other’s presence, suggesting that these two species could interfere with each other (Pereira et al. 2016). It has been suggested that differences in the foraging strategies displayed by these wasps may render *V. vulgaris* with a competitive advantage over *V. germanica* in certain scenarios (Harris et al. 1994).

In the 1980s the region known as Patagonia (Southern Argentina) was invaded by *V. germanica* (Fabricius; Hymenoptera) and some 30 years later *V. vulgaris* (Linnaeus; Hymenoptera) was first detected (Willink 1980; Masciocchi et al. 2010a). Sequential invasion by these two eusocial wasps has been observed elsewhere. In New Zealand, for example, *V. germanica* first arrived in 1945 and has since spread widely throughout the country, and 30 years later, *V. vulgaris* arrived and displaced it from many environments (Sandlant and Moller 1989; Harris et al. 1991). Despite the fact that both species coexist throughout the invaded areas (for more than 10 years in Argentina and almost 50 in New Zealand; Masciocchi et al. 2019; Schmack et al. 2021), little is known about the factors determining co-occurrence and relative abundances of *V. vulgaris* and *V. germanica* in such areas. Congeneric species that overlap their geographic distribution provide an excellent opportunity to explore the mechanisms for coexistence.

The sequential invasion of *V. germanica* and *V. vulgaris* in NW Patagonia (Argentina) offers a unique opportunity to study a variety of ecological and applied

questions regarding the interactions between both. Also, it allows us to inquire about the role of competition as related to invasion success, and the strategies that promote the final outcome. Specifically, the objective of our study was to explore niche overlap between *V. germanica* and *V. vulgaris*, to determine whether co-occurrence is a consequence of resource partitioning.

Materials and methods

Study sites and field experiments

This study was carried out under natural conditions in scrubland areas, within the Nahuel Huapi National Park, Patagonia, Argentina (41°S, 72°W). This area, located close to the city of Bariloche, is defined as an appropriate habitat for both wasp species (e.g., a disturbed, tree-less zone, with an annual rainfall of ca. 800 mm, mostly concentrated during the winter months). The most characteristic plant species that describes the area is the native bamboo *Chusquea culeou*, and woody shrubs *Embothrium coccineum* and *Fuchsia magellanica*. Other species of the genus *Berberis* are also present. All assays were carried out in different sites where both *Vespula* species are known to be abundant. Experiments were conducted during March 2014, on sunny days with no wind, between 10 AM and 5 PM, to minimize the effects of weather (i.e., daily temperatures) on wasp activity.

We selected 12 sites of ca. 1 ha and in each, 10 transects were established (each located 10 m apart from one another) where we searched for wasp nests. Each nest was marked, geo-referenced and the species was identified. Nest density was chosen as an estimator of wasp abundance (Archer 1985, 2001; Barlow et al. 2002; Estay and Lima 2010). To estimate niche overlap between *V. germanica* and *V. vulgaris*, we selected 10 of the marked nests for each species. Using an entrance trap to catch returning foragers (adapted from Harris and Oliver 1993; Fig. 1), we captured foragers returning to their nests, counted, and classified all prey collected by them to investigate differences in diet composition. Traps were placed at the entrance of each nest (simultaneously, to avoid differences related to sampling times) causing a minimal disturbance to the colonies, and we ensured foragers did not establish alternative entrances. After 10 min of placing, the inner part of the trap was removed, and trapped foragers were anesthetized with CO₂. The assay was repeated twice for each nest with a difference of two days. Prey items were identified to the order level with a digital magnifying glass to 40X level and the help of specialists.

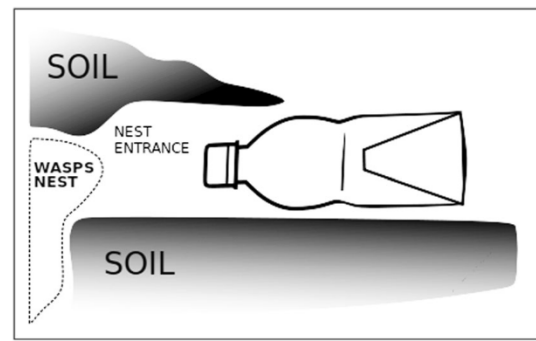


Fig. 1 Trap design used to capture forager returning to nest (extracted and modified from Harris and Oliver 1993)

Competitive interaction models

To assess the existence of competitive interactions between *V. germanica* and *V. vulgaris*, we ran the Lotka-Volterra model for interspecific competition (Volterra 1926; Lotka 1932; Takeuchi 1996; Neal 2004; Momo and Capurro 2006). This model may be written with an explicit intraspecific competition coefficient as a set of coupled equations:

$$V. \text{ germanica} \frac{dN_{VG}}{dt} = r_1 N_{VG} \left(1 - \frac{N_{VG} + \alpha N_{VV}}{K_1} \right)$$

$$V. \text{ vulgaris} \frac{dN_{VV}}{dt} = r_2 N_{VV} \left(1 - \frac{N_{VV} + \beta N_{VG}}{K_2} \right),$$

where N_{VG} represents the size of *V. germanica* population, measured as nest density (nest/ha), r_1 is its intrinsic growth rate, K_1 is maximum population density in the study area (i.e., the carrying capacity), and α is the competition coefficient. A similar equation is written for *V. vulgaris*, indicated by the subindex *VV*. The competition coefficients α and β represent the reduction in growth of one species caused by each additional individual of the other (Momo and Capurro 2006). Therefore, the term αN_{VG} represents the effects of *V. vulgaris* on *V. germanica* populations and βN_{VV} represents the effects of *V. germanica* on *V. vulgaris*.

The values of N_{VG} , N_{VV} were obtained from sites where they coexisted and K_1 and K_2 from sites where each species was found by itself. We assumed that the intrinsic growth rates were similar for both wasp species (Moller 1991; Donovan et al. 1992; Leathwick 1997; Leathwick et al. 1999). The model simulation was done with different initial densities since *V. vulgaris* arrived after *V. germanica*. *V. germanica* initial density was equal to its K , while *V. vulgaris* initial values for N were considered to be 0.08, estimated under the assumption that this species needs at least 1 nest to establish, divided by the 12 sites chosen in our sampling design.

The competition coefficients were estimated from two possible scenarios: using overlap indices as competition coefficients (Loman 1986) or calculating the coefficients of competition from isocline equations. In the first case, we assumed diet to represent competitive interactions since both species are opportunistic, generalist foragers of insects and carrion. The competition coefficients were calculated from the asymmetric index of niche overlap of MacArthur and Levins (1967) as

$$M_{jk} = \frac{\sum_i^n p_{ij} \cdot p_{ik}}{\sum_i^k p_{ij}^2} \text{ and } M_{kj} = \frac{\sum_i^n p_{ij} \cdot p_{ik}}{\sum_i^k p_{ij}^2},$$

where p_{ij} and p_{ik} are the proportions of resource i used by species j and k , respectively. This index is asymmetric and allows obtaining a competition coefficient for each species.

In the other case, we estimated competition coefficients from the isocline equations, for which we assumed that time of co-occurrence of both wasp species was long enough to allow for equilibrium population densities. With values of N and K , we estimated the value of the factors converting an individual of one species into an individual of another species (Volterra 1926; Lotka 1932; Hairston 1980). Thus, both species of *Vespula* will be in equilibrium when

$$\frac{dN_{VG}}{dt} = 0 \text{ and } \frac{dN_{VV}}{dt} = 0;$$

this occurs when populations stop growing. In this case, the equations were

$$N_{VG} = K_{VG} - \alpha N_{VV} \text{ and } N_{VV} = K_{VV} - \beta N_{VG}.$$

The competition coefficients were calculated as

$$\alpha = (N_{VG} - K_{VG}) / -N_{VV},$$

$$\beta = (N_{VV} - K_{VV}) / -N_{VG},$$

Statistical analysis

The non-parametric *Kruskal–Wallis* test was used to compare diet composition of *V. germanica* and *V. vulgaris* foragers. Analyses were performed using the R statistical environment (R Core Team 2020). Lotka–Volterra models and phase diagrams were run and plotted with *deSolve* (Soetaert et al. 2010) and *ggplot2* packages of R statistical environment (Wickham 2016).

Results

Vespula germanica and *V. vulgaris* diet

A total of 2022 *V. germanica* foragers were trapped at the nest entrance, of which 245 (12%) entered with prey. Of the total prey items recovered, 78% were insects and the rest were remains that could not be identified. For *V. vulgaris*, a total of 1936 workers were captured, of which 202 (10.4%) carried prey. Of these prey items, the majority (89%) were insects. Regarding the composition of the diet, there are differences between some types of prey that *V. germanica* and *V. vulgaris* brought to their nests (*Kruskal–Wallis* test, $P < 0.05$; Fig. 2). The prey identified for *V. germanica* were, for the large part, insects belonging to the Diptera (36%) and Orthoptera (18%) orders, while Hemiptera (35%) and Coleoptera (19%) were the predominant orders in the diet of *V. vulgaris*.

Competitive interaction models

The competition coefficients for *V. germanica* and *V. vulgaris*, calculated from diet overlap indices using the MacArthur and Levins' asymmetric index, were 0.53 and 0.54, respectively. In turn, coefficients calculated from the isocline equations were 0.076 for *V. germanica* and 0.197 for *V. vulgaris*. The number of nests per hectare in co-occurrence sites were $N_{VG} = 3.14$ for *V. germanica* and $N_{VV} = 4.71$ for *V. vulgaris*. The density in sites where each species was found alone were $K_{VG} = 3.5$ nest/ha and $K_{VV} = 5.33$ nest/ha. With these data, the population growth dynamics of both species was modeled under two possible scenarios (Figs. 3 and 4).

According to the model using diet as competitive resources, populations of *V. vulgaris* grew exponentially until they reached densities of 4.73 nests/ha, at which point they would remain at a stable equilibrium. However, populations of *V. germanica* decreased to equilibrium density of 1.03 nests/ha, in approximately 20-year-long simulations (Fig. 3). Under this predictive scenario, the phase diagram showed that isoclines intersect at positive densities for both species ($x = 1.03$, $y = 4.73$; Fig. 5), while, using the coefficient of competitions from the isocline equations (Fig. 6), populations of *V. vulgaris* grew exponentially until 4.71 nests/ha and *V. germanica* declined slightly resulting in the current density of 3.14 nests/ha (Fig. 4).

Since under two scenarios both α and β take values less than one, the following inequalities are obtained: (1) $K_1 < K_2/\beta$ and (2) $K_2 < K_1/\alpha$ (Fig. 5 and 6). Therefore, the carrying capacity of each species is less than the

Fig. 2 Average percentage (\pm standard error) of different arthropod orders in *V. germanica* (blue bars) and *V. vulgaris* (red bars) diets ($N=10$ nests). **Indicates significant differences ($P < 0.05$) between wasp species according to the Kruskal–Wallis test

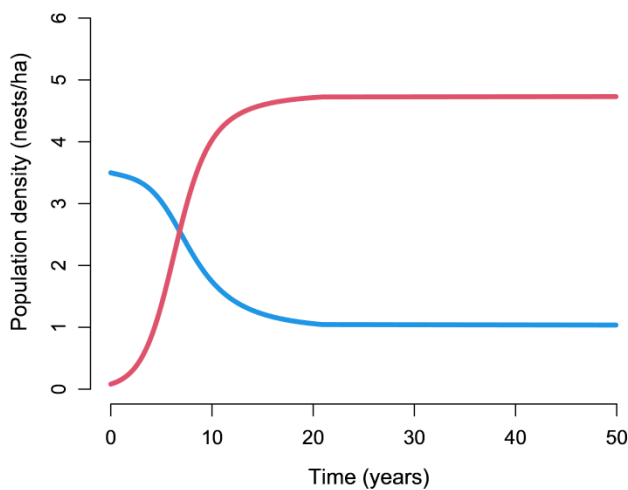
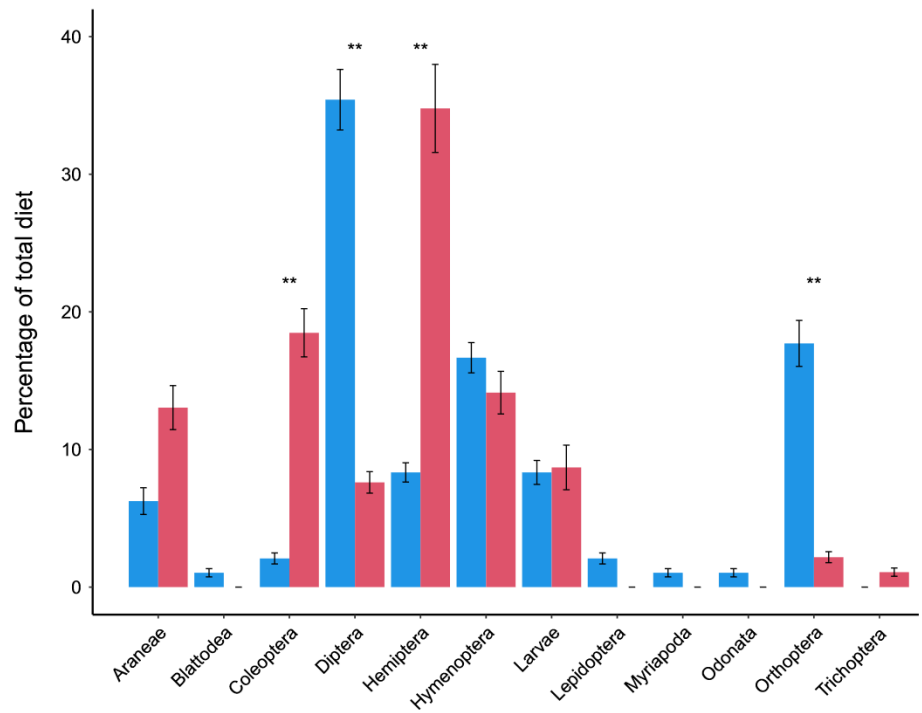


Fig. 3 Lotka-Volterra model prediction of *V. germanica* (blue line) and *V. vulgaris* (red line) population growth in time (years) based on parameters estimated from the diet overlap indices and abundances of each species

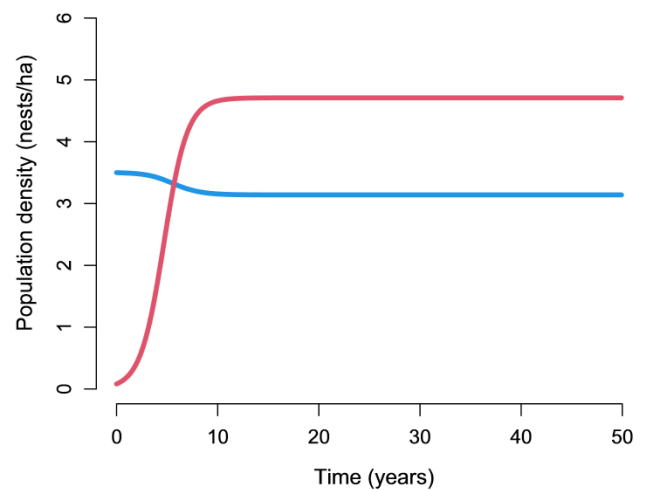


Fig. 4 Lotka-Volterra model prediction of *V. germanica* (blue line) and *V. vulgaris* (red line) population growth in time (years) based on parameters estimated from the isocline equations and abundances of each species

equivalent in individuals of the other species, suggesting that intraspecific competition is more important than interspecific competition.

Discussion

The objective of our study was to explore niche overlap and competition between two invasive social wasps, *V. germanica* and *V. vulgaris*, to determine whether co-occurrence is a consequence of resource partitioning. Both wasps share common morphological and behavioral aspects and, outside their native range, are often found

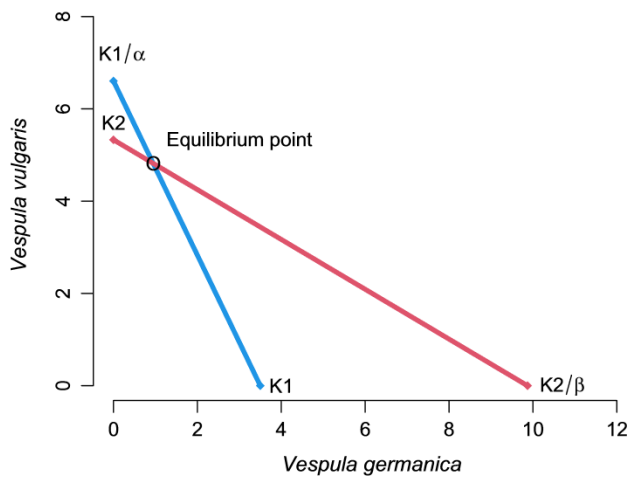


Fig. 5 Graphical representation (phase diagram) of competition for prey consumption between *V. germanica* (blue line) and *V. vulgaris* (red line). Lines represent the specific zero growth rate isoclines that intersect at positive abundances (equilibrium point; $x=1.03$, $y=4.73$)

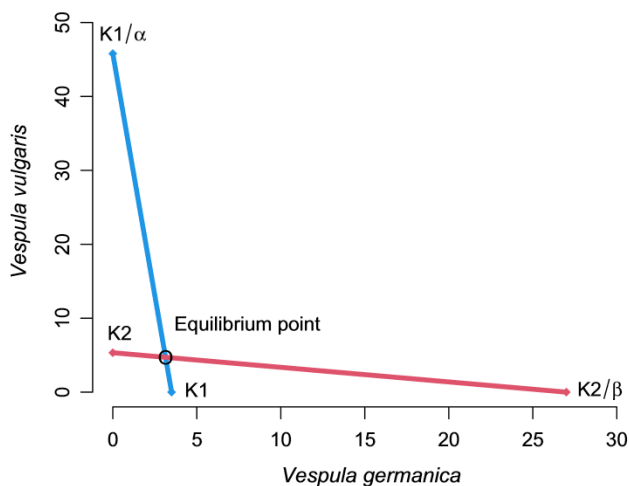


Fig. 6 Graphical representation (phase diagram) of competition for resources between *V. germanica* (blue line) and *V. vulgaris* (red line) with assumed equilibrium population densities. Lines represent the specific zero growth rate isoclines that intersect at positive abundances (equilibrium point; $x=3.14$, $y=4.71$)

together in similar habitats suggesting the existence of some strategy that allows for coexistence. Here, we showed by means of a simple phenomenological model based on field collected data that, for the NW Patagonia conditions, food resource does not play a central role in competitive interaction between two *Vespa* species.

We observed that preys collected by both *Vespa* species were different. *V. germanica* foraged mostly on insects belonging to Diptera and Orthoptera orders. In contrast, the diet of *V. vulgaris* consisted mostly of the orders Hemiptera and Coleoptera. In Chile, Mangunacelaya et al. (1986)

found that the most consumed orders by *V. germanica* were Araneae, Lepidoptera, and Diptera. In New Zealand some authors compared diets of both species noting some differentiation, with *V. germanica* foraging more Diptera and fewer Araneae, Hemiptera, and Lepidoptera than *V. vulgaris* (Harris 1991; Harris and Oliver 1993; Schmack et al. 2021). Undoubtedly, exact proportions will vary at each site, depending on the local abundance of prey, reflecting the opportunistic behavior of both species. However, the observed differences suggest that *V. vulgaris* and *V. germanica* partition their prey to some degree, that could lead to a reduction in niche overlapping.

By preying on a wide range of arthropods, both *Vespa* species have the potential to impact on natural ecosystems. In NW Patagonia, little is known about the relative abundance of most native arthropod species. However, based on our results using morphological techniques only, and considering previous works here and elsewhere (Beggs et al. 2011, Pietrantuono et al. 2018, Potter-Craven et al. 2018), a significant impact of these wasps on the native arthropod community may be expected. In line with this, Schmack et al. (2021) quantified prey dietary composition of *V. vulgaris* and *V. germanica* in New Zealand, using next-generation sequencing of DNA, and concluded that these species consumed mostly native arthropod species with Lepidoptera representing the major prey order in both wasps' diet. Although visual identification as used in the present work is often used to compare diet composition, a molecular approach ensures the accuracy of prey species identification, which coupled with extensive background knowledge may allow for more precise and specific conservation measures.

Vespa germanica and *V. vulgaris* coexist in many environments where they have invaded. Given their similarity in biology, these species may have developed strategies to avoid or reduce competition. In New Zealand and in Patagonia, it has been noted that both species partition resources spatially, as *V. vulgaris* are found foraging in the shrubland, at mid-height level while *V. germanica* are more commonly seen at the ground level (Harris et al. 1991; Masciocchi et al. 2019). Additionally, in the north-east coast of New Zealand, differences among *V. vulgaris* and *V. germanica* diet were found also among seasons (Schmack et al. 2021), while, in Argentina, Pereira et al. (2016) found that *V. germanica* significantly avoids *V. vulgaris* visual and odor cues in bioassays with free-flying wasps arriving to protein baits. The coexistence observed by these generalist invaders at some locations could be related with resource foraging behavior partitioning.

Species with a generalist feeding habit are expected to be more flexible than specialists due to their foraging niche partitioning capacity (Wilson and Yoshimura 1994). The opportunistic and generalist foraging habits of *V. germanica* and *V. vulgaris* may be the reason why competitive exclusion

is prevented. Previous work done in NW Patagonia (Argentina), 10 years before the arrival of *V. vulgaris*, determined that Araneae and Coleoptera were part of the most common prey items in the diet of *V. germanica* (Sackmann et al. 2000). Surprisingly, at present, we showed that those items are consumed to a greater extent by *V. vulgaris* than by *V. germanica*, suggesting that current diets may have shifted to reduce competition. Moreover, Schmack et al. (2021) evaluated prey richness and niche width suggesting that considerable differentiation exists among *Vespula* species, having *V. germanica* the most species rich diet and broadest trophic niche. Despite the “lower” competition coefficients found here, these past works may at least partly explain why *V. germanica* could coexist with *V. vulgaris*. Our findings are consistent with theoretical predictions about the relationship between flexibility and the degree of specialization and may explain why *V. germanica* and *V. vulgaris* cohabit in much of the invaded range.

To obtain competition coefficients, we modeled *V. germanica* and *V. vulgaris* interaction under two possible scenarios. Those coefficients obtained from the isocline equations (Hairston 1980) are different from those inferred from the overlap indices (Loman 1986). Coefficients calculated from the diet analyzed were very similar (0.53 and 0.54), suggesting that these species have resolved the conflict over food resources, coexisting for more than 10 years. But, other unknown variables (e.g., nesting sites) may be also designing the interaction between these invasive wasps. A recent study carried out in New Zealand suggested that these species may coexist by shifting their ecological niche given that spatial, dietary and temporal partitioning was noted (Schmack et al. 2021). It is likely that spatial segregation across different habitats as observed in New Zealand may also occur in Patagonia over the coming years. However, little is still known about the reasons why *V. vulgaris* may reach higher densities in a short time window, even displacing *V. germanica* from many environments. The competition coefficient estimated from isocline equations for *V. vulgaris* in our study is 2 times larger than that of *V. germanica*. This could be the reason why *V. vulgaris* is able to invade environments previously occupied by a similar congeneric species and even reach higher densities. It would seem that, no matter the sequence of arrival, *V. vulgaris* may always reaches higher densities throughout the invaded environments (Beggs et al. 2011).

It is known that models simplify reality and may not describe appropriately all the complex biological processes involved among interacting species. However, they may provide estimates of the process results, and have been shown to be useful in predicting population growth of competing species (Carusela et al. 2009; Torre et al. 2017; Chalmandrier et al. 2021; Deng et al. 2021; Tamura et al. 2021). Fort (2018) concluded that the Lotka-Volterra

model, despite its simplicity, is a useful quantitative tool for describing the equilibrium species abundances and can make accurate predictions. Even when competing species are at equilibrium densities, a retrospective analysis, such as that done here, may allow us to estimate competition parameters providing a useful basis for predictive analysis of future invasions (Curto et al. 2021). Based on our results, management strategies for these invasive wasps should focus on species-specific practices since, no matter the arrival order, the population density of *V. vulgaris* is expected to be greater than that of *V. germanica*. Accordingly, studies on the impact and habits of the former are warranted.

The outcome of invasions depends on several attributes of both the species involved and the invaded range, including in this the resistance provide by the established communities and prior invasions. Our study is a first step to document the interaction between *V. germanica* and *V. vulgaris* in Argentina and provides an additional example of the use of the Lotka-Volterra modeling approach. We conclude that the co-occurrence of both species of wasps in Patagonia is likely possible because of resource partitioning between them. In turn, we suggest the preference for different preys and intraspecific competition as a plausible explanation for the coexistence of *V. germanica* and *V. vulgaris* in the invaded range. Improving our understanding of the interaction between invasive species may help develop appropriate techniques for managing undesired invasive social wasp populations.

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Author contribution statement AJP, MM, and JJC conceived the idea; AJP and MM collected the data; AJP analyzed the data and developed the mathematical models; all the authors were involved in writing the manuscript.

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Availability of data and material All raw data are sorted at digital Institutional Repository of INTA (Instituto Nacional de Tecnología Agropecuaria), through the link <http://hdl.handle.net/20.500.12123/10582>, and access will be unrestricted upon acceptance.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

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