BIODIVERSITY RESEARCH

Determinants for the successful establishment of exotic ants in New Zealand

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ABSTRACT

Biological invasions can dramatically alter ecosystems. An ability to predict the establishment success for exotic species is important for biosecurity and conservation purposes. I examine the exotic New Zealand ant fauna for characteristics that predict or determine an exotic species' ability to establish. Quarantine records show interceptions of 66 ant species: 17 of which have established, 43 have failed to establish, whereas nests of another six are periodically observed but have failed to establish permanently (called 'ephemeral' establishment). Mean temperature at the highest latitude and interception variables were the only factors significantly different between established, failed or ephemeral groups. Aspects of life history, such as competitive behaviour and morphology, were not different between groups. However, in a stepwise discriminant analysis, small size was a key factor influencing establishment success. Interception rate and climate were also secondarily important. The resulting classification table predicted establishment success with 71% accuracy. Because not all exotic species are represented in quarantine records, a further discriminant model is described without interception data. Though with less accuracy (65%) than the full model, it still correctly predicted the success or failure of four species not used in the previous analysis. Techniques for improving the prediction accuracy are discussed. Predicting which species will establish in a new area appears an achievable goal, which will be a valuable tool for conservation biology.

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Keywords

Biological invasions, body size, climate tolerance, discriminant analysis, Formicidae, interception rate.

INTRODUCTION

Our ability to predict species that will invade or spread outside of their range has improved through retrospective analyses of a wide variety of traits. Duncan *et al.* (2001) placed such determinants into three categories: historical factors, life-history traits and climatic suitability. Of the historical factors, increasing introduction rate or propagule pressure is a common feature found to significantly enhance establishment success in birds, weeds and mammals (Kolar & Lodge, 2001). Introduction rates are a critical factor for the invasion success and can substantially alter predictions of invasion success (Duncan, 1997). Behavioural flexibility has been found to be important for exotic bird success in New Zealand (Sol & Lefebvre, 2000), as well as climatic suitability (Blackburn & Duncan, 2001). An ability to tolerate climatic conditions has been used as a predictor for establishment for a number of taxa, including mammals in Australia (Forsyth *et al.*, 2004) and fish introduced to the North American Great Lakes (Kolar & Lodge, 2002).

Invasive ants can substantially alter and even devastate entire ecosystems (e.g. Christian, 2001; O'Dowd *et al.*, 2003). As with most invertebrates, climate is thought to play a large role in determining their distribution (Kaspari *et al.*, 2000). Climate tolerance models have been developed for a number of the most important invasive ants, such as the red imported fire ant, *Solenopsis invicta* Buren (Morrison *et al.*, 2004). Additional factors are also likely to be important in determining invasion success and ant distribution, including introduction rates and behaviour. However, limited data are available on introduction rates for most invertebrate taxa, as species such as ants are seldom intentionally introduced. Previous work has indicated that behaviour and functional group classification can be important for predicting the establishment of exotic ants (McGlynn, 1999a). Morphology may also be important as non-native ants generally appear to be smaller than their non-invasive relatives (Passera, 1994; McGlynn, 1999b).

In New Zealand, the native ant fauna is species-poor with an estimated current total of only 35 ant species, 24 of which are

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established exotics. Species-poor ant communities may be comparatively susceptible to biological invasion, as the likelihood of species with similar life histories to the invader is reduced (Andersen, 1997). The limited species richness in New Zealand may thus be useful, as it allows a focus specifically on the characteristics of the invader, rather than both on invader and on the receiving community. In this paper, I assess the role of historical factors, life-history traits and climatic suitability, as predictors for exotic ant establishment in New Zealand.

METHODS

Historical factors

The New Zealand quarantine authorities have maintained records of ant species intercepted at ports and airports. I used two data sets: interceptions from 1966 to 1982 (Richardson, 1979; Keall, 1981a; Townsend, 1984) and the more recent period 1997–2003 (unpublished data). These records were used to identify potential invaders and as a proxy for 'introduction effort' or 'propagule pressure'. A total of 80 ant species were recorded over this time. Fourteen species were excluded because of a lack of specimens for morphological data. Seven other established species were not intercepted and were also excluded from the analysis.

The remaining ant species were categorized into three groups: 17 established ant species, 6 that ephemerally established and 43 that have failed. Species used in this analysis are presented in Appendix S1 in Supplementary Material.

The 'ephemeral' establishment category was developed for species that have been observed to nest on New Zealand soil, but which have failed to establish permanently. Establishing a nest must allow a greater chance for permanent establishment than when a propagule of possibly only a few workers is intercepted at the border. However, solely because a nest is observed in New Zealand does not mean that a species will become established. For example, the Australian ant, *Myrmecia brevinoda* Forel, was observed in Auckland in 1948, 1965 and 1981 (Keall, 1981b). Though government authorities made no attempt at control in the two early dates, and killed only one nest in 1981, this large and aggressive species has not since been observed. Also in the ephemeral category are the tramp species that have been observed nesting around ports during yearly surveys, undertaken since 2001. These species were *Anoplolepis gracilipes* (F. Smith), *Monomorium floricola* (Jerdon), *Paratrechina longicornis* (Latreille), *Solenopsis geminata* (Fabricius), *S. invicta* Buren and *Tapinoma melanocephalum* (Fabricius). These are tramp species that are widely observed in the Pacific region (Wilson & Taylor, 1967), with the exception of *S. invicta*. Because isolated nests of these species have been observed since the first survey in 2001, I assumed that they are also likely to have previously nested in New Zealand but have failed to establish during the last century. Species such as *A. gracilipes* have been recorded throughout much of the Pacific for almost a century (Wilson & Taylor, 1967). Prior to 2001, no eradication attempts had been made by the government on these species, yet none have established.

Introduction rates from the two periods (1966–82 and 1997–2003) were averaged to produce one interception variable for the discriminant analysis. The number of countries from which each species was intercepted was counted. For the purpose of this analysis, Hawaii was considered separate from mainland USA. Similarly, the Society Islands were considered separate from mainland Tahiti.

The 'pest' status of each of the ant species was inferred from the total number of published citations on each species from the FORMIS database (Wojcik & Porter, 2003). This database is a compilation of 30,971 references from the scientific literature on ants, spanning the period 1670–2002. In initial trials with this database, I searched for references containing the words 'tramp' or 'pest' to estimate the pest status of each ant species. However, some relevant literature was excluded by this method. Instead, the total number of citations for each species was used as an index of 'pest' status.

Life-history traits

Competition is generally thought to exert a strong influence on ant communities (Hölldobler & Wilson, 1990). However, information on this and other life-history traits is limited for many of the ant species intercepted. Accordingly, I categorized ant behaviour based on the functional grouping described by Brown (2000). Because climate was included as a separate variable, hot- and cold-climate specialists were reassigned to other categories based on their genus. Species were thus placed into five groups, ranked from low to high aggression: (1) Cryptic and specialized predator species: ants that forage primarily in the soil and litter, having little interaction with other species or predators that have limited interaction with other ants, including the genera *Hypoponera* and *Myrmecia*; (2) Subordinate Camponotini: species that can co-occur with the dominant Dolichoderines but are behaviourally submissive and often nocturnal feeders, including the genera *Camponotus* and *Polyrhachis*; (3) Opportunists: unspecialized, weedy species characteristic of disturbed habitat, though opportunist species like *P. longicornis* is dominant over *Camponotus* in the Pacific (Lester & Tavite, 2004); (4) Generalized Myrmicinae: these rapidly recruit to and defend clumped food resources, including the genera *Pheidole* and *Monomorium*, and *Oecophylla smaragdina* (Fabricius); and (5) Dominant Dolichoderinae: abundant, highly active and aggressive species, exerting a strong competitive influence on other ants, including the *Iridomyrmex* and *Linepithema*. The behaviour category for each species is given in Appendix S1 in the Supplementary Material.

Morphological measurements were taken from specimens in the New Zealand Ministry of Agriculture and Forestry's National Plant Protection Reference Laboratory in Auckland, New Zealand. These collections were from specimens intercepted over the last century. Measurements consisted of the length of the right hind tibia, the head width, and Weber's length (diagonal measurement from the anterior margin of the pronotum to the posterior extremity of the metapleural lobe). I chose a variety of measurements because leg length alone has been shown to decrease disproportionately to body size in 142 ant species from five subfamilies (Kaspari & Weiser, 1999; Espandaler & Gómez, 2001). In addition, many ant species are polymorphic. Consequently, two sets of measurements were made, one set from the smallest ant and the other from the largest ant in the collection.

Individual species may not be true replicates for the analysis as they may have evolved under similar ecological conditions. Unfortunately, I could not perform phylogenetically independent contrasts as ant systematics is not well understood. As in Kolar and Lodge (2002), to reduce the likelihood that a significant association was because of phylogenetic similarity, I included a variable that ranked ant subfamilies by degree of derived characters using Baroni Urbani (1989). Additionally, I also tested for the most obvious phylogenetic confounds by comparing the establishment success in the subfamily Myrmicinae (28 species) to all other subfamilies (38 species), as in Sol and Lefebvre (2000). No significant difference was observed between the two groups ($\chi^2 = 0.015$, d.f. = 1, $P = 0.904$), indicating phylogenetic independence at this level of analysis.

Climatic suitability

Many of the ant species examined here are known from only one or a few locations. Therefore, instead of attempting to derive a climate envelope for each species, I a priori decided to include temperature data from only the most extreme latitude. This method may still have some bias, as it assumes that a species will have been able to extend its range poleward until it is limited by temperature. Global climate data for monthly temperature and precipitation values were obtained from the International Panel for Climate Change for the period 1961–90 (New *et al.*, 1999). The precipitation surfaces were summed to create a surface of mean annual precipitation, and the minimum and maximum monthly precipitations for each half-degree grid cell. Monthly averages of the mean, minimum and maximum daily temperatures were used to derive the mean and the extremes during the hottest and coldest months of the year. Consequently, the minimum temperature was the average daily minimum in the month with the coolest temperature.

Statistical analysis

Data were considered normally distributed if $P > 0.05$ in Kolmogorov–Smirnov tests, with distributions examined in histograms. Several variables were positively skewed and were consecutively transformed using log, square root, or cube root functions until a normal distribution was obtained in Kolmogorov–Smirnov tests. A Box-Cox transformation ($Y' = [Y^{\lambda} - 1]/\lambda$) was used for the minimum temperature variable, as it was negatively skewed (Quinn & Keough, 2002). A backward-stepwise analysis discriminant was used, as this test is likely to perform better when there are correlations among the variables (SYSTAT, 2002). Two analyses were performed: one with and one without the interception data. The latter may be useful for predicting the success of future invasive ants that have not been previously intercepted. Jackknife procedures were used for cross-validation purposes.

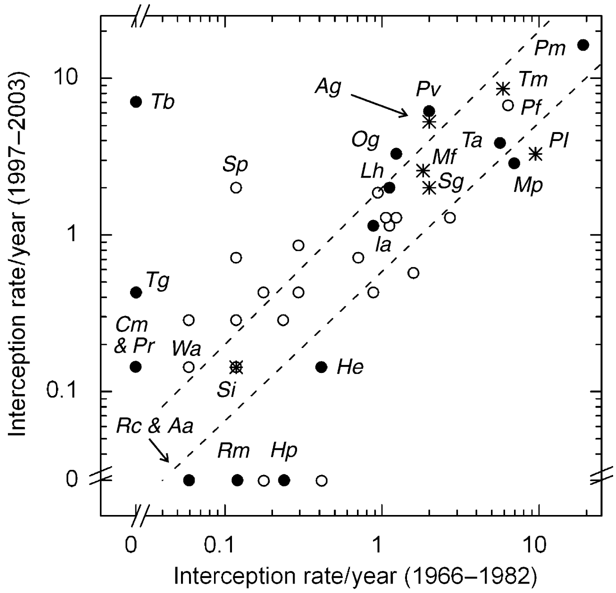

Figure 1 The yearly interception rate of exotic ants into New Zealand during the periods 1966–82 and 1997–2003, used as an index of propagule pressure. The lower dashed line indicates half the rate of introduction between the two time periods, whereas the upper dashed line shows a rate in 1997–2003 double that of 1966–82. Exotic species established (●): Aa = *Amblyopone australis*; Cm = *Cardiocondyla minutior*; He = *Hypoponera eduardi*; Hp = *Hypoponera punctatissima*; Ia = *Iridomyrmex anceps*; Lh = *Linepithema humile*; Mf = *Monomorium floricola*; Mp = *Monomorium pharaonis*; Og = *Ochetellus glaber*; Pv = *Paratrechina vaga*; Pm = *Pheidole magacephala*; Pr = *Pheidole rugosula*; Rc = *Rhytidoponera chalybaea*; Rm = *Rhytidoponera metallica*; Sp = *Strumigenys perplexa*; Ta = *Technomyrmex albipes*; Tb = *Tetramorium bicarinatum* and Tg = *Tetramorium grassii*. Non-established species are (○), and highlighted are Pf = *Pheidole* fervens; Sp = *Solenopsis papuana* and Wa = *Wasmannia auropunctata*. Species that have been observed to nest, but not established (*) are Ag = *Anoplolepis gracilipes*; Mf = *Monomorium floricola*; Pl = *Paratrechina longicornis*; Sg = *Solenopsis geminate*; Si = *Solenopsis invicta* and Tm = *Tapinoma melanocephalum*.

RESULTS

A total of 2075 records of ant interceptions were used in this analysis. The average yearly interception rates were 78.0 (during 1966–82) and 85.3 (during 1997–2003). Interception rates were highest for *Pheidole megacephala* (Fabricius) at an average of 17.67 $year^{-1}$ for the period of 1966–82, which was similar to that observed for the second duration of 1997–2003. However, 13 species more than doubled and 12 more than halved their interception rate between these periods. Despite the median rate for established species being over twice as high as for those that have failed to establish, no significant differences were observed in interception rates between failed, ephemeral or successfully established species (Fig. 1, Table 1). Several species were unique to each time period (Fig. 1). Some species were able to establish despite an apparently low introduction rate (e.g. *Amblyopone australis*

Table 1 Median values for the variables used to predict the establishment of exotic ants. Data are shown with the range and *P* values from the Kruskal–Wallis test, comparing medians

	Established		Ephemeral		Failed		
Variable	Median	Range	Median	Range	Median	Range	K–W *U* test
Historical factors							
Interception rate (notification year^{-1})	0.28	0.03–17.67	2.92	0.13–7.23	0.1	0.03–6.53	0.002
Countries, intercepted (total, 1966–2003)	3	1–27	13.5	2–28	2	1–17	0.008
Citations (in database FORMIS)	5	0–1180	243.5	15–2965	24.5	16–631	0.018
Climatic data at the most southern or northern recorded location							
Mean temperature (°C)	13.4	2.5–23.6	15.4	9.2–25.1	19.6	−7.3–28.0	0.037
Minimum temperature (°C)	2.5	−14.1–18.0	1.3	0.4–20.7	9.3	−31.3–22.0	0.059
Maximum temperature (°C)	25.7	14.5–31.7	29.4	20.9–30.6	29.3	14.9–41.2	0.158
Mean precipitation (mm day^{-1})	2.7	0.9–6.0	2.8	1.6–5.9	3.1	1.0–6.6	0.219
Minimum precipitation (mm day^{-1})	1.4	0.1–2.9	2.2	1.3–3.3	2.2	0.0–4.4	0.086
Maximum precipitation (mm day^{-1})	4.1	1.2–10.6	6.9	1.9–10.5	4.9	1.7–13.3	0.188
Life-history traits							
Aggressive behaviour index	3.0	1.0–5.0	3.5	3.0–4.0	3.0	1.0–5.0	0.258
Smallest ant; head width (mm)	0.55	0.38–1.63	0.57	0.32–0.70	0.61	0.29–3.48	0.593
Smallest ant; hind right tibia (mm)	0.49	0.29–1.24	0.58	0.24–2.02	0.54	0.19–3.85	0.940
Smallest ant; Webers (mm)	0.86	0.53–2.33	0.94	0.48–1.62	0.84	0.40–4.58	0.985
Largest ant; head width (mm)	0.66	0.40–2.53	0.59	0.46–1.24	0.73	0.29–3.80	0.782
Largest ant; hind right tibia (mm)	0.54	0.29–1.60	0.96	0.44–1.94	0.62	0.19–4.20	0.667
Largest ant; Webers length (mm)	0.92	0.53–3.93	1.16	0.77–1.66	1.04	0.38–4.86	0.821
Phylogeny	2.0	1.0–4.0	1.5	1.0–3.0	3.0	1.0–4.0	0.747

Erichson, 0.03 year^{-1}), whereas others did not establish despite a much higher interception rate (e.g. *A. gracilipes*, 3.64 years^{-1}).

The group of ephemerally established ants were generally characterized by high interception rates, except for *S. invicta*. Additionally, ephemerally established species were observed to originate from significantly more countries than those species in the other categories. For example, *P. longicornis* was intercepted from 28 different countries. The number of citations for each species was also significantly higher for the ephemeral ant species, with the highest number being recorded for *S. invicta* (Table 1). A high percentage of these references come from North America, perhaps creating some bias in this statistic. Invasive species may attract much more scientific study there than in some other countries.

Significant differences between successful, ephemeral and failed species were observed in the temperature data. Those species that established in New Zealand were significantly more likely to be observed in locations elsewhere with cooler mean and minimum temperatures, and with lower minimum precipitation rates (Table 1, Fig. 2).

For all the morphological variables, no significant differences were observed between established, ephemeral and failed exotic ant species ($P \geq 0.593$, Table 1). However, data indicated that only smaller ant species became established. In the analysis of tibia length for the smallest ant in each species, the largest of the established species was *Rhytidoponera chalybaea* Emery at 1.24 mm. Fourteen of the failed species had a hind tibia length of up to three times greater (Fig. 2).

Behavioural and phylogenetic factors were not significantly different between the groups (Table 1), indicating that aggression level or relatedness did not influence establishment success.

Discriminant analysis

Of the 17 independent variables, eight were selected for prediction in the backward stepwise discriminant analysis (Table 2). The first function explained 69% of the variance and the associated three-way MANOVA showed a significant difference between the three groups on the first discriminant function (Pillia trace = 0.669, $F = 3.58$, d.f. = 18, $P < 0.001$). The most important standardized factors in the first function were the tibia length of the largest and smallest ants. Behaviour was excluded from the analysis, as were most of the temperature variables except for the maximum temperature. The same variables were used in the second function, wherein the first loading was the minimum rainfall followed by the interception rate. The resulting plot shows overlap between all three groups (Fig. 3a).

The classification matrix categorized species into those that would successfully establish, fail or establish briefly before dying out (ephemeral establishment). The model correctly predicted 12 of the 17 species that have successfully established in New Zealand (Table 3). The four species that were incorrectly predicted to not have established species, with posterior probabilities *for* establishment: *Hypoponera eduardi* (Forel) 0.495, *Paratrechina vaga* (Forel) 0.452, *R. chalybaea* 0.378, and *Tetramorium grassii* (Emery) 0.497.

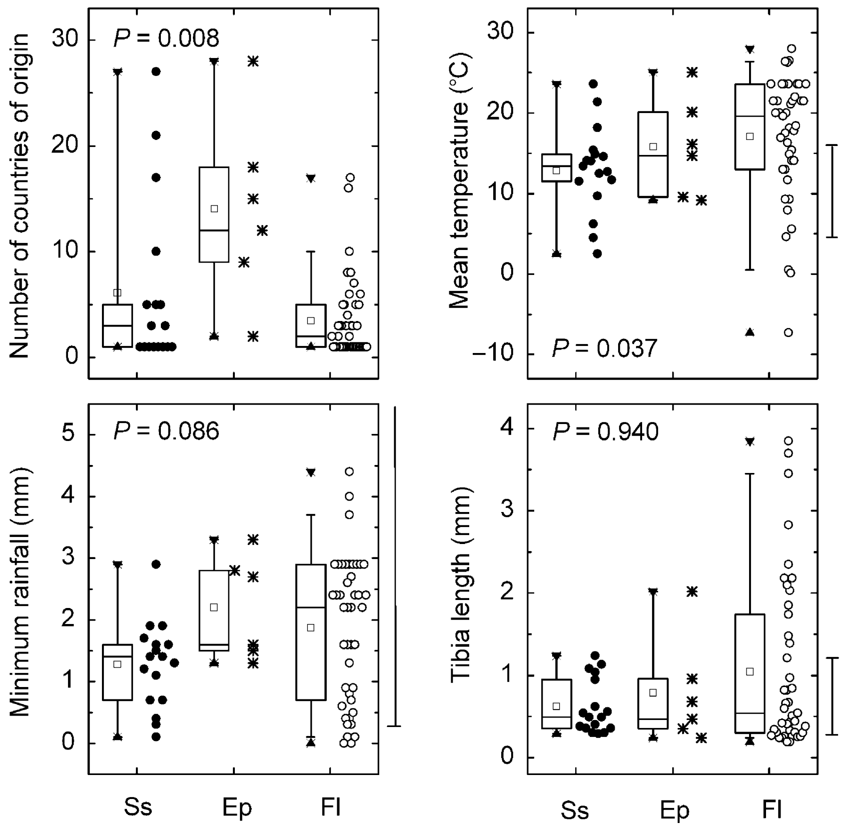

Figure 2 Examples of the distribution of variables used to predict the success (Ss), ephemeral establishment (Ep) or failure (Fl) to establishment by exotic ants in New Zealand. *P* values are Kruskal–Wallis tests comparing medians. The bars to the immediate right of the graphs show the range of temperatures or rainfall in New Zealand, or the range in tibia lengths for endemic ants.

Table 2 Standardized loadings for the first and second canonical discriminant functions, from the backward stepwise discriminant analysis. Loadings are shown for (a) the results from the analysis with all variables, and (b) the analysis excluding interception rate data

	(a) With interception data		(b) Without interception data	
Discriminant function	First	Second	First	Second
Interception rate	0.039	1.179	Excluded	Excluded
Number of countries	−0.788	−0.735	Excluded	Excluded
Citations			0.831	0.180
Mean temperature			0.474	1.026
Minimum Temperature				
Maximum temperature	−0.288	−0.774		
Mean rainfall	1.166	0.874		
Minimum rainfall	−1.181	−1.164		
Maximum rainfall				
Shortest headwidth			−2.012	0.581
Shortest tibia length	2.276	−0.811		
Shortest Weber's length				
Longest headwidth	1.491	0.117	−1.466	−0.209
Longest tibia length	−3.777	0.451		
Longest Weber's length			3.324	0.075
Behaviour				
Phylogeny				

Table 3 The classification matrix from the backward-stepwise discriminant analysis, predicting the number of species would successfully establish, fail, or establish briefly before dying out. The jackknifed classification matrix is shown in brackets. (a), the results from the analysis with all variables, and (b) the analysis excluding interception rate data

	Success	Ephemeral	Fail	Correct (%)
(a) Full model				
Success, *n* = 17	12 (8)	1 (2)	4 (7)	71 (47)
Ephemeral, *n* = 6	0 (0)	6 (5)	0 (1)	100 (83)
Fail, *n* = 43	11 (12)	3 (4)	29 (27)	67 (63)
Total, *n* = 66	23 (20)	10 (11)	33 (35)	71 (61)
(b) No interception data				
Success, *n* = 17	9 (5)	1 (2)	7 (10)	53 (29)
Ephemeral, *n* = 6	0 (0)	6 (6)	0 (0)	100 (100)
Fail, *n* = 43	12 (12)	3 (7)	28 (24)	65 (56)
Total, *n* = 66	21 (17)	10 (15)	35 (34)	65 (53)

The important invasive species *A. gracilipes*, *S. invicta*, *S. geminata*, *Pa. longicornis* and *Ta. melanocephalum* were correctly classified into the ephemeral group (posterior probabilities for establishment $P < 0.001$–0.017). The established species, *Ph. megacephala*, was incorrectly predicted as being ephemeral. Three other species which have failed to establish but were given a high probability as being ephemerally established were

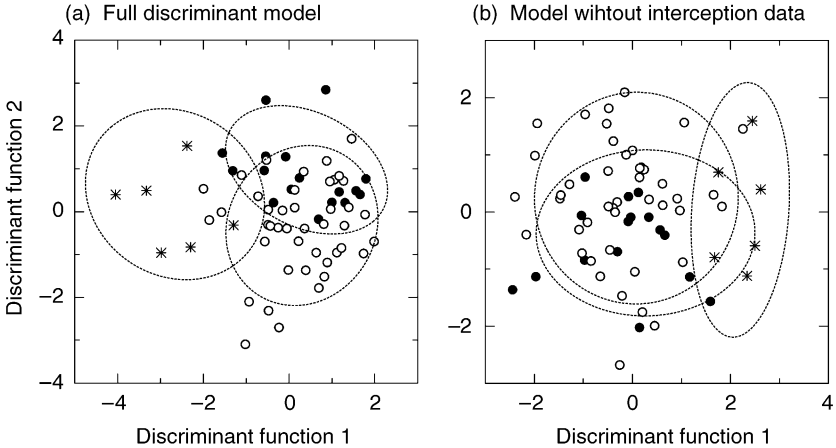

Figure 3 Discriminant function scores for each ant species. (a) the scores from the stepwise model that included interception rate data. Such data are not available for all species entering New Zealand, so (b) shows the scores from the analyses which excluded interception rate information. The three groups are the successfully established exotic species (●), non-established or failed species (○), and species that are occasionally observed in New Zealand but have not become permanently established, i.e. ephemeral species (*). Confidence ellipses are 75%, centred on the centroid of each group.

Camponotus pennsylvanicus (De Geer), *O. smaragdina* and *Paratrechina bourbonica* (Forel).

The weakest predictive ability for the model was the classification of species that have actually failed to establish. Eleven failed species were misclassified as established, including some widespread invasive species such as *Lasius niger* (Linnaeus), *Monomorium destructor* (Jerdon), *Solenopsis papuana* (Emery), *Tetramorium simillimum* (Smith) and *Wasmannia auropunctata*. The posterior probabilities *for* establishment of these species ranged between 0.454 and 0.765. An examination of the climatic data indicated these species occur elsewhere in climates similar to that of New Zealand (except for *S. papuana*), but these had relatively low rates of interception (0.10–1.99 interception year^{-1}).

Discriminant analysis without interception data

Excluding the interception data allows predictions for novel ant species not previously observed. Only five variables were retained in the resulting discriminant model. The first function explained 58% of the variance and the associated three-way MANOVA showed a significant difference between the three groups on the first discriminant function (Pillia trace = 0.416, $F = 3.156$, d.f. = 10, $P = 0.001$). The most important variables in the model were still morphological. The discriminative and predictive ability for this analysis was much less than for the previous model (Table 3, Fig. 3b). Here only 65% of ants were correctly assigned in the full model, 53% in the jackknifed classification matrix. Some of the same species were misclassified in both models, including *W. auropunctata*, which was classified as being successfully established in New Zealand (Fig. 4).

Inputting data into the model for four species not previously included in the analysis further tested the efficacy of the model that excluded interception records. The ant species were *Monomorium sydneyense* and *Doleromyrma darwiniana* (Forel), which are both established in New Zealand; *M. brevinoda* Forel, an ephemeral species observed with one nest in Auckland but not established; and *Cardiocondyla wroughtonii* (Forel), a Pacific tramp species not established. Despite not giving the model the current establishment status, the calculated posterior probabilities correctly predicted the establishment of the first two species.

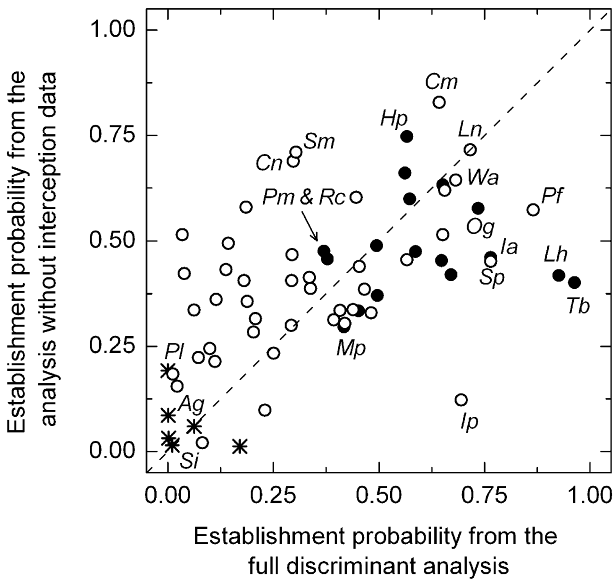

Figure 4 Posterior probabilities for exotic ant establishment in New Zealand, based on the Malahanobis distances from the discriminant analyses with or without interception rate data. The three groups are the established exotic species (●), non-established species (○), and species that are occasionally observed in New Zealand but have not become permanently established (*). Species abbreviations are as in Fig. 1. The dashed line represents a 1 : 1 relationship.

The failure of the remaining two species was also predicted, though *M. brevinoda* was given a low probability for ephemeral establishment (Table 4).

DISCUSSION

The discriminant analysis with all variables including interception rate gave an overall correct classification of 71%, with the lowest predictive ability for those species that would fail to establish. Using similar analytical techniques Kolar and Lodge (2002) were able to predict successful and failed fish invaders with the great accuracy of 87% (83% in Jackknife validation). In the sections that follow I discuss why it may be difficult to discriminate ants

Table 4 Validation of the model predicting the establishment of ants in New Zealand, using the discriminant analysis model without interception data. These species were not included in the previous analyses as there are no records of interception. All species are Australian

Species	Current status in New Zealand	Posterior Probability		
		Establish	Ephemeral	Fail
Monomorium sydneyense Forel*	Established	0.68	0.00	0.32
Doleromyrma darwiniana (Forel)†	Established	0.66	0.00	0.34
Myrmecia brevinoda Forel‡	Not present	0.24	0.00	0.76
Cardiocondyla wroughtonii (Forel)§	Not present	0.45	0.05	0.50

*First recorded in New Zealand in 2001, unpublished information. Populations have been observed to over-winter, are present and expanding in 2004 (Stringer & Lester, unpublished information).
†Recorded in New Zealand by Keall & Somerfield (1980).
‡A nest recorded in Auckland by Keall (1981b), but has since not been observed.
§Never recorded as being in New Zealand, but are known as tramp species elsewhere in the Pacific (Wilson & Taylor, 1967).

likely to be successful from those that would fail to establish in New Zealand, and what further data might be necessary in order for an improved predictive ability.

Interception rate and climate

Several of the ant species which have so far failed to establish in New Zealand have invaded human modified environments in similar or cooler climates elsewhere, such as *W. auropunctata* and *L. niger* in Europe (Baroni Urbani & Collingwood, 1977; Wetterer & Porter, 2003). Perhaps as a consequence, both these species were misclassified in my model as likely to be already successfully established in New Zealand. To determine the role of interception rate on this misclassification, I lowered the interception rate for both species to 0.03 interception year^{-1}. The model then correctly ascribed these species to failed establishment and an overall increase in classification accuracy to 77% for successful ant establishment. This result is indicative of the vital role of introduction data in the correct prediction of establishment success, a result that has also been observed for birds and mammals (Case, 1996; Wolf *et al*., 1998; Forsyth *et al*., 2004). These studies have indicated that a minimum number of individuals need to be released to achieve establishment, for example, releases of at least seven or more mammals generally resulted in successful establishment in Victoria, Australia (Forsyth *et al*., 2004). Ant colony size also has a large influence on establishment success and survival. Larger colonies of red imported fire ants are able to survive for longer durations in stressful conditions (Kaspari & Vargo, 1995) and Argentine ant colonies are more competitive with larger numbers of workers (Holway & Case, 2001). Despite the problems with the interception data, the increased discrimination ability of the model with interception records demonstrated the value of this information.

Interception data used in my analysis were probably not equivalent to 'introduction effort', as defined in previous studies. As quarantine authorities are unlikely to discover every occasion an ant enters the country, I used these data as an indicator for the likely propagule pressure. This method is more likely to be accurate for species that frequently enter the country. There is likely to be some bias caused by quarantine authorities examining some imports more than others. Further, New Zealand quarantine authorities recorded only the ant species, and not the size of the colonies, the time of the year, or whether the colony included reproductive individuals. All of these factors are likely to vary between species and are likely to influence the probability of establishment success. Some ant species may be associated with particular crops and time periods, affecting the likelihood of their establishment. For example, during the 1997–2003 period, the interceptions of *Paratrechina minutula* (Forel) were in October or November and always on Fijian taro. The cool weather during these months may reduce the establishment probability for this species.

'Ephemeral' establishment

An exotic species may establish in a new area and survive for only a few generations before going extinct (Mack *et al*., 2000). I feel that a classification that describes failed establishment, despite high opportunity, is a useful category for such an analysis as this. Another example of such an ephemeral establishment would be the release and establishment of guinea pigs near Dunedin, New Zealand. After a release of 206 guinea pigs, a large colony was established, but subsequently went extinct (Druett, 1983). Consequently, we know much more about the establishment probability for this species than we would just based on the release of a few individuals with no further information.

In my analysis, the probability of successful establishment for the ants classified as ephemeral was extremely low. These are ants that have generally established throughout much of the Pacific as long as a century ago (Wilson & Taylor, 1967). The high rate of interception for these species over the last 40years suggests that if they were going to establish here, they would likely have done so by now. The example of *M. brevinoda* (Keall, 1981b) appears to suggest that such a brief establishment before local extinction can occur for ants in New Zealand. My classification of other ephemeral species in New Zealand is based on the recent observation of nests, which I assume to be also indicative of the previous nesting here prior to the annual surveys of ports in late summer that are currently undertaken since 2001. That ephemeral species had an extremely low probability of establishment in the discriminant models may be an accurate prediction or a by-product of the statistical analysis technique. However, such previous ephemeral establishment seems likely for species such as *A. gracilipes*, which is widely distributed throughout the Pacific for nearly a century (Wilson & Taylor, 1967). Climate envelope models have indicated that New Zealand is too cold to allow the permanent establishment of this species (R.J. Harris, unpublished data). Other species which were given a high probability as ephemerally established were *O. smaragdina* and *P. bourbonica*. It is possible that these species have been present in New Zealand over the last century, though have not been recorded. The other species with a high probability for ephemeral establishment (43%) was *Ph. megacephala*. This dominant invader of other areas is rare in New Zealand with an extremely restricted distribution (Lester *et al*., 2003), apparently limited here by climate (Berry *et al*., 1997).

Perhaps the exception in the ephemeral category is *S. invicta*, which has a relatively low interception rate probably because of its low occurrence in the Pacific. However, the global model of Morrison *et al*. (2004) is in agreement with my categorization, for they predict reproduction of colonies in New Zealand to be 'unlikely' or at best 'possible'. The ephemeral establishment category is somewhat subjective. However, the category is useful to determine ultimately failed species that may otherwise be predicted as successful.

Taxonomic issues

A further factor adding noise to the model is likely to be the distribution of subspecies, which may have varying climate tolerances. For example, *Camponotus maculatus subsp. tortuganus* is known from Florida (Smith, 1930). However, this species has also been recorded from Churchill (Manitoba, Canada) but as a different subspecies and variety *Camponotus maculatus subsp. vicinus var. plurabilis* (McClure, 1943). For my analysis, quarantine authorities had not determined specimens to subspecies level. Therefore, I used the extreme location data at the species-level, despite the low probability for an ant making its way to New Zealand from Churchill.

The taxonomic status of other species may also have contributed noise to the models. For example, the established exotic species called *P. vaga* in New Zealand is probably not the same species established throughout the Pacific and is thought more likely to be another species of Australian origin (S.O. Shattuck, pers. comm.). These results highlight the importance of taxonomic studies.

The role of morphology and behaviour

In both analyses, aspects of ant size were the most important variables defining establishment success. This result has been previously observed, with McGlynn (1999b) demonstrating that non-native ants tend to be smaller than native species, although this was not always observed to be the case for my data (Fig. 2). Small size has been associated with tramp ant species elsewhere (Passera, 1994) and is a characteristic for the successful establishment of other insects (Lawton & Brown, 1986). The reasons for size being a key characteristic in establishment success remain obscure. Smaller insects have a higher intrinsic rate of increase, but this correlation is not sufficiently strong to allow a sound prediction for introduced species (Simberloff, 1989). Other experiments have shown that ants with smaller legs may be more behaviourally competitive, able to escape larger predators and obtain food in substrate with smaller interstitial spaces (Farji-Brener *et al*., 2004). Several different hypotheses were suggested as mechanisms by McGlynn (1999b), including theories on inter- and intraspecific competitions, life histories and climate in regulating colony size. Competitive behaviour was not a significant variable in my discriminant analysis, likely because of the established species having a wide range of competitive behaviour scores.

CONCLUSIONS

McGlynn (1999a) suggested life history behaviours such as queen number, unicoloniality, interspecific aggression and generalized foraging and nesting to be crucial for predicting future invaders. Such data are not available for all the ant species used in my analysis, although they may improve predictive ability. Nevertheless, validation of the model (Table 4) indicates that the variables that were included have predictive ability that may aid managers in decision-making. Recent ant incursions over the last year to New Zealand include *A. gracilipes* and *Pheidole fervens* Smith. The use of the ephemeral establishment category clearly indicated that we should be much more concerned about the *Ph. fervens* incursion than that of *A. gracilipes*, despite the reputation of the latter (Holway *et al*., 2002; O'Dowd *et al*., 2003). Identification of these 'high risk' species would enable a focus on specific entry pathways. Such predictive ability would thus be a powerful tool to slow the spread of invasive species.

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SUPPLEMENTARY MATERIAL

The following material is available online at
www.blackwell-synergy.com/loi/ddi

Appendix S1 Ant species, establishment probabilities and behavioural categories

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