Modelling the impacts of an invasive species across landscapes: a hierarchical approach

We develop a hierarchical modelling approach to estimate the extent of ecological impacts of the invasive Asian paper wasp across different landscapes in New Zealand. We used: i) a baseline distribution layer (modelled via MaxEnt); ii) Asian paper wasp nest density (from >460 field plots, related to their preferences for specific land cover categories); and iii) and their foraging intensity (rates of foraging success, and the time available to forage on a seasonal basis). Using geographic information systems this information is combined and modelled across different landscapes in New Zealand. The highest densities of Asian paper wasps were in herbaceous saline vegetation, followed closely by built-up areas, and then scrub and shrubland. Nests densities of 34 per ha, and occupancy rates of 0.27 were recorded for herbaceous saline vegetation habitats. However, the extent of impacts of the Asian paper wasp remains relatively restricted because of narrow climate tolerances and spatial restriction of preferred habitats. A hierarchical approach based on geographic information systems and species distribution models, in combination with factors such as distribution, density, and predation, create a powerful tool that allows the extent of impacts of invasive species to be assessed across large spatial scales. These models will be useful for conservation managers as they provide easy visual interpretation of results, and can help prioritise where direct conservation action or control of the invader are required.

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Introduction

Species distribution models (SDMs), which can be used to predict a species' potential occurrence across a landscape, have become a key part of ecological research and conservation planning (Guisan & Thuiller, 2005; Thuiller et al., 2008; Elith & Leathwick, 2009; Franklin, 2013). Such models can explore more than just distribution, and are increasingly being used for a range of biodiversity applications such as modelling the habitats of communities, ecological refuges, potential impacts under climate change, and biotic interactions (Araújo & Luoto, 2007; Bradley, 2013; Porto, Carnaval & da Rocha, 2013; Ross & Howell, 2013).

However, one aspect of SDMs that is less utilised is analyses of the impacts of invasive species across large spatial scales. Yet SDMs are ideal for this type of study because they capture localised impacts (at sites) and can extend these impacts across larger spatial scales using geographic information systems (GIS). Predicting impacts across landscapes is an extremely useful tool for invasive species, and may highlight the need for direct conservation action or control of the invader.

Social insects form a large part of the invasive invertebrate literature because they usually have a wide host range, feed at a range of trophic levels, can reach very high densities, often have noticeable effects on prey, and are commonly associated with human trade (Suarez, Holway & Ward 2005; Snyder & Evans 2006; Wilson, Mullen & Holway 2009; Ward et al., 2010; Roura-Pascual et al. 2011; Roy HE et al., 2011). Four species of paper wasps (*Polistes*) are invasive around the globe (Beggs et al., 2011): *P. versicolor* (Olivier) in the Galápagos; *P. dominula* in North America; and *P. humilis* (Fabricius) and *P. chinensis antennalis* Perez in New Zealand.

In New Zealand, *P. chinensis antennalis*, commonly known as the Asian paper wasp (APW), was first recorded in 1979, and has subsequently spread rapidly across much of the North Island and several locations in the South Island (Clapperton, Tilley & Pierce, 1996). Although the distribution and nesting biology of the APW is well known (Clapperton, Tilley & Pierce, 1996; Yamane, 1996; Clapperton & Dymock, 1997; Clapperton & Lo, 2000), little has been published on its ecological impacts. Densities of paper wasps can reach up to 210 nests/ha (Clapperton 1999), and although densities of 20-40 nests/ha are more common, this still translates into ~1000–2000 wasps/ha, who are responsible for many 10,000s of prey captured per season (Clapperton 1999).

Paper wasps do not naturally occur in New Zealand (along with many other groups of social insects (Ward et al 2006)), and consequently, there are concerns that APW could have a

37 significant impact on native biodiversity, particularly on the larvae of butterfly and moths, which

38 are heavily preyed upon (Clapperton 1999; Ward & Ramón-Laca 2014).

39   In this paper we used a hierarchical approach, built on a potential distribution layer

40 (modelled via MaxEnt), and hierarchically added, land-cover-specific densities, and foraging

41 intensity, to develop a comprehensive model of the spatial extent of the impacts of Asian paper

42 wasps across New Zealand.

43 **Materials and Methods**

44 **Distribution**

45 *Occurrence data*

46 In total, 253 geo-referenced occurrence records of the presence of Asian Paper wasps (APW)

47 were obtained from (a) published literature (Clapperton 1999) (n = 71); (b) Museum collections

48 (n = 112); (c) field surveys in 2012 (n = 22); and (d) through a publicity campaign asking

49 members of the public for sightings of the APW (n = 48; only records that were supported by

50 photographic evidence were used, e.g. a worker wasp, or nest, both of which are very distinct).

51 Specimens from museum collections are held in the Auckland War Memorial Museum

52 (Auckland), the New Zealand Arthropod Collection (Auckland), Te Papa (Wellington),

53 Entomology Research Museum (Lincoln University), and Otago Museum (Dunedin).

54 *Environmental variables*

55 Environmental layers used were elevation (m), growing degree days (at a 10°C base), annual

56 rainfall (mm), solar radiation (MJm $^{-2}$day $^{-1}$), maximum annual temperature (°C), and minimum

57 annual temperature (°C). Environmental layers came from the National Institute of Water and

58 Atmospheric Research, except for elevation which is available from Landcare Research LRIS

59 portal (http://lris.scinfo.org.nz/). Each environmental layer was created at 500 m (25 ha) spatial

60 resolution. The nesting biology of paper wasps is known to be strongly influenced by such abiotic

61 variables (Yamane, 1996).

62 *Model method*

63 Distribution models were generated using MaxEnt (Version 3.3.3) to discriminate the

64 environments associated with the presence of APW from the rest of the landscape (Phillips,

65   Anderson & Schapire, 2006; Elith et al., 2011). MaxEnt models were trained with a random
66   sample of 75% of the species occurrence data, and the remaining 25% was used to test model
67   performance (Guisan & Zimmermann 2000). We used 50 model runs on random subsamples of
68   the occurrence data to assess uncertainty of the SDM predictions. We evaluated models using the
69   Area Under the Curve (AUC) metric. The MaxEnt output is a logistic probability with values
70   between 0 (low probability) and 1 (high probability).

71   As the occurrence dataset was not constructed using a systematic sampling approach, a
72   geographic sampling bias may occur (Phillips et al., 2009; Syfert, Smith & Coomes, 2013).
73   Therefore, we created a sampling bias grid in MaxEnt using a quartic kernel density layer (Figure
74   1) to correct for this bias as recommended (Phillips et al., 2009; Syfert, Smith & Coomes, 2013).
75   To provide a surface that highlights both suitable and unsuitable habitats, we require a threshold
76   value that outlines a minimum value that constitutes a suitable habitat. After reviewing the
77   continuous raster output and the nominal threshold values from the MaxEnt models, we selected
78   the average 10% minimum threshold for all 50 MaxEnt runs to define the minimum probability
79   of a suitable habitat. This value was selected as it provides flexibility to account for the variation
80   in quality of the input data.

81   **Density**
82   We used previous information on habitat preferences of the APW in combination with land cover
83   satellite imagery to undertake field surveys to generate density estimates and occupancy rates of
84   APW. In a hierarchical approach, we then combined these land cover-specific densities with the
85   MaxEnt distribution model to generate density estimates of APW across New Zealand.

86   *Land cover*
87   Asian paper wasps occur across a range of native 'open-canopy-habitats' such as grassland,
88   marshland and shrubland, where nests are typically found within short (<2 m high) plants
89   (Clapperton, 1999; Clapperton & Lo, 2000). They are also common in urban areas, with nests
90   found in residential gardens and on wooden fences. Although the habitat preferences of APW are
91   well established, there is little information on their densities within these habitats.
92   In order to select habitats for field surveys to generate density estimates, we used the
93   LCDB-3 database (LCDB NZ Land Cover Database, 2012) derived from the 2007–2008 LUCAS
94   satellite imagery, which classifies land cover into 33 classes. Three land cover classes are highly

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95   suitable for APW: i) built-up area (BUA); ii) herbaceous saline vegetation (HSV); and iii) scrub

96   and shrubland (SAS).

97   Some land cover classes were not surveyed because they are not suitable for APW (e.g.

98   water bodies; bare or lightly vegetated surfaces; artificial surface (such as roads)); are too

99   disturbed to allow nests to develop (e.g. cropland; pasture); or are not preferred (e.g. forest types,

100 alpine vegetation) (Clapperton, 1999). We considered some land cover classes (orchard vineyard

101 & other perennial crops (OVPC); herbaceous freshwater vegetation (HFV); tall tussock grassland

102 (TTG)) to be possibly suitable but of very low preference (due to high disturbance and unsuitable

103 vegetation to construct a nest), and did not survey these classes but instead estimated a nominal

104 value of three nests per ha and occupancy rate of 0.03.

105 *Field surveys*

106 During January to March 2012 we surveyed the three most suitable land cover classes: built-up

107 area (BUA); herbaceous saline vegetation (HSV); scrub and shrubland (SAS). We walked slowly

108 through plots (10 x 10 m) checking vegetation for nests of APW (Table 1). We believe we

109 achieved a high detection rate as nests are larger and more obvious from January to March.

110 However, as it is possible we failed to detect all nests, our densities are conservative. All plots

111 were in the Auckland region.

112 **Foraging Intensity**

113 Paper wasps are generalist predators of invertebrates, and we inferred their effects on biodiversity

114 through foraging intensity as measured by: i) their foraging success of prey capture, and ii) the

115 time available to forage.

116 *Foraging success rate*

117 The foraging of APW has been studied at three sites in northern New Zealand (Clapperton, 1999).

118 We used some of this published data to derive a foraging success rate based on: i) the return of

119 foraging wasps ("traffic rate"; average 0.33 per minute; range 0.23–0.46); ii) the proportion of

120 wasps that carried material back to the nest (average 0.30; range 0.25–0.38), and iii) the

121 proportion of material that represented a prey item (as opposed to liquid food or nesting material)

122 (average 0.75; range 0.70–0.80, excluding the value 0.12 as an outlier). Multiplying these data

123 gives a foraging success rate of 4.5 prey captured/nest/hour (range 2.4–8.4).

124 *Foraging time available*

125   Available foraging time to AWP was estimated by examining "sunshine hours" across New

126   Zealand. Paper wasps do not forage at night or in periods of rain (Clapperton, 1999). Sunshine

127   hours accounts for periods of cloud cover and rain, which reduce foraging, but are also

128   topographically very accurate, and take into consideration the landscape effects of slope and

129   gullies, etc. We used hourly sunshine data (MJm $^{-2}$, obtained from the National Institute of Water

130   and Atmospheric Research, 500 m spatial resolution), and summed these across days, months,

131   and the period February to April (when paper wasps are active).

132   Foraging success and the total time available to forage (for the period February to April,

133   when paper wasps are active) was multiplied together, and then hierarchically combined with

134   land cover specific densities and the MaxEnt distribution model to develop a comprehensive

135   model of the spatial extent of the impacts of Asian paper wasps across New Zealand.

136   **Results**

137   **Distribution**

138   The MaxEnt model predicted that coastal and lowland regions of the North Island are

139   highly suitable for the APW, with potential to extend inland and inhabit considerable areas of the

140   middle and lower North Island (Figures 2, 3). Suitable sites in the South Island are largely

141   restricted to northern regions and the eastern lowland. However, coastal areas of the West Coast

142   and Central Otago (where the APW have been present in Alexandra for over a decade) are also

143   predicted to be suitable (Figures 2, 3). The average test AUC of the MaxEnt models was 0.846

144   (+/− 0.013).

145   These distributions correspond very well to an intolerance of cooler mountainous and wet

146   regions. Jackknife tests of variable importance showed elevation contributed the highest gain, and

147   was the variable containing the most information by itself (possibly because elevation is strongly

148   correlated with temperature and rainfall). Solar radiation was the variable that decreased the gain

149   the most when it is omitted, and contains the most information that is not present in other

150   variables. Contribution to the MaxEnt model gain ranked solar radiation (43.5%) as the most

151   important variable, followed by growing degree days (26.1%) and elevation (21.5%).

152   **Density**

153 A total of 466 plots were surveyed, where average densities of AWP nests ranged from 0 – 34

154 nests per ha (Table 1). The highest densities were in herbaceous saline vegetation (HSV),

155 followed closely by built-up areas (BUA) and then scrub and shrubland (SAS) (Kruskal-Wallis,

156 H = 21.53, d.f. = 2, P <0.001, Table 1). No nests were found in forest plots. A high proportion of

157 plots had no nests (Figure 4), thus the occupancy rate of APW in plots was generally low, with

158 only 15% of plots occupied by at least one nest. However, occupancy was higher in HSV (0.27)

159 and BUA (0.23) compared with SAS (0.09). Three nests was the maximum found in a plot (n = 2

160 plots).

161 Extrapolation of suitable land cover across New Zealand shows over 874,000 ha is

162 estimated to be suitable for APW (Table 1). However, this is greatly reduced (to 92,000 ha) when

163 rates of occupancy are included. A combination of density and occupancy data estimates the total

164 number of APW nests in New Zealand in the region of 1.5 million per year (Table 1).

165 **Foraging Intensity**

166 Based on the estimated total number of nests across the entire country (1,568,118, Table 1), and

167 the estimates of foraging success and foraging time available (Table 2), the APW is responsible

168 for consuming an estimated 3-4 billion prey items during a single season. Total sunshine hours

169 from different locations throughout New Zealand for the February-April period were very similar

170 (Table 2). Consequently, there was little difference in terms of the number of prey items

171 consumed from different locations around New Zealand (Figure 5).

172 **Discussion**

173 Site-based studies provide important details about the impacts of an invasive species; however,

174 these are often very limited in spatial scale. Because of this limitation it remains unknown

175 whether the stated impacts also occur at other sites (or habitats, etc.). This is particularly true in

176 areas that have different abiotic conditions that could directly affect the biology of an invasive

177 species.

178 Creating a hierarchical approach based on key features of an invasive species

179 (distribution, density, foraging intensity) and that incorporates species distribution modelling

180 SDM) and geographic information systems (GIS) allows the extent of impacts to be examined

181 across large spatial scales. The ability to "scale-up" impacts across large spatial scales could be

182 extremely useful for pest management, particularly to provide a greater assessment of the

183   possible impacts of an invasive species in the early stages of its invasion, before it reaches
184   equilibrium.

185   Despite forming a large part of the exotic fauna worldwide, the impacts of invasive
186   invertebrates have received disproportionality less attention compared with the impacts of plants
187   and vertebrates, especially for impacts associated with natural ecosystems (Kenis et al., 2009;
188   Roy et al., 2011). Although the threat posed by invasive invertebrates towards natural ecosystems
189   is well recognised, evidence is scare and limited to a few well-known examples (Kenis et al.,
190   2009; Brockerhoff et al. 2010). However, New Zealand is well known for understanding the
191   impacts of invasive invertebrates, particularly ants and social wasps in natural ecosystems (Ward
192   2007; Beggs et al. 2011). The impacts of paper wasps are also of concern, especially because the
193   native invertebrate fauna did not evolve alongside a diverse and abundant social insect fauna, and
194   thus could be particularly susceptible to such predators. The potential impacts of such highly
195   predacious and generalist arthropods have recently been highlighted (Snyder & Evans, 2006).

196   Although consuming an estimated 3-4 billion prey per year, the overwhelming impression
197   of APWs across New Zealand is that the extent of their impacts is very restricted (e.g. Figure 5).
198   A large proportion of the country is climatically unsuitable for their establishment, and because of
199   their strong habitat preferences they are then further restricted. However, localised, or habitat-
200   specific impacts, may be considerable. Recent research shows the APW prey on a large diversity
201   of endemic caterpillars in the HSV habitat (Ward & Ramón-Laca, 2014). Further assessment of
202   the impacts of APWs should be directed towards HSV habitat because it had the highest nest
203   density and occupancy rates.

204   Several aspects could be further examined to improve modelling. In particular, there is
205   some uncertainty with the potential distribution in the Central Otago region (e.g. Queenstown),
206   where their presence has been recorded for over a decade (Harris, 2002). More locality records
207   from Central Otago would help reduce this uncertainty. Determining density and occupancy rates
208   from other regions around New Zealand would also be valuable. The current values are based on
209   field plots around Auckland (upper North Island). It is possible that density and occupancy rates
210   may be less in other regions because APWs have (and are) spreading southward and these regions
211   are less likely to be at equilibrium for density and occupancy. Additionally, improved estimates of
212   how abiotic factors interact with nest and foraging activity are also important to understand the
213   rates of predation by the APW.

214   **Conclusion**

215 A hierarchical approach based on GIS and SDMs, in combination with factors such as
216 distribution, density, and specific impacts on biodiversity (in this case predation) create a
217 powerful tool that allows the extent of impacts of invasive species across large spatial scales to be
218 assessed. These models will be useful for conservation managers as they provide easy visual
219 interpretation of results, and can help prioritise where direct conservation action or control of the
220 invader are needed, but can also highlight gaps in models where better information is needed.

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Figure 1

Sampling bias grid in MaxEnt using a quartic kernel density to correct for geographic sampling bias in occurrence data.

The scale is a logistic probability with values between 0 (low probability; blue) and 1 (high probability; orange–red). Inset boxes visually show the sampling density kernel for different regions

Value

0

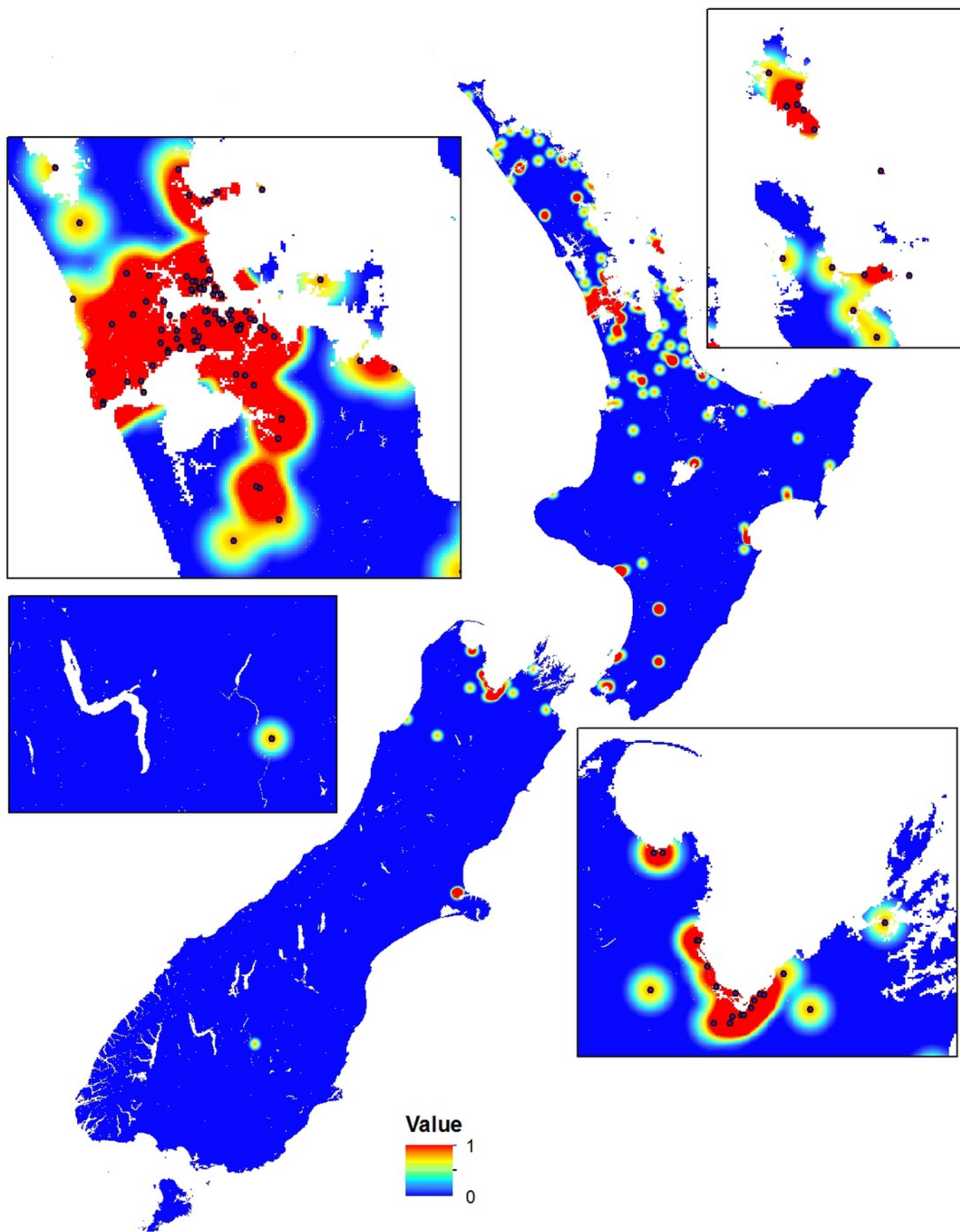



Figure 2

Potential distribution of the Asian Paper Wasp using MaxEnt.

The scale is a logistic probability with values between 0 (low probability; blue) and 1 (high probability; orange–red).

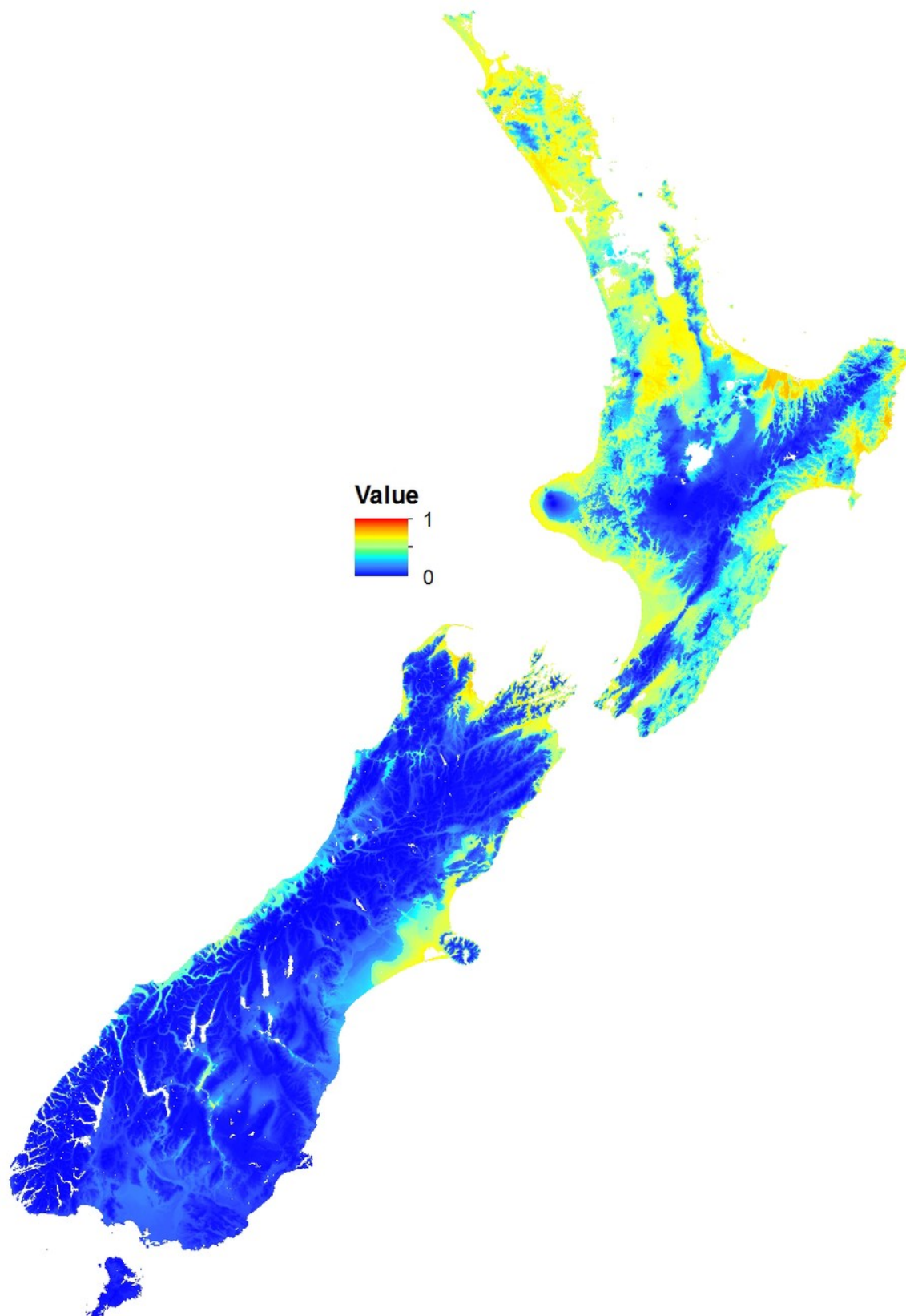



Figure 3

Potential distribution of the Asian Paper Wasp (based on a 10% threshold in MaxEnt). Unsuitable (light), suitable (dark).

North Island

West Coast

Canterbury

South Island

Central Otago

Figure 4

The proportion of field survey plots with zero (white), one (light grey), two (dark grey), three (black) nests.

Land cover classes are: herbaceous saline vegetation (HSV), built-up areas (BUA), and scrub and shrubland (SAS).

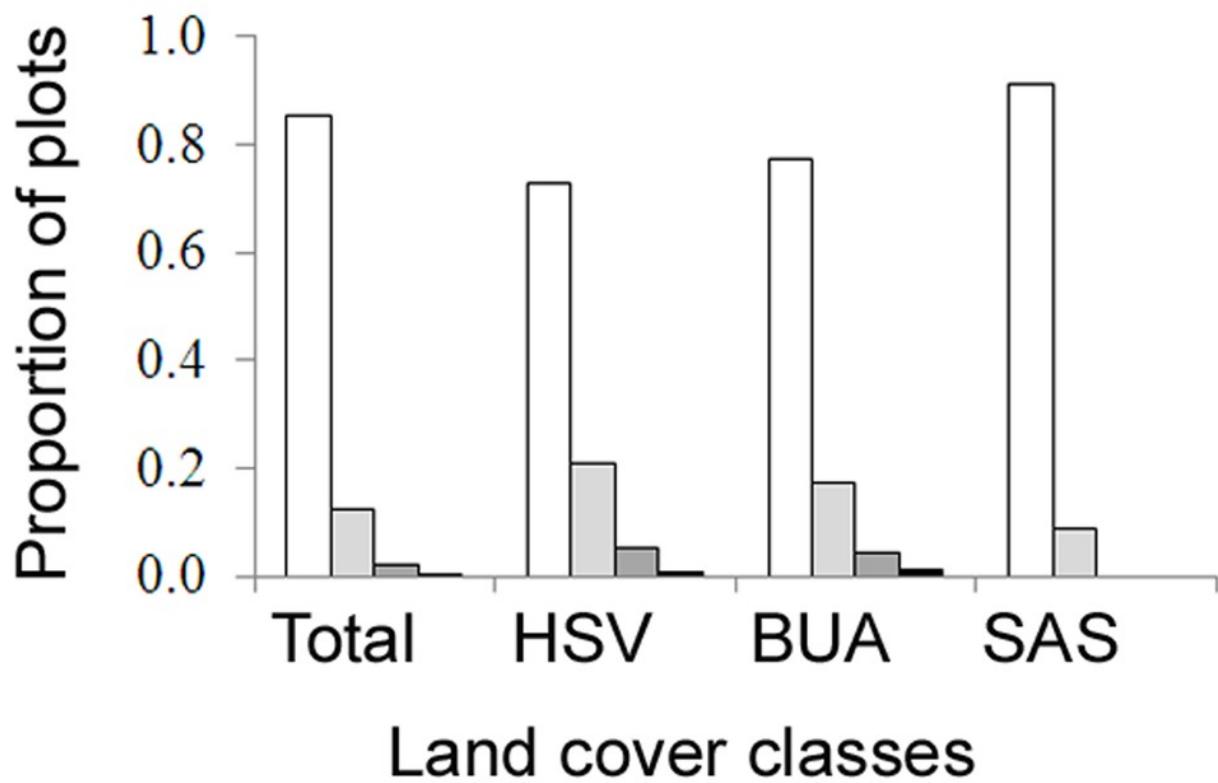
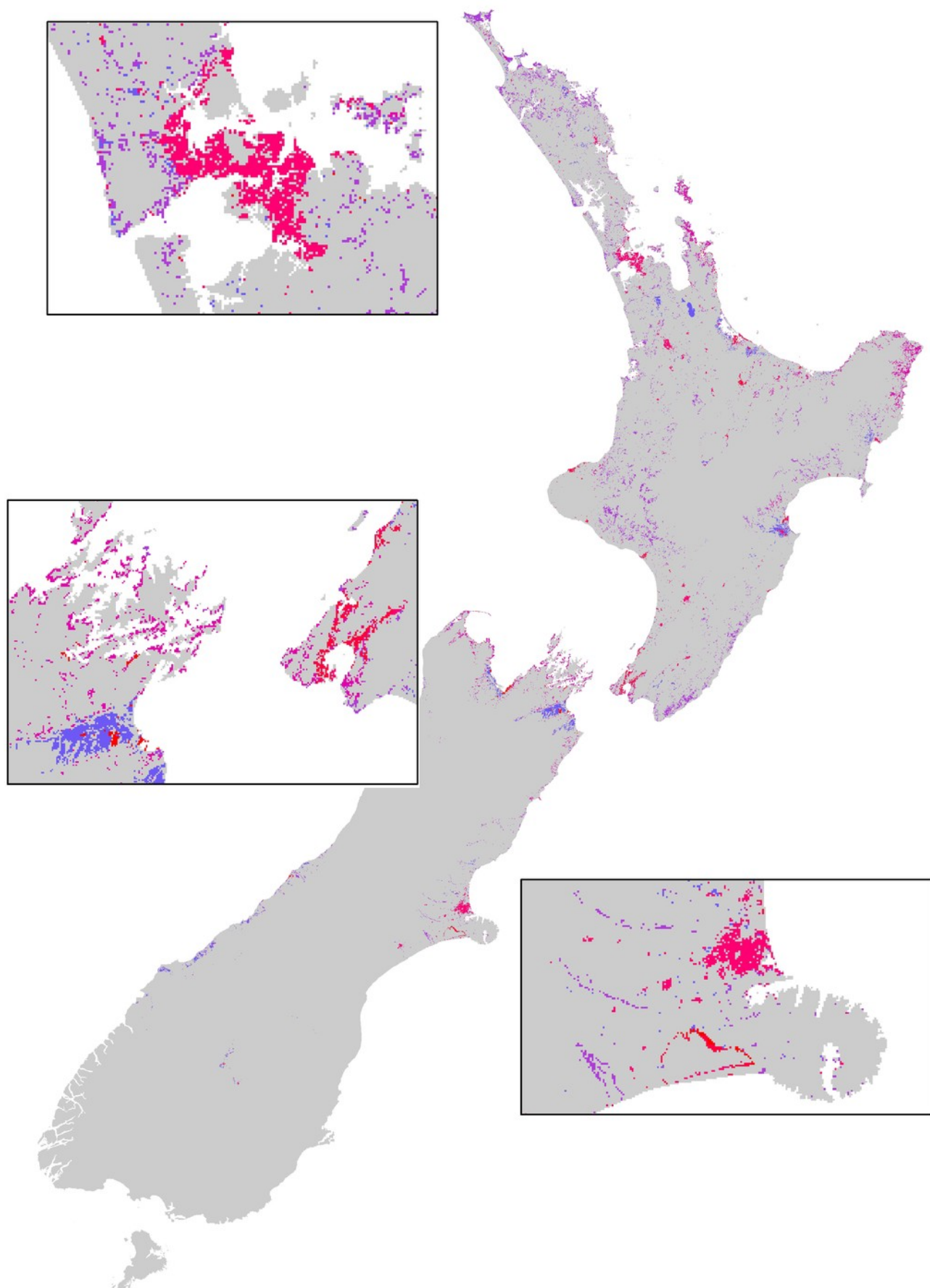



Figure 5

The extent of the impacts of the Asian Paper wasp across New Zealand based on a hierarchical combination of potential distribution, land-cover density, and foraging intensity.

The colours represent a relative scale of impacts from grey (no impact) to blue–purple (lower impacts) to pink–red (highest impacts). Inset boxes visually show the extent of impacts for different regions.

Estimates of the total area occupied and total number of nests for the Asian Paper Wasp

Data extrapolated across New Zealand from field surveys (plots) of density and occupancy for specific land cover classes. *nominal values (see methods)

Table 1. Estimates of the total area occupied and total number of nests for the Asian Paper Wasp extrapolated across New Zealand from field surveys (plots) of density and occupancy for specific land cover classes. *nominal values (see methods)

Land cover class	Total potential (ha)	Plots	Nests	Occupancy	Total occupied (ha)	Average density	Total nests
HSV	13 050	114	39	0.27	3 523	34	119 799
BUA	146 275	93	27	0.23	33 643	29	975 654
SAS	567 100	206	18	0.09	51 039	9	459 351
OVPC	100 575	0		0.03*	3 017	3*	9 051
HFV	47 125	0		0.03*	1 413	3*	4 241
TTG	250	0		0.03*	7	3*	22
Forest	0	53	0	0	0	0	0
Total	874 375	466	84	0.15	92 642	18	1 568 118

Total sunshine hours for different locations throughout New Zealand

Table 2. Total sunshine hours for different locations throughout New Zealand.

Latitude (S)	Location	Annual	Feb/Apr season	Within potential distribution
–36.85	Auckland	1949	519	yes
–37.77	Hamilton	1954	529	yes
–37.67	Tauranga	2169	576	yes
–39.49	Napier	2161	550	yes
–40.36	Palmerston North	1852	526	yes
–41.30	Wellington	1986	553	yes
–43.47	Christchurch	2040	528	yes
–45.02	Queenstown	1927	545	outside?
–45.86	Dunedin	1594	407	outside
–46.41	Invercargill	1649	421	outside