Long-Term Coexistence of Two Invasive Vespid Wasps in NW Patagonia (Argentina)

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1 Title: Long-term coexistence of two invasive vespid wasps in NW Patagonia (Argentina)¹

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19 Running head: coexistence between two exotic social wasps

20
21 Community ecology – original research

¹**Authors' contributions** AJP, MM and JJC conceived the idea; AJP and MM collected the data; AJP analyzed the data and developed the mathematical models; all authors were involved in writing the manuscript.

22   **Abstract**

23   In Patagonia (Argentina) two non-native vespids wasps became established in the last decades.
24   *Vespula germanica* was first detected in 1980 while *V. vulgaris* arrived some 30 years later. Both
25   species can have a strong negative impact on agriculture, natural environment and on outdoor
26   human activities. Invasion success -the establishment and spread of a species- may be influ-
27   enced negatively by the degree of interaction with the resident native community, and alien
28   species already present. The sequential arrival of these two wasps allows us to understand key
29   questions of invasion ecology. Additionally, recognizing the outcome of the invasion by vespids
30   in Patagonia -a region lacking native social wasps-, may help plan species-focused mitigation
31   and control strategies. We explored long term species coexistence through the deterministic
32   Lotka-Volterra competition model, using site-specific field data on prey captured (to estimate
33   niche overlap) and current nest densities in sites. Food items carried by workers were similar but
34   there is some degree of segregation. *V. germanica* nest density in shared sites, and in sites
35   without coexistence, were 3.14 and 3.5 respectively, being higher for *V. vulgaris* with 4.71 and
36   5.33. The model predicts stable co-existence of both species in the invaded range, yet a higher
37   abundance of *V. vulgaris* should be expected. Added to evidence on other foraging behavioral
38   attributes of both wasp species and the invasion patterns observed in other regions, it is likely
39   that the prior presence of *V. germanica* does not contribute significantly to the biotic resistance
40   of the invaded range for *V. vulgaris*.

41   **Keywords:** *Vespula germanica*, *Vespula vulgaris*, biotic resistance, biological invasion, Lotka-
42   Volterra

43 Introduction

44 Competition is considered as one of the major forces responsible for shaping the distribution of
45 species in space and time (Tilman 1982; Connor and Simberloff 1983; Begon et al. 2006). For
46 more than a century, questions about species competition remain to fascinate researchers. This
47 is largely because understanding competition can help, not only understand how species in
48 communities are organized, but also address management problems including the conservation
49 of rare species (DeCesare et al. 2010), forecasting climate change impacts (Chu et al. 2016)
50 and the control of biological invasions (MacDougall et al. 2009).

51 It is widely accepted that competition plays a key role in any invasion process (Mack et al. 2000;
52 Vilà et al. 2011; Pyšek et al. 2012). Competitive interactions can contribute to biotic resistance -
53 the reduction of invasion success- as it may hinder the establishment and spread of an invasive
54 species in the new environment. In general, it is claimed that the presence of resident
55 competitors in the arrival area may affect invasion of new species by reducing their access to
56 resources due to exploitation or interference. Competition then, may negatively affect
57 reproduction and population growth rates of non-native species in the new areas (Davis 2009).

58 However, biotic resistance does not only occur between native and an invasive species.
59 Competitive interactions have been observed between naturalized exotic species, and new alien
60 species (Simberloff and Von Holle 1999). For example, it has been shown that *Linepithema*
61 *humile*, an invasive ant native to South America, competes with other species in the invaded
62 range (i.e., California, USA), reducing foraging success and survival, as well as the
63 establishment of new ant colonies (Holway and Case 2001; Kabashima et al. 2007). According
64 to the principle of competitive exclusion, the coexistence of two species is not possible if they
65 compete for at least one resource that is limiting for both, so that the "stronger" competitor tends

66 to eliminate the "weaker" species by competition (Gause 1934; Begon et al. 2006). However, if
67 resources are not limiting as may often occur in invaded areas, arriving species may also be
68 negatively affected by resident natives or non-native competitors, if the efficiency in resource
69 exploitation is different, and best foods are monopolized by the best competitor (Masciocchi et
70 al. 2010).

71 In nature, the existence of competitive interactions is still hard to assess as for most
72 communities modeled by competition, this maybe have occurred in some past time (Connell
73 1980). However, competition may be inferred through an understanding of species behaviors
74 and the identification of overlapped niche requirements, such as similar feeding habits (Grangier
75 and Lester 2012; Pereira et al. 2013). Else, the performance of exclusion experiments (Fox et al.
76 1985) or the use of mathematical modeling may allow us to infer the existence and
77 consequences of competition (Kaplan et al. 2010; Vet et al. 2018).

78 The "Lotka-Volterra Model" is a remarkable example of a simple equation system approach to
79 resource competition elaborated by Albert Lotka and Vito Volterra in the 1920's (Wangersky
80 1978). This classical approach has been generalized to multiple species engaging in all types of
81 ecological interactions (Solé and Bascompte 2012). The generalized simple Lotka-Volterra
82 equation is frequently employed to model communities due to its ease of parameterization and
83 well-established mathematical properties (Gamarra et al. 2005; Warren et al. 2019). Theory
84 supporting the Lotka-Volterra model rests on the assumption that species interactions play a
85 major role in structuring a community. According to Wilson et al. (2003), taking a mean-field
86 approximation of those interactions across the community enables us to calculate a distribution
87 of target species densities that determines, to a large degree, the temporal development of the
88 ecological community, including the success of biological invasions.

89 Several species of social wasps (Hymenoptera: Vespidae) have shown to be remarkably
90 successful invaders of new territories around the world (Spradbery and Richards 1973;
91 Clapperton et al. 1989; Wilson and Holway 2010; Masciocchi and Corley 2013; Lester and
92 Beggs 2019). In the last decades, two of the most notorious species, *Vespula germanica* and *V.*
93 *vulgaris*, have invaded Australia, New Zealand and South America, rapidly becoming very
94 common insects within the new range (Beggs et al. 2011). In the 1980's the region known as
95 Patagonia (Southern Argentina) was invaded by *V. germanica* (Fabricius; Hymenoptera) and
96 some 30 years later *V. vulgaris* (Linnaeus; Hymenoptera) was first detected (Willink 1980;
97 Masciocchi et al. 2010). Both species of Vespidae are native to Europe and North Africa and co-
98 exist in large parts of their native range (Delmotte and Marchal 1982; Dvorak and Landolt 2006).
99 Throughout the invaded range, however, both these wasps are recognized as having strong
100 negative impact on agro-industrial economic activities, the natural environment and outdoor
101 human events, due to their venomous sting, aggressive behavior and efficient, opportunistic
102 foraging abilities (Clapperton 1989; Yeruham et al. 2002; Beggs et al. 2011; MacIntyre and
103 Hellstrom 2015).

104 Sequential invasion by these two eusocial wasps has been observed also elsewhere. In New
105 Zealand, for example, *V. germanica* first arrived in 1945 and since spread widely throughout the
106 country, but 30 years later, *V. vulgaris* arrived and displaced it from many environments
107 (Sandlant and Moller 1989; Harris et al. 1991). Both species are defined as opportunistic
108 predators and scavengers, with food preferences affected by the development of their colonies
109 and the availability of the environment (Akre and MacDonald 1986; Barr et al. 1996; Spurr 1995;
110 Pereira et al. 2013). Even though both species are seen as generalists, their diet and phenology
111 are very similar, suggesting an overlap in food preferences and foraging behavior (mainly
112 protein-rich foods) towards the end of summer and autumn when colonies need to feed future
113 reproductive individuals (gynes and males; Sackmann et al. 2000). Moreover, feeding activities

observed for both wasp species may be disrupted by each other's presence, suggesting that these two species could interfere between each other (Masciocchi et al. 2019). 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; Pereira et al. 2016). Given that there is no evidence of regions invaded only by *V. vulgaris* or of an invasion sequence led by *V. vulgaris*, the role played by either species on the invasion process of the other remains unknown, with strong practical implications.

The recent invasion of *V. germanica* and *V. vulgaris* in NW Patagonia offers a unique opportunity to study a variety of ecological and applied questions regarding the future of these species in terms of invasion success of each species and their geographical spread. In this study, we explore the potential role played by *V. germanica* on the invasion process of *V. vulgaris* wasps in Patagonia, using the classical Lotka-Volterra model. Based on the similarities in foraging habits and diets between both species, our hypothesis is that the presence of *V. germanica*, prior to the arrival of *V. vulgaris*, adds biotic resistance, affecting the final outcomes of the invasion process.

Materials and Methods

Study sites and field experiments

The 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 wasps (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*

137 species are known to be abundant. Experiments were conducted during March of 2014, on
138 sunny days with no wind, between 10 AM and 5 PM, to minimize the effects of weather (i.e.,
139 daily temperatures) on wasp activity.

140 We selected 12 sites of ca. 1 ha and in each, 10 transects were established (each located 10 m
141 a part from another) where we searched for all wasp nests. Each nest found was marked, geo-
142 referenced and the species was identified. Nest density was chosen as an estimator of wasp
143 abundance (Archer 1985, 2001; Barlow et al. 2002; Estay and Lima 2010). To estimate niche
144 overlap between *V. germanica* and *V. vulgaris*, we selected 10 of the marked nests for each
145 species. Using an entrance trap to catch returning foragers (adapted from Harris and Oliver
146 1993; Fig. 1), we captured, counted, and classified all prey collected by foragers returning to
147 their nests. Traps were placed at the entrance of each nest (simultaneously, to avoid differences
148 related to sampling times) causing a minimal disturbance to the colonies, and we ensured
149 foragers did not establish alternative entrances. After 10 minutes of placing, the inner part of the
150 trap was removed, and trapped foragers were anesthetized with CO₂. The assay was repeated
151 twice for each nest with a difference of two days. Prey items were identified with a digital
152 magnifying glass to 40X level and the help of specialists.

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

158
$$V. germanica \frac{dN_{VG}}{dt} = r_1 N_{VG} \left(1 - \frac{N_{VG} + \alpha N_{VV}}{K_1} \right)$$

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

159

160 where N_{VG} represents the size of *V. germanica* population, measured as nest density (nest/ha),
 161 r_1 is its intrinsic growth rate, K_1 is maximum population density in the study area (i.e., the
 162 carrying capacity) and α is the competition coefficient. A similar equation is written for *V. vulgaris*,
 163 indicated by the subindex VV . The competition coefficients α and β represent the reduction in
 164 growth of one species caused by each additional individual of the other (Momo and Capurro
 165 2006). Therefore, the term αN_{VG} represents the effects of *V. vulgaris* on *V. germanica* populations
 166 and βN_{VV} represents the effects of *V. germanica* on *V. vulgaris*.

167 The values of N_{VG} , N_{VV} , K_1 and K_2 were obtained from the number of nests of each species in the
 168 sites where they coexisted (N) and, from sites where each species was found by itself, we
 169 estimated K . We assumed that the intrinsic growth rates were similar for both wasp species
 170 (Moller 1991; Donovan et al. 1992; Leathwick 1997; Leathwick et al. 1999).

171 The competition coefficients were calculated from the asymmetric index of niche overlap of
 172 MacArthur and Levin (1967) as:

$$M_{jk} = \frac{\sum_i^n p_{ij} \cdot p_{ik}}{\sum_j^k p_j^2} \quad M_{kj} = \frac{\sum_i^n p_{ij} \cdot p_{ik}}{\sum_k^j p_k^2}$$

173

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

176 To determine the equilibrium abundance of *V. germanica* and *V. vulgaris* populations (i.e., the
177 intersection of the zero isocline), we did a phase diagram, and the isoclines were analyzed
178 (Edelstein-Keshet 1988; May and McLean 2007). Both species of *Vespula* will be in equilibrium
179 when:

180
$$\frac{d N_{VG}}{dt} = 0 \text{ y } \frac{d N_{VV}}{dt} = 0$$

181 this occurs when populations stop growing. In this case, the equations are:

182
$$N_{VG} = K_{VG} - \alpha N_{VV} \text{ y } N_{VV} = K_{VV} - \beta N_{VG}$$

183 These two equations define two lines called zero-growth isoclines.

184 *Statistical analysis*

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

190 **Results**

191 *V. germanica* and *V. vulgaris* diets

192 A total of 2022 *V. germanica* foragers were trapped at the nest entrance, of which 245 (12%)
193 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, 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. On the other hand, Hemiptera (35%) and Coleoptera (19%) were the predominant orders in the diet of *V. vulgaris*.

Competitive interaction models

The competition coefficient for *V. germanica*, calculated using the MacArthur and Levins' asymmetric index, was 0.53. The number of nests per hectare in coexistence sites, and in sites where each species was found by itself, were $N_1 = 3.14$ and $K_1 = 3.5$ respectively. On the other hand, the coefficient of competition for *V. vulgaris* was 0.54, with $N_2 = 4.71$ and $K_2 = 5.33$. With these data, the population growth dynamics of both species was modeled (Fig. 3).

According to the model, populations of *V. vulgaris* grew exponentially until they reached densities of 4.83 nests/ha, at which point they would remain at a stable equilibrium. However, populations of *V. germanica* grew to a maximum density of 1.65 nests/ha but then declined to equilibrium values of 0.85 nests/ha, in approximately 20 year-long simulations (Fig. 3).

The phase diagram showed that isoclines intersect at positive densities for both species ($x = 0.85$, $y = 4.83$; Fig. 4). Since both α and β take values less than one, the following inequalities are obtained: (1) $K_1 < K_2/\beta$ and (2) $K_2 < K_1/\alpha$. Therefore, the carrying capacity of each species is less than the equivalent in individuals of the other species, suggesting that intraspecific competition overmatches competition among both species.

216 Discussion

217 *Vespula germanica* and *V. vulgaris* are both truly social wasps that are successful invaders
218 found in the same regions in different parts of the world. This, added to the fact that they often
219 become remarkably common insects in the invaded range and are considered pests, has made
220 the the center of considerable research attention (e.g., Akre and MacDonald 1986; Bashford
221 2001; Beggs et al. 2011; Buteler et al. 2021). Both wasps share common morphological and
222 behavioral aspects and are often found together in similar habitats, outside their native range.
223 Here we show, by means of a simple phenomenological model fed on field collected data that,
224 for the NW Patagonia conditions, co-existence is the most likely long-term outcome in which *V.*
225 *vulgaris* will be the most common species, despite the fact that it arrived three decades later.

226 Knowledge about biology and ecology of pest species is important to manage invasive social
227 wasps. Current control methods for *Vespula* wasps are directed towards the destruction of nests
228 and the application of toxic baits, however their success is often variable and poses a risk for
229 non-target species. Next-generation pest control technologies, including synthetic lures, have
230 been proposed as part of an alternative solution (Masciocchi et al. 2019). Based on our co-
231 existence results, future management strategies suggest that local site studies on the
232 preponderance of a given *Vespula* spp., may be needed, to focus species-specific practices.
233 Since the population density of *V. vulgaris* is expected to be 5 times greater than that of *V.*
234 *germanica*, studies on the impact and habits of the former are warranted.

235 Our results also show that, in general, the diet of these wasps was similar, however preys
236 collected were different. *V. germanica* foraged, mostly, on insects belonging to Diptera and
237 Orthoptera orders. In contrast, *V. vulgaris* had a diet composed for the most part of insects of
238 Hemiptera and Coleoptera orders. In Chile, Mangunacelaya et al. (1986) found that the most

consumed orders by *V. germanica* are Araneae, Lepidoptera and Diptera. In New Zealand, diets of both species were compared noting that Diptera was the most abundant prey component for both *V. germanica* and *V. vulgaris*. However, some differentiation was observed, with *V. germanica* foraging more Diptera and less Araneae, Hemiptera and Lepidoptera than *V. vulgaris* (Harris and Oliver 1993). 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 could suggest that *V. vulgaris* and *V. germanica* present a prey partitioned consumption behavior that could potentially lead to reduction in niche overlap. According to Harris (1991), *V. germanica* foragers return to nests with heavier prey loads than *V. vulgaris*, making in comparison, fewer trips. However, the higher foraging efficiency reported for *V. vulgaris* does not seem to have a significant effect in Patagonia. Our results suggest the coexistence of both species. Future studies could evaluate these characteristics to determine the magnitude of these variables.

Given their similarity in biology, and overlap in nesting sites and diet, these species may have developed strategies to avoid or reduce competition. In New Zealand and Patagonia, it has been noted that both species have spatial resource partitioning, where *V. vulgaris* were found foraging in the shrubland, mid height level while *V. germanica* were more commonly seen foraging at the ground level (Harris et al. 1991; Masciocchi et al. 2019). In line with this, Pereira et al. (2016) found that *V. germanica* significantly avoids *V. vulgaris* visual and odour cues in bioassays with free-flying wasps arriving to protein baits. Together these findings suggest that interspecific competition may not determine the interactions among both wasps and could explain co-existence as the most likely long-term outcome.

In regards of the invasion process described for these social wasps, it is likely that intraspecific competition plays a role. Pusceddu et al. (2018) showed that social facilitation, given by local

enhancement, promoted agonistic competition between *Vespula* wasps, suggesting that individuals from different colonies, that find themselves at the same foraging site, will defend their own prey item from other conspecifics. Competitive interactions between individuals of *V. germanica* during feeding, even when the food resource is not scarce, also have been described by Parrish and Fowler (1983). This evidence suggest that no invasion meltdown process occurs among these very similar vespids, but instead a quota of biotic resistance is added to *V. vulgaris* invasion by the prior arrival of the competing species, *V. germanica*. Unfortunately, all reported invasions by both these wasps have occurred in a similar sequence, so we cannot ascertain whether *V. vulgaris*' invasion could mitigate the establishment of *V. germanica*, although this is also a site-dependent process as both species are generalists and opportunistic.

Models of resource competition play an important role in ecology. Lotka-Volterra phenomenological model allows us to understand if and by how much, species affect each other without knowing the mechanism behind that interaction (Looijen 1998). It is a good simple model to introduce a first approximation into the study of species interactions, however it has been highly criticized for its simplicity. Still, several studies had used this model to successfully analyze interactions between species recently (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 is a useful quantitative tool for describing the equilibrium species abundances and make accurate predictions.

Understanding the interplay between invasive species and invasion process, is a key issue related to their invasion ecology (e.g., biological meltdown, biotic resistance), population outcomes and species-specific management. 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 Lotka-Volterra modelling approach. We provided information, with field

287 data, indicating that the coexistence of both species of wasps is likely in Patagonia. In turn, we
288 suggested that the preference for different preys and intraspecific competition could be a
289 plausible explanation to the coexistence observed in Argentina. Improving our understanding of
290 the interaction between invasive species may help to develop appropriate techniques for
291 managing undesired invasive social wasp populations.

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295 **Declarations**

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298 **Conflicts of interest** The authors declare that they have no conflict of interest

299 **Ethics approval** Not applicable

300 **Consent to participate** Not applicable

301 **Consent for publication** Not applicable

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

305 **Code availability** Not applicable

306 **Authors' contributions** AJP, MM and JJC conceived the idea; AJP and MM collected the data;
307 AJP analyzed the data and developed the mathematical models; all authors were involved in
308 writing the manuscript.

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488 Figures legends

489 **Fig. 1**

490 Trap design used to capture forage returning to nest (extracted and modified from Harris and
491 Oliver 1993)

492 **Fig. 2**

493 Average percentage ($\pm$ standard error) of different arthropods orders in *V. germanica* (blue bars)
494 and *V. vulgaris* (red bars) diets (N = 10 nests). ** indicates significant differences ($P < 0.05$)
495 between wasp species according to the Kruskal-Wallis

496 **Fig. 3**

497 Lotka-Volterra model prediction of *V. germanica* (blue line) and *V. vulgaris* (red line) population
498 growth in time (years) based on parameters estimated from the abundances and diets of each
499 species

500 **Fig. 4**

501 Graphical representation (phase diagram) of competition for preys consumption between *V.*
502 *germanica* (blue line) and *V. vulgaris* (red line). Lines represents the specific zero growth rate
503 isoclinas that intersect at positive abundances (equilibrium point; $x=0.85$, $y=4.83$)

Figures

Fig. 1

Fig. 2

Fig.3

Fig. 4