Biogeography and anthropogenic impact shape the success of invasive wasps on New Zealand's offshore islands

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Abstract

Aim: The theory of island biogeography predicts that the susceptibility of an island to invasion is determined by its isolation and size. However, many island ecosystems have been intensely modified by humans. Here, we investigated the biogeographic, biotic and anthropogenic drivers of invasive social wasps on 36 offshore islands.

Location: Islands off the east coast of New Zealand's North Island.

Taxa: Vespula germanica (Fabricius, 1793), Vespula vulgaris (Linnaeus, 1758) and Polistes chinensis antennalis (Fabricius, 1793), Polistes humilis (Fabricius, 1781).

Methods: We used GIS software for in situ randomization of plots on each island (36 islands, 409 plots) and conducted 5-min wasp counts to estimate wasp abundance. Wasp abundance and canopy cover were recorded at each plot. Island isolation was measured using GIS software. Data on island size, human settlement and the presence of introduced rats (Rattus spp.) were collated from the literature and island managers. The number of boat docks per island was counted from satellite images. A generalized linear mixed-effect model (GLMM) was fitted to identify drivers of Vespula and Polistes abundance on offshore islands.

Results: The abundance of Vespula was negatively correlated with island isolation and canopy cover, yet positively correlated with island size. Vespula were also more abundant on islands that have been settled by humans. The abundance of Polistes was negatively correlated with canopy cover. Finally, results did not support the notion that invasive wasps were associated with introduced rats on New Zealand's offshore islands.

Conclusions: Our findings highlight the importance of biogeographic factors, such as island size and isolation, for species invasions, and suggest that intact forest cover could contribute to biotic resistance to invasive wasps in island ecosystems. Studies of invasive species should consider the joint effects of biogeographic, biotic and anthropogenic factors to best inform conservation management.

Keywords: biological invasion, conservation biogeography, human disturbance, social insects
Invasive species can radically alter the ecosystems they invade (Vilà et al., 2011). The success of an invader is largely determined by the biogeographic characteristics of the receiving ecosystem (Crowl, Crist, Parmenter, Belovsky, & Lugo, 2008; Ficetola et al., 2010; Frost et al., 2019; Moles, Gruber, & Bonser, 2008; Thuiller et al., 2010). Islands are geographically isolated and thereby less likely to be invaded than mainland (MacArthur & Wilson, 1963; Simberloff, 2009). Paradoxically, they are also species depauperate relative to equivalent mainland areas and therefore less resistant to invasion (D’Antonio & Dudley, 1995). Islands therefore represent model ecosystems for studying the biogeographic processes that determine invasion success (Marvier, Kareiva, & Neubert, 2004).

The biotic resistance hypothesis posits that species rich communities are more resistant to invasion than less diverse communities (Balestri, Vallerini, Menicagli, Barnaba, & Lardicci, 2018; Bartomeus, Sol, Pino, Vicente, & Font, 2012; Elton, 1958). Large islands hold more species than smaller islands (“species-area relationship.” MacArthur & Wilson, 1963) and should therefore be more resistant to invasion. However, humans have substantially reduced the species richness of many island ecosystems through deforestation for agricultural and residential use (Corlett, 1992; Mooney & Hobbs, 2000). Additionally, human transport breaks down geographical barriers and facilitates the dispersal of exotics to even the most remote islands (Capinha, Essl, Seebens, Moser, & Pereira, 2015; Gallardo, Zieritz, & Aldridge, 2015; Helmus, Mahler, & Losos, 2014). A holistic approach that considers biogeographic, biotic and anthropogenic factors is therefore required to understand how they jointly determine invasion success.

Social wasps cause considerable ecological and economic damage in the ecosystems they invade (Beggs et al., 2011; MacIntyre & Hellstrom, 2015). Their success has been attributed to their social behaviour, polyphagous diet and the ability to initiate a colony with a single mated queen (Hanna et al., 2014; Lester & Beggs, 2019; Moller, 1996). *Vespula* and *Polistes* have been particularly successful in New Zealand (Beggs et al., 2011). *Vespula* reach peak densities in Southern Beech (Nothofagaceae) forests (Lester et al., 2013; Moller, Tilley, Thomas, & Gaze, 1991), where they compete with native birds (Gardner-Gee & Beggs, 2013), lizards and invertebrates for carbohydrate resources, predate native insects (Beggs, 2001; Burne, Ritchie, Gruber, & Lester, 2017) and alter multiple components of the decomposer subsystem (Wardle et al., 2010). Similarly, *Polistes* predate native invertebrates (Kumar, Longino, Colwell, & O’Donnell, 2009; Richter, 2000; Ward & Ramón-Laca, 2013) and dominate food resources otherwise available to native species (Gamboa, Greig, & Thom, 2002; Ward & Ramón-Laca, 2013). Despite their substantial impact on native ecosystems, to date, no study has investigated invasive social wasps on New Zealand’s offshore islands.

The islands surrounding New Zealand are important refugia for many endangered endemic species. Here, we investigated the effect of biogeographic, biotic and anthropogenic factors on the abundance of invasive *Vespula* and *Polistes* on 36 islands off the New Zealand "mainland". Specifically, we tested five predictions. First, because species richness increases with island size (MacArthur & Wilson, 1963) and richness can be a form of resistance to invasion (Elton, 1958), we predicted wasp abundance to be negatively correlated with island size. Second, because propagule pressure decreases with distance from the source pool (i.e., mainland, Lockwood, Cassey, & Blackburn, 2009), we predicted wasp abundance to be negatively correlated with island isolation. Third, wasps generally prefer open habitats (Clapperton, Tilley, & Pierce, 1996; Dvořák, Castor, & Roberts, 2008) and forage more efficiently under direct sunlight (Kovac, Stabentheiner, & Brotschneider, 2015). Open habitats are also readily colonized by exotic insects and thereby facilitate their invasion (Morales & Aizen, 2002). We therefore predicted wasp abundance to be negatively correlated with canopy cover. Fourth, because wasps are often associated with human settlements and stowaway on transport vessels (Masciocchi & Corley, 2013), we predicted wasp abundance to be positively correlated with human settlement and boat access. Finally, although the underlying mechanism is unknown, *Vespula* disappeared following the eradication of introduced rats (*Rattus* spp.) on three of New Zealand’s offshore islands (Bellingham et al., 2010). To explore this further, we tested the prediction that *Vespula* abundance is associated with the presence of introduced rats.

## 2 METHODS

### 2.1 Study site

This study was conducted on 36 islands off the east coast of New Zealand’s North Island (Figure 1). Between January and May 2018, we measured social wasp abundance in relation to biogeographic factors (island size and isolation), biotic factors (canopy cover and presence of introduced rats) and anthropogenic factors (presence of settlement and number of boat docks).

For each island, 10 plot locations were a priori randomized with a minimum distance of 40 m to the next plot using ArcGIS 10.5.1 (Environmental Systems Research Institute (ESRI) 2011). In the field, these plots were located using a GPS (Garmin Series 64). Plots that could not be safely accessed were substituted with new plots located at the nearest accessible locale. Islands up to 400 ha in size were allocated 10 plots. To account for variability in larger islands, 1 plot was added for each additional 400 ha in island size. The large size of Great Barrier Island (27,761 ha) and a high proportion of inaccessible private land on Kawau Island required a change of protocol: 11 plots were surveyed in a representative 800 ha sized area in the north-western part of Great Barrier Island, and 10 plots were surveyed in an accessible 400 ha area on Kawau Island.
2.2 | Wasp abundance

We adapted the traditional “5-min bird count” (Dawson & Bull, 1975) to measure wasp abundance. Wasps were visually recorded by trained observers, the bright aposematic coloration in *Vespula* and distinct flight patterns in *Polistes* facilitated visual detection. Traditional methods that had been developed in high wasp density locales (e.g., baited traps and strip searching for nests, Beggs et al., 1998) were tested in preliminary studies, but proved to be inefficient in detecting individuals in low density locales. In contrast, we found that the point-count method was sensitive to record wasp abundance also at low densities. Prior to the standard sampling, the method was tested with multiple observers and yielded consistent results. Ninety per cent (472) of the total counts were performed by a single observer (the first author of this study). The remaining 10% of the total counts were conducted by one additional trained observer. At each plot, individual German (*Vespula germanica*) and common (*V. vulgaris*) wasps, as well as Australian (*Polistes humilis*) and Asian (*P. chinensis antennalis*) paper wasps, were recorded visually within a range of approximately 75 metres in a 360 degree radius around the observer. *Vespula* wasps were counted individually, while *Polistes* wasps were recorded in categories 1 (0–5 individuals), 2 (5–10 individuals), 3 (10–20 individuals), 4 (20–40 individuals), 5 (40–80 individuals) since their abundance was too high in some places to count individuals; for later analyses, categories were considered to represent count data ranging from 5 to 80 recorded individuals. Monitoring was conducted between 9 a.m. and 5 p.m. and only on days where the temperature exceeded 18°C. No monitoring was conducted during rain or strong winds. To ensure that our estimates were representative, monitoring was repeated the following year (January–April 2019) on 10 of the 36 islands, given that wasp densities can fluctuate annually (Barlow, Beggs, & Barron, 2002; Lester et al., 2013).

2.3 | Determinants of wasp invasion

To explore whether wasp abundance was higher on smaller islands, we extracted island area values (ha) from Atkinson and Taylor (1991). Island size ranged from 8 ha (Poroporo Island, Bay of Islands) to 27,761 ha (Great Barrier Island, Hauraki Gulf).

To test whether wasp abundance was greater on less isolated islands, we measured island isolation as the shortest distance to the closest mainland using ArcGIS. Island isolation ranged from 0.39 km (Moturoa Island, Bay of Islands) to 47.5 km (Burgess Island, Mokohinau Islands). Due to their large size and close proximity to surrounding islands, Great Barrier Island and Waiheke Island were treated as mainlands in the calculation of island isolation, given that they are likely source pools for the smaller islands surrounding them (see Harbaugh, Wagner, Allan, & Zimmer, 2009).

To test whether wasps were more abundant on islands with less canopy cover, we estimated canopy cover at each plot following a visual method (Bunnell & Vales, 1990) that describes crown completeness as the proportion of sky that is obscured by tree crowns.
at a single point. The percentage of sky covered by canopy cover decreases with both the absence of tree crowns as well as gaps within the tree crowns (Vales & Bunnell, 1985). Canopy cover was comprised of both native and exotic plant species. The absence of canopy cover is associated with high amounts of exotic plant species (Charbonneau & Fahrig, 2004) that can provide resources for exotic insects (Morales & Aizen, 2002).

To determine whether wasp abundance was greater on islands that have been settled by humans, we collated data on human settlement on islands from Atkinson and Taylor (1991). Presence of human settlement was defined as currently inhabited by people other than conservation rangers or farmed. Abandoned ranger houses, meteorological stations, sheds and jetties did not count as human settlement. Early human settlement, defined as the permanent occupation at some period during pre-European times, was a poor predictor of wasp abundance in a preliminary test and was excluded from later models.

The number of boat docks was used as a proxy for the intensity of boat visitation. We hypothesized that frequent boat visitations increases the risk of transporting wasps to islands. To test whether wasp abundance was greater on islands with high boat visitation, we manually counted the number of boat docks on each island from Google Maps 2017 satellite images.

To investigate whether wasp abundance was higher on islands that have introduced rats, we collated data on the presence of introduced Polynesian (Rattus exulans), Norway (R. norvegicus) and ship rats (R. rattus) from conservation researchers and island managers and the Department of Conservation.

### 2.4 Statistical analysis

We used generalized linear mixed-effect models (GLMM) applying model selection and model averaging (Burnham & Anderson, 2002). We fitted separate GLMMs for Vespula and Polistes abundances recorded in both years (2018 and 2019). A Poisson regression model was used to test the effects of the fixed variables island size and isolation (biogeographic factors), canopy cover and introduced rats (biotic factors), and human settlement and number of boat docks (anthropogenic factors) on wasp abundance (Table 1). To account for the hierarchical design of our study, we included “plot nested within island” and “year” as crossed random effects in all GLMMs. To obtain standardized parameter estimates, we standardized all predictor parameters prior to analysis to zero mean and unit variance (Becker, Chambers, & Wilks, 1988). To test for potential interaction effects between the two genera, the abundance of Polistes was included in the initial model predicting Vespula abundance and vice versa. We found that the abundance of one genus did not affect the abundance of the other and subsequently removed this variable from the models. Consistently, the abundance of Vespula and Polistes was not correlated (n = 524 counts, Pearson’s cor < −.01, p > .05).

We generated separate global Poisson regression models following the procedure described above for Vespula and Polistes, respectively. We then derived a full set of models with all possible combinations of fixed effects from each global model. Next, we applied an information theoretic approach to determine a set of best models, including all models within a range of ΔAICc ≤ 2 (Akaike’s information criterion for small sample sizes) relative to the best model. To gain weighted averages of parameter estimates from the respective set of best models, model averaging was used (Burnham & Anderson, 2002). The “lm4” package was used to fit GLMMs (Bates et al., 2012), and the “MuMIn” package was applied for model averaging (Barton, 2016). All statistical analyses were performed in the R environment (v 3.4.1, R Core Development Team).

### 3 RESULTS

#### 3.1 Invasive wasps on offshore islands

Invasive wasps were found on 35 of 36 (97%) islands off the mainland of New Zealand (Figure 1, Tables 2 and 3). Aorangi Island, (Poor Knights Islands), was the only island in our study where neither Vespula nor Polistes wasps were recorded. Vespula wasps occurred on 27 of the 36 islands (75%), while Polistes wasps were found on 34 islands (94%). The abundance of both wasp species varied from island to island (Tables 2 and 3). Across both years (2018, 2019) and all islands, we observed a mean abundance ± standard error of 4.03 ± 1.38 Vespula individuals per plot per 5-min count while the mean abundance of Polistes was 5.40 ± 0.49 individuals. The highest mean abundance of Vespula was recorded on Great Mercury Island (78 individuals per plot per 5-min). The highest mean abundance of Polistes was recorded on Rotoroa Island (33 individuals per plot per 5-min).

#### 3.2 Drivers of Vespula abundance

Vespula abundance was determined by an interplay of island isolation, island size, canopy cover and human settlement: large islands, islands closer to the mainland, human inhabited or farmed islands, and islands with little canopy cover had higher Vespula abundance than small, more distant, uninhabited islands and islands with greater canopy cover (Table 4, Figure 2a-d). Although there was no significant relationship between rat presence and Vespula abundance, rat presence was included in the set of supported models explaining Vespula abundance on islands (Table 4). The number of boat docks was not correlated with Vespula abundance and was not included in any of the supported models.

#### 3.3 Drivers of Polistes abundance

Polistes abundance was negatively correlated with canopy cover such that higher abundance of Polistes wasps was recorded on islands with little canopy cover (Table 4, Figure 3). The effects of
human settlement and number of boat docks were non-significant, but were included in the set of supported models explaining Polistes abundance on islands (Table 4). Island size and isolation and the presence of rats were not significantly associated with Polistes abundances and not included in any of the supported models.

4 | DISCUSSION

We asked how biogeographic, biotic and anthropogenic factors affect the distribution and abundance of invasive Vespula and Polistes on New Zealand’s offshore islands. Invasive wasps were present on almost all (97%) of the 36 New Zealand offshore islands surveyed, with Polistes being more widely distributed than Vespula. Although the two genera responded differently to the factors considered, canopy cover was an important predictor for both. The abundance of Polistes was only associated with canopy cover, while canopy cover, island size and isolation and human settlement were related to the abundance of Vespula.

Results supported the hypothesis that Vespula are least abundant on strongly isolated islands. Similar trends have been documented for other invasive species (Hartman & Eastman, 1999; Nordström & Korpiämäki, 2004) and are thought to result from the reduced propagule pressure experienced by more isolated islands (Lockwood et al., 2009). In contrast, the abundance of Polistes was not associated with isolation. Differences in the abundance-isolation relationship might result from differences in dispersal ability. Vespula are stronger fliers than Polistes (400 and 72 metres, respectively, Masciocchi & Corley, 2013; Suzuki, 1978), suggesting that Vespula should be less influenced by isolation than Polistes. Surprisingly, we observed the opposite pattern, suggesting that the different responses to island isolation do not result from differences in flight capacity. Results might instead represent differences in the propensity of the different genera to reach islands as stowaways.

We hypothesized that large islands support fewer wasps than smaller islands because they are more species rich (MacArthur & Wilson, 1963). Species rich islands are thought to be more resistant to invasion because native species already occupy most niches, leaving few vacant to invasion (Bartomeus et al., 2012; Elton, 1958).

In contrast, we found that Vespula were more abundant on large islands. Although species richness naturally scales with island size, this relationship might be reversed by the tendency of humans to inhabit and modify large islands. Indeed, the majority of settlements in our study were located on large islands (t test, degrees of freedom = 35, T = 1.808, p = .079). Our results suggest that human activity can obscure—or even reverse—the signal of biogeographic factors, such as island size (see also Rizali et al., 2010).

It is well understood that anthropogenic impact facilitates the spread of invasive species across the globe (Ficetola et al., 2010; Gallardo et al., 2015; Helmus et al., 2014; MacDougall & Turkington, 2005; Pyšek et al., 2010). For instance, human land use has been associated with the presence of invasive plants in forests in New Zealand (Sullivan, Timmins, & Williams, 2005) and North America (Gavier-Pizarro, Radeloff, Stewart, Huebner, & Keuler, 2010). The spread of invasive ants and termites has also been linked to human impact (Evans, Forschler, & Grace, 2013; King & Tschinkel, 2008; Rizali et al., 2010), such as habitat fragmentation (Suarez, Bolger, & Case, 1998) and human infrastructure (Hochmair & Scheffrahn, 2010; Roura-Pascual et al., 2011). Accordingly, the abundance of Vespula was higher on islands with human settlement than on uninhabited islands. In contrast, Polistes were not associated with human settlement, suggesting that Vespula are more synanthropic than Polistes (Dvořák et al., 2008). Overall, our findings provide further evidence for the link between anthropogenic impact and the abundance of invasive insects, but also suggest idiosyncratic responses for different taxa.

We found that Vespula and Polistes were most abundant on islands with low canopy cover. The New Zealand mainland and offshore islands have been subject to significant deforestation following Polynesian and European settlement (McGlone, 1989; Ministry for the Environment & Statistics New Zealand, 2019; Wilmshurst et al., 2014). Deforestation might increase wasp abundance as Vespula and Polistes prefer open habitats (Beggs et al., 2011; Clapperton et al., 1996; Gamboa, Austin, & Monnet, 2018), for instance because low canopy cover increases solar radiation thereby reducing energetic expenditure of wasps (Kovac et al.,

| Parameter          | Range             | Description                                      | Hierarchy |
|--------------------|-------------------|-------------------------------------------------|-----------|
| Island size        | 0–27,761 ha       | Island size in hectare                          | Island    |
| Island isolation   | 0–47.5 km         | Distance to the mainland/next island >9,000 ha in kilometres | Island    |
| Canopy cover       | 0%–100%           | Percentage of sky covered by canopy             | Plot      |
| Rats               | Present or absent | Absence = 0, presence = 1 of rats               | Island    |
| Human settlement   | Present or absent | Absence = 0, presence = 1 of settlement and farming | Island    |
| No. of boat docks  | 0–79              | Number of boat docks on an island               | Island    |

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**TABLE 1** Six potential drivers of Vespula and Polistes abundance on 36 New Zealand’s offshore islands, as analysed in generalized linear mixed-effect models

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Diversity and Distributions
| Island          | # Plots | Size (ha) | Isolation (km) | Canopy cover (%) | Rats | Settlement | # Boat docks | Vespula abundance | Polistes abundance |
|----------------|---------|-----------|----------------|------------------|------|------------|-------------|-------------------|--------------------|
| Motuekanui     | 10      | 34        | 1              | 45 ± 11.2        | 1    | 0          | 0           | 0.0 ± 0.0         | 90 ± 3.6           |
| Unupukapuka    | 10      | 220       | 1              | 23 ± 10.7        | 0    | 0          | 1           | 2.7 ± 0.7         | 29.0 ± 6.4         |
| Moturoa        | 10      | 157       | 0              | 15 ± 4.7         | 0    | 1          | 1           | 4.7 ± 0.7         | 1.0 ± 1.0          |
| Moturua        | 10      | 162       | 2              | 45 ± 12.4        | 1    | 1          | 1           | 1.8 ± 0.5         | 4.5 ± 2.0          |
| Poroporo       | 10      | 8         | 1              | 44 ± 10.4        | 0    | 0          | 0           | 0.9 ± 0.3         | 1.0 ± 0.7          |
| Motuarohia     | 10      | 66        | 2              | 24 ± 9.3         | 0    | 0          | 1           | 0.6 ± 0.2         | 2.5 ± 0.8          |
| Tawhitirahi     | 10      | 163       | 24             | 39 ± 12.9        | 0    | 0          | 0           | 0.0 ± 0.0         | 3.5 ± 2.1          |
| Aorangi         | 10      | 110       | 23             | 68 ± 14.9        | 0    | 0          | 0           | 0.0 ± 0.0         | 0.0 ± 0.0          |
| Burgess         | 10      | 56        | 48             | 9 ± 8.0          | 0    | 0          | 0           | 0.0 ± 0.0         | 5.5 ± 2.2          |
| Aotea (Great Barrier) | 11 | 27,761  | 17             | 55 ± 11.0        | 1    | 1          | 21          | 2.5 ± 0.6         | 1.8 ± 1.8          |
| Rakitu (Arid)  | 10      | 328       | 3              | 44 ± 14.3        | 1    | 0          | 0           | 1.0 ± 0.5         | 1.0 ± 1.0          |
| Motuhaku       | 10      | 43        | 3              | 16 ± 10.0        | 1    | 0          | 0           | 1.6 ± 0.5         | 10.0 ± 1.8         |
| Okokewa (Green)| 10      | 8         | 9              | 25 ± 7.5         | 1    | 0          | 0           | 0.1 ± 0.1         | 2.5 ± 2.0          |
| Nelson          | 10      | 12        | 0              | 30 ± 10.6        | 1    | 0          | 0           | 4.2 ± 1.2         | 0.0 ± 0.0          |
| Kaikoura       | 13      | 535       | 1              | 37 ± 8.7         | 1    | 1          | 1           | 3.0 ± 1.2         | 4.2 ± 1.7          |
| TeHauturu o-Toi (Little Barrier) | 17 | 3,083 | 22             | 57 ± 8.1         | 0    | 0          | 0           | 0.0 ± 0.0         | 6.8 ± 4.8          |
| Motutaiko      | 10      | 24        | 1              | 15 ± 8.7         | 1    | 0          | 0           | 1.8 ± 0.7         | 6.5 ± 1.5          |
| Rangihua       | 10      | 65        | 0              | 1 ± 0.5          | 1    | 0          | 1           | 1.4 ± 0.6         | 3.5 ± 2.0          |
| Kawau          | 10      | 2050      | 2              | 48 ± 9.6         | 1    | 1          | 79          | 2.4 ± 0.7         | 3.0 ± 2.1          |
| Repanga (Cuvier)| 11   | 170       | 24             | 40 ± 13.4        | 0    | 0          | 1           | 0.0 ± 0.0         | 6.8 ± 2.3          |
| Motuora        | 10      | 86        | 4              | 35 ± 10.2        | 0    | 0          | 0           | 1.4 ± 0.6         | 3.5 ± 1.3          |
| Tiritiri Matangi | 10  | 196       | 4              | 23 ± 10.0        | 0    | 0          | 1           | 0.0 ± 0.0         | 7.5 ± 2.5          |
| Ahuahu (Great Mercury) | 15 | 1,860 | 6              | 22 ± 7.9         | 0    | 1          | 2           | 9.6 ± 6.8         | 1.0 ± 0.7          |
| Whakau (Red)   | 10      | 225       | 14             | 63 ± 8.9         | 0    | 0          | 0           | 0.0 ± 0.0         | 3.0 ± 2.0          |
| Korapuki       | 10      | 18        | 6              | 78 ± 7.8         | 0    | 0          | 0           | 0.0 ± 0.0         | 0.5 ± 0.5          |
| Otata          | 10      | 15        | 19             | 48 ± 13.0        | 0    | 0          | 0           | 1.0 ± 0.5         | 2.0 ± 2.0          |
| Rakino         | 10      | 148       | 6              | 20 ± 5.4         | 0    | 1          | 1           | 1.4 ± 1.0         | 2.0 ± 1.1          |
| Rangitoto–Motutapu | 19 | 3,881  | 4              | 28 ± 7.5         | 0    | 1          | 2           | 2.8 ± 0.5         | 1.3 ± 0.6          |
| Waiheke        | 33      | 9,333     | 5              | 30 ± 5.4         | 1    | 1          | 32          | 7.5 ± 1.7         | 9.5 ± 2.3          |

(Continues)
### Table 2 (Continued)

| Island                  | # Plots | Size (ha) | Isolation (km) | Canopy cover (%) | Rats | Settlement | # Boat docks | Vespula abundance | Polistes abundance |
|-------------------------|---------|-----------|----------------|------------------|------|------------|--------------|-------------------|--------------------|
| Rotoroa                 | 10      | 90        | 12             | 15 ± 8.8         | 0    | 1          | 1            | 3.1 ± 0.8         | 33.0 ± 8.7         |
| Motuihe                 | 10      | 195       | 4              | 16 ± 7.6         | 0    | 1          | 1            | 2.1 ± 0.7         | 175 ± 5.2          |
| Browns                  | 10      | 58        | 1              | 12 ± 6.3         | 0    | 0          | 0            | 1.3 ± 1.0         | 2.0 ± 1.3          |
| Aldermen                | 10      | 96        | 19             | 44 ± 13.6        | 0    | 0          | 0            | 0.0 ± 0.0         | 0.0 ± 0.0          |
| Whakahau (Slipper)      | 10      | 247       | 4              | 20 ± 10.6        | 1    | 1          | 1            | 0.9 ± 0.4         | 1.5 ± 1.1          |
| Motiti                  | 10      | 690       | 10             | 13 ± 7.0         | 1    | 1          | 1            | 1.0 ± 0.3         | 8.0 ± 4.2          |
| Moutohora               | 10      | 173       | 7              | 52 ± 14.1        | 0    | 0          | 0            | 0.0 ± 0.0         | 2.5 ± 2.0          |

**Note:** For each island, the mean abundance of *Vespula* and *Polistes* (mean number of individuals/plot/5-min) was based on individual counts for *Vespula* and abundance categories for *Polistes* in 2018. Islands are ordered from North to South.

### Table 3

| Island                 | # Plots | Size (ha) | Isolation (km) | Canopy cover (%) | Rats | Settlement | # Boat docks | Vespula abundance | Polistes abundance |
|------------------------|---------|-----------|----------------|------------------|------|------------|--------------|-------------------|--------------------|
| Te Hauturu o-Toi (Little Barrier) | 17     | 3,083     | 22             | 57 ± 3.3         | 0    | 0          | 0            | 0.0 ± 0.0         | 6.5 ± 3.3          |
| Repanga (Cuvier)       | 11      | 170       | 24             | 34 ± 13.5        | 0    | 0          | 1            | 0.0 ± 0.0         | 13.5 ± 5.9         |
| Ahuahu (Great Mercury) | 15      | 1,860     | 6              | 26 ± 9.2         | 0    | 1          | 2            | 78.3 ± 44.5       | 3.3 ± 1.4          |
| Whakau (Red)           | 10      | 225       | 14             | 49 ± 10.4        | 0    | 0          | 0            | 0.9 ± 0.8         | 9.0 ± 5.2          |
| Korapuki               | 10      | 18        | 6              | 72 ± 10.9        | 0    | 0          | 0            | 0.0 ± 0.0         | 2.0 ± 2.0          |
| Otata                  | 10      | 15        | 19             | 47 ± 12.6        | 0    | 0          | 0            | 0.0 ± 0.0         | 0.5 ± 0.5          |
| Rakino                 | 10      | 148       | 6              | 8 ± 3.2          | 0    | 1          | 1            | 2.4 ± 0.8         | 4.5 ± 0.9          |
| Rangitoto–Motutapu     | 19      | 3,881     | 4              | 27 ± 8.4         | 0    | 1          | 2            | 2.7 ± 0.9         | 1.3 ± 0.7          |
| Motuihe                | 10      | 195       | 4              | 9 ± 3.3          | 0    | 1          | 1            | 0.5 ± 0.3         | 8.0 ± 1.7          |
| Aldermen               | 10      | 96        | 19             | 33 ± 12.1        | 0    | 0          | 0            | 0.0 ± 0.0         | 0.5 ± 0.5          |

**Note:** For each island, the mean abundance of *Vespula* and *Polistes* (mean number of individuals/plot/5-min) was based on individual counts for *Vespula* and abundance categories for *Polistes* in 2019. Islands are ordered from North to South.
Furthermore, the removal of canopy cover is often associated with the establishment of exotic plant species (Charbonneau & Fahrig, 2004) that could facilitate invasion by wasps via the enhanced provision of nectar and arthropod prey (Morales & Aizen, 2002). Deforestation also reduces biodiversity (Barlow et al., 2016; Brook, Sodhi, & Ng, 2003), which can result in lower biotic resistance to invasion (Chapin et al., 2000; Mooney & Hobbs, 2000; Oliver et al., 2015). Independent of the exact mechanism, there is evidence that New Zealand’s forested ecosystems are less invaded by introduced social insects (Probert, Ward, Beggs, Allison-Maxwell, & Stanley, 2020), therefore protecting and restoring native forest may help to inhibit the success of invasive wasps on New Zealand’s offshore islands.

Measuring wasp abundance can be challenging; especially in areas with low wasp densities. Attraction of wasps to baited traps is highly variable (e.g., Harris, Moller, & Tilley, 1991; Masciocchi, Unelius, & Buteler, 2019). Density estimates using Malaise traps and nest searching in strip plots are correlated, suggesting that these non-baited methods are relatively robust for estimating wasp abundance (Beggs et al., 1998). However, these latter two techniques were developed in New Zealand’s southern beech forests where wasp abundance is high (Moller et al., 1991; Thomas, Moller, et al., 2015).

### Table 4

| Parameter       | Models | Estimate | SE  | p    |
|-----------------|--------|----------|-----|------|
| Vespula Size    | 2      | 0.534    | 0.234 | 0.023* |
| Vespula Isolation | 2     | -1.99    | 0.399 | <.001*** |
| Vespula Canopy cover | 2    | -0.336   | 0.029 | <.001*** |
| Vespula Human settlement | 2    | 1.521    | 0.513 | 0.003** |
| Vespula Rats    | 1      | 0.042    | 0.281 | 0.881 |
| Polistes Canopy cover | 3    | -0.526   | 0.027 | <.001*** |
| Polistes Human settlement | 1    | 0.079    | 0.245 | .747 |
| Polistes Boat docks | 1     | 0.021    | 0.094 | .822 |

Note: For each fixed parameter, the number of models containing the respective factor and their estimate, standard error (SE) and p-value are presented. Model averaging was based on all models within a range of ΔAICc ≤ 2.

* *, **, and *** denote p < .05, p < .01, and p < .001, respectively.

### Figure 2

The abundance of *Vespula* (mean number of individuals/plot/5-min) on New Zealand’s offshore islands was associated with (a) island isolation (km), (b) island size (ha) and (c) canopy cover (%). *Vespula* were also more abundant on islands that have been settled by humans (d). Closed circles denote mean values for each island. Shaded areas around fitted trend lines indicate 95% confidence intervals. Axes of continuous predictors and response variables are log-transformed.
This suggests that forests that provide honeydew are prolific (Beggs, 2001; Beggs et al., 2011; Gardner-Gee & Beggs, 2009). This finding suggests that, while island geography and canopy cover are important predictors of wasp abundance, the robustness of our findings is also supported by the fact that we surveyed the abundance of wasps over two years, revealing similar patterns in both years for both genera, although, prior research has demonstrated that wasp abundance can fluctuate annually (e.g., Barlow et al., 2002; Lester et al., 2013).

While biogeographic theory is a useful tool for understanding invasion dynamics on islands, biotic interactions between the invaders and the receiving community are also important determinants of invasion success (Ficetola, Thuiller & Mlaud, 2007). Vespula wasps scavenge protein from cadavers and exploit old rodent burrows as nesting sites (Spradberry, 1973), introduced rats could therefore facilitate wasp invasion. However, here we found no evidence for a link between rat presence and wasp abundance on islands. In our study, the highest abundance of Vespula was actually recorded in kanuka (Kunzea ericoides) forest on Great Mercury Island, where endemic honeydew-producing scale insects are prolific (Gardner-Gee & Beggs, 2009). This finding suggests that, while island geography and canopy cover are important predictors of wasp abundance, the availability of carbohydrate resources such as honeydew is also very important (Beggs et al., 2011; Gardner-Gee & Beggs, 2009). In fact, the highest densities of Vespula recorded to date occur in New Zealand’s indigenous beech forest (Thomas et al., 1990), where honeydew-producing scale insects are prolific (Beggs, 2001; Beggs & Wardle, 2006). This suggests that forests that provide honeydew resources are associated with high wasp numbers, while a canopy cover without such trees may be less suitable for wasps than open habitats. Consistently, we found that islands that were covered by forest without honeydew resources had the lowest abundance of wasps.

Our study shows that social wasps are highly successful invaders on New Zealand’s offshore islands. Their invasion success may be explained by their opportunistic feeding behaviour, the absence of predators and the availability of nesting sites on these islands (Lester & Beggs, 2019). While we show that the ocean between offshore islands and the New Zealand mainland may act as a barrier to wasp invasion (at least for Vespula), anthropogenic impact such as settlements and deforestation was important for the invasion success of both wasp genera on islands. The findings revealed by our study therefore suggest that the protection and restoration of native forest should be prioritized in the conservation of island ecosystems and could help to mitigate the ecological consequences of insect invasion for native ecosystems.

**ACKNOWLEDGEMENTS**

We thank David Paterson, Obi Bayliss and Jesse Gifkins for support during field research. We are very grateful to the Department of Conservation, island owners, caretakers and their families for supporting the logistics of field research. We thank Matthew Biddick for helpful comments on earlier drafts of this paper. This research project is funded by MBIE-SSIF funding for Landcare Research to the Biota Portfolio, the Rotary Club of Newmarket (Bob Stewart Environmental Award) and the Biological Heritage National Science Challenge.

**CONFLICT OF INTEREST**

None.

**DATA AVAILABILITY STATEMENT**

All data available at: Schmack et al. 2019 submitted with DOI, https://doi.org/10.5061/dryad.zkh189368

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BIOSKETCH

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How to cite this article: Schmack JM, Schleuning M, Ward DF, Beggs JR. Biogeography and anthropogenic impact shape the success of invasive wasps on New Zealand's offshore islands. Divers Distrib. 2020;26:441–452. https://doi.org/10.1111/ddi.13021