BIODIVERSITY RESEARCH

The diversity and origin of exotic ants arriving in New Zealand via human-mediated dispersal

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ABSTRACT

The number of exotic ant species being dispersed to new regions by human transportation and the trade pathways responsible for this are poorly understood. In this study, the taxonomic diversity, trade pathways, and origin of exotic ants intercepted at the New Zealand border were examined for the period 1955–2005. Overall, there were a total 4355 interception records, with 115 species from 52 genera. The 10 most frequently intercepted genera, and the 20 most frequently intercepted species contributed > 90% of all records. Many of the species frequently intercepted are regarded as invasive species, and several are established in New Zealand. The most intercepted species was *Pheidole megacephala*. Despite a relatively low trade relationship, a high proportion (> 64%) of the exotic ants which were intercepted originated from the Pacific region. However, the majority of species intercepted from the Pacific was exotic to the region (71%), or to a lesser extent, wide-ranging Pacific native species. No endemic species from the Pacific were intercepted. The effectiveness of detecting exotic ant species at the New Zealand border ranged from 48–78% for different trade pathways, indicating a number of species remain undetected. Trade routes associated with specific geographical regions represent a major filter for the arrival of exotic ant species. Despite the importance of the Pacific as a frequent pathway, we suggest that the future establishment of exotic ant species in New Zealand is likely to be mitigated by a renewed focus on trade routes with cool temperate regions, particularly Australia.

Keywords

Biological invasions, biosecurity, border, trade, Formicidae, invasive species, Pacific.

INTRODUCTION

It is well recognized that biological invasions occur along an invasion pathway, typically divided into initial dispersal, establishment, and spread (Vermeij, 1996; Heger & Trepl, 2003). Initial dispersal is the fundamental stage upon which all other stages are reliant. Only those species that successfully pass through the initial dispersal filter proceed along the invasion pathway. However, there is relatively little information on this critical stage, with most of the knowledge regarding biological invasions relating to the establishment and spread stages (Kolar & Lodge, 2001; Puth & Post, 2005).

Global trade and transportation by humans has greatly extended the capacity of many species to become established in regions outside their natural range (Drake *et al.*, 1989; Mooney & Drake, 1989; Williams, 1994; Sandland *et al.*, 1999; Floerl & Inglis, 2004). Trade routes essentially represent pathways for invasion, with transport hubs (shipping ports, airports, mail centres) acting as important foci for the arrival and spread of exotic species (Ricciardi & Rasmussen, 1998; Floerl & Inglis, 2004). The likelihood that a new region will receive exotic species is largely influenced by the presence of, or proximity to, a major port of entry (Mack *et al.*, 2000). Accurate estimates of arrival rates of exotic species are required to develop risk assessments for specific trade pathways and species; however, there have been few opportunities to quantify arrival rates of exotic species (Work *et al.*, 2005).

Two recent international examples serve to show the number and diversity of insects being transported by human trade. Stanaway *et al.* (2001) surveyed the floors of empty sea containers arriving in Brisbane, Australia over a 6-month period. They demonstrated that containers were regularly exposed to timber, agricultural, and nuisance arthropod pests. Thirty-nine per cent of containers were found to be contaminated with arthropods. In

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a much larger study, Work *et al.* (2005) examined several types of cargo entering the USA; refrigerated and non-refrigerated marine cargo, air cargo, and cargo across the USA–Mexico border. During 1997–2001, they estimated a new insect species was intercepted every 54 inspections. However, projected estimates suggested that inspectors only detected 19–28% (non-refrigerated marine cargo) and 30–50% (USA–Mexico border) of insects. Work *et al.* (2005) also found that the number of insect species detected from maritime cargo (refrigerated) entering the USA was poor, compared to other cargo pathways.

Invasive ant species are currently receiving considerable attention from around the globe, with increasing evidence of economic and agricultural impacts, health effects on humans, displacement of native species, and disruption to natural ecosystems (Williams, 1994; Christian, 2001; Holway *et al.*, 2002; O'Dowd *et al.*, 2003). Previous estimates suggest at least 150 species of ants have arrived at new regions accidentally through global trade (McGlynn, 1999). There is also increasing evidence that human transportation is the major explanation for the range expansion within a region of established invasive ant species (Suarez *et al.*, 2001; Ward *et al.*, 2005). However, few regions have undertaken a comprehensive assessment of exotic ant species and the mechanisms behind their arrival and establishment (Deyrup *et al.*, 2000; Harris *et al.*, 2005). Recently, Suarez *et al.* (2005) examined historical records of human transportation and the interception of exotic ant species in the USA. This is one of the few examples for any taxonomic group that provides information on the number, diversity, and type of species that have had the opportunity to overcome the initial barrier to invasion. Such data are important in predicting why some species become successful biological invaders while other species do not (Lester, 2005; Suarez *et al.*, 2005).

New Zealand has a very small native ant fauna (11 species). This is probably because of its long (> 80 million years) geographical isolation from Australia, which has presented an extreme limitation to the natural dispersal of ants (distance of > 2500 km). However, through human trade 28 exotic ant species have become established. Ants are the second most common family of insects intercepted at the New Zealand border (Keall, 1980; after armoured scale insects, Homoptera: Diaspididae). The recent arrival of the Argentine ant, *Linepithema humile*, has led to considerable attention towards the risk and potential impacts posed by invasive ant species to New Zealand (Hartley & Lester, 2003; Lester *et al.*, 2003; Harris *et al.*, 2005; Ward & Harris, 2005; Ward *et al.*, 2005). However, in general the biology and distribution of established exotic ant species remains very poorly known.

In a major review of biological invasions, Mooney & Drake (1989) posed several fundamental questions relevant to the initial dispersal stage of biological invasions; who are the invaders, how do they get there, and where do there come from? Reducing the threat of new invasions requires a focus on the ways humans facilitate the transport of species to new areas (Hayes, 2003; Floerl & Inglis, 2004). The aim of this paper is to provide statistics on the taxonomic diversity, trade pathways, and origins of exotic ant species being unintentionally transported by humans. We use exotic ant species that have historically arrived at the New Zealand border as a case study. Additionally, estimates of the number of species and the effectiveness of detecting exotic ant species in border inspections are evaluated. An understanding of the pathways used by exotic ants to arrive in New Zealand, and the origins of the exotic species, will be of major practical benefit to biosecurity authorities in New Zealand, but patterns within the data may also be relevant to other geographical regions.

METHODS

The New Zealand Ministry of Agriculture and Forestry Quarantine Service (MQS) is part of the Ministry of Agriculture and Forestry (MAF), and is responsible for examining cargo, goods, and mail that are imported, and people that arrive, into New Zealand. MQS personnel sample cargo in shipments that arrive via maritime vessels or air transport. Because New Zealand is an island nation, shipments via land vehicles crossing the border are not relevant.

Products transported through different cargo pathways vary significantly in their quantity, size, and shape, and therefore, the sampling units used for MQS inspections also vary. In general, the sampling unit from air cargo represents the collection of items described by the accompanying manifest for a given shipment. At airports, approximately 9000 people per day arrived in New Zealand (Hayden & White, 2003). For the period 1993–99, approximately 11.4–15.7% of passengers declared risk items and 1.5–2.3% (detected rate) did not declare such items (Hayden & White, 2003).

For maritime cargo, sampling unit are containers (6 m and 12 m in length). Three sampling approaches are taken to detect exotic species; (1) cargo with high-risk packing are selected for inspection; (2) cargo that is certified as free from contamination is verified by randomly sampling 10% of the cargo; and (3) a proportion of cargo is inspected on the basis of estimated risk; 100% of very high-risk goods are examined, with low-risk goods examined less (to as low as 5%). Examples of high-risk goods include: soil, wood, hay, sea containers, nursery stock, and vehicles. Low-risk goods include: mail, personal items, and treated building material. Prior to 2004, approximately 20% of maritime containers were inspected by MQS personnel that arrived annually into New Zealand. For example, in 1999–2000, over 350,000 maritime containers arrived in New Zealand, of which 27.8% were inspected and of those, 24.8% were contaminated and required quarantine action (Hayden & White, 2003). In 2003, over 550,000 sea containers arrived into New Zealand (MAF, unpublished data). However, since 2004, all sea containers entering New Zealand are now examined. High-risk commodities are still examined by MQS personnel, but low-risk goods are examined by trained inspectors at transitional facilities (an approved facility for the purpose of storage, treatment, quarantine, or destruction of uncleared goods away from ports of entry).

Details of positive detections of exotic ant species are recorded in a MAF database of interception records. Two sets of border interception records were obtained from MAF to determine the exotic ants arriving into New Zealand.

Historical port of entry (POE) records

Previously published MAF records for the period 1955–2003 were used to provide a historical background on the exotic ant species that have been intercepted at the New Zealand border. Published records were obtained for five time periods: for 1955–65 from Manson & Ward (1968), 1966–72 from Richardson (1979), 1973–78 from Keall (1981), 1979–82 from Townsend (1984), and unpublished records of 1983–2003 from MAF. The validity of species names was checked using Bolton (1995), and subfamily nomenclature follows Bolton (2003). For historical records, ants detected on fresh produce, nursery stock, and plant products were required to be identified at the National Plant Pest Reference Laboratories (NPPRL) of MAF. Other pathways were at the discretion of the quarantine officer as to whether the ants are submitted for identification.

All Ants, All Pathways records

During the period December 2004 to June 2005 (inclusive), MQS undertook an assessment of 'All Ants, All Pathways' (AAAP). The aim of this assessment was to characterize all the exotic ant species entering New Zealand. During the AAAP period *all* ants from *all* pathways which were detected were required to be submitted for identification.

The major difference between the AAAP period and historical port of entry (POE) records is that analysis and interpretation of data based on historical POE records need much greater caution, and are less useful for statistical analyses. With the historical POE records there is far greater uncertainty of (1) what ant species were detected during quarantine sampling but *not* sent for identification and subsequent databasing; (2) the sampling procedures varied over such a long time period (50 years), and were less stringent than compared with present-day procedures; and (3) only since 2004 have all low-risk goods from maritime containers been examined. Thus the AAAP assessment represents the best data set to fully characterize the efficiency of detection of exotic ant species entering New Zealand.

AAAP records were obtained from MAF, and reclassified into four trade pathways: air cargo, air passengers, maritime cargo, and total cargo. Country information from POE records was reclassified into a region of origin: Australia, Pacific, Europe, Asia, the Americas, and Africa/Middle East. Commodity information was also reclassified into larger subsets of information: containers (air/maritime), timber, fresh produce, vehicle (cars, equipment, machinery), and personal effects (including mail).

To evaluate the effectiveness of inspections at detecting exotic ant species during the AAAP time period, the number of species arriving through four trade pathways (maritime cargo, air cargo, air passengers, and total cargo) was estimated, using sample-based rarefaction procedures in EstimateS software version 7.5 (Colwell, 2005). In these analyses, specimens identified only to genus were treated as a unique species. For example, if there were three records of '*Camponotus*', these records are treated as one species but kept separate from other named *Camponotus*. This approach avoids overestimating effectiveness (by not ignoring unidentified species) and also avoids over-inflating rarefaction curves (by not treating each unidentified records as a species). Abundance data were not used, because such data are not always accurately recorded in border interceptions, where the emphasis is on detecting the presence or absence of a species (Venette *et al.*, 2002). Additionally, the number of worker ants is not an accurate measure of abundance, because the fundamental unit of ants is the colony (Hölldobler & Wilson, 1990). Therefore, AAAP records were coded as binary data.

Three sets of rarefaction curves were used to estimate the number of exotic ant species within a trade pathway (see Work *et al.*, 2005). The observed number of exotic ant species detected through MQS interceptions (AAAP records) was defined as the 'best-case' scenario. In this scenario, the observed rarefaction curves only represent the best-case scenario if they reach an asymptote. If an asymptote is not reached, it indicates that sampling has underestimated the number of species arriving in each trade pathway. In trade pathways where no asymptote is reached, a 'probable' and 'worst-case' scenario were calculated using the Chao 2 estimator of species richness (Colwell, 2005). A probable scenario was assessed using the Chao 2 estimator. A worst-case scenario was assessed using the Chao 2 +1 standard deviation, which can be considered the upper limit of the total number of species (both detected and undetected).

The Chao 2 estimator is particularly useful for data sets which have many rare species (Colwell & Coddington, 1994; Colwell, 2005). This estimator up-weights the importance of singletons and doubletons (species with a score of one and two, respectively). This effect accelerates the rarefaction curve towards an asymptote, and thus an estimate of the number of species that would have been detected given increased sampling effort (Colwell & Coddington, 1994). Data sets with high numbers of singletons and doubletons indicate sampling is incomplete. The default parameters in EstimateS were used, with 50 runs, and the classic formula for the Chao 2. The efficiency of detecting exotic ant species within each trade pathway was evaluated using the number of observed species divided by the Chao 2 estimate of species richness.

RESULTS

Historical port of entry records

From 1955 to 2003 there were 4355 POE records of ants intercepted at the New Zealand border. Of these, 1036 records (23.8%) were identified to genus level, and 3213 (73.8%) were identified to species level. Within such a large data set, some taxonomic issues relating to species-level identification may arise. Nevertheless, we are confident that the identified species are representative of the actual species arriving at the border because if species-level identification could not be made, or was doubtful, specimens were only identified to genera.

A total of 110 species were intercepted from 51 genera (Appendix). Forty-four species have only one record (singletons), and 12 species have only two records (doubletons). Nine subfamilies were represented in the POE records, although species from Myrmicinae,

Table 1 The number of species from different subfamilies intercepted at the New Zealand border (POE records 1955–2003), and the number of exotic species established in New Zealand (as of 2005). Global ant species data from Bolton (1995). *Includes records of ants from the recently separated subfamilies Ponerinae, Ectatomminae, and Amblyoponinae (Bolton, 2003)

Subfamily	POE records (%)	Established (%)	Global ant species (%)
Myrmicinae	40 (36.4)	15 (53.6)	4377 (48.4)
Formicinae	33 (30.0)	2 (7.1)	2458 (27.2)
Dolichoderinae	19 (17.3)	5 (17.9)	554 (6.1)
Ponerimorphs*	14 (12.7)	6 (21.4)	1299 (14.4)
Myrmeciinae	2 (1.8)	0	89 (1.0)
Pseudomyrmecinae	1 (0.9)	0	197 (2.2)
Dorylinae	1 (0.9)	0	61 (0.7)

Table 2 The 10 most frequently recorded ant genera intercepted at the New Zealand border (POE records 1955–2003)

Genera	Total records	Percentage of total	Records to genus only
Pheidole	1470	34.6	327
Paratrechina	584	13.7	149
Monomorium	391	9.2	51
Tetramorium	337	7.9	24
Camponotus	308	7.2	195
Tapinoma	238	5.6	26
Technomyrmex	188	4.4	15
Solenopsis	114	2.7	20
Iridomyrmex	110	2.6	68
Anoplolepis	91	2.1	1
All other genera	418	9.6	160

Formicinae, and Dolichoderinae were the most frequently intercepted (Table 1). Species from POE records differed significantly from ants in general with respect to taxonomic composition at the level of the subfamily ($\chi^2 = 26.28$, d.f. = 4, $P < 0.01$, Table 1), with proportionally fewer Myrmicinae but more Dolichoderinae in POE records.

Additionally, there was a significance difference between the proportion of species in POE records vs. all established exotic species in New Zealand ($\chi^2 = 9.83$, d.f. = 4, $P < 0.05$, Table 1). There are currently 28 exotic species of exotic ants established in New Zealand (Ward, 2005), of which 15 were recorded in the POE records (Appendix).

The most intercepted genus was *Pheidole* (34.7% of total), and the 10 most frequently intercepted genera contributed 90.1% of all records (Table 2). The most intercepted species was *Pheidole megacephala* (27.7% of all records), and this was also the most frequently recorded species in each time period (range for time periods 14.4–32.4%). Overall the twenty most frequently intercepted species contributed > 90% of all records (range for time periods 83.3–95.7%).

All ants, all pathways records

During this period (December 2004–June 2005) 344 detection records of exotic ants from 319 positive inspections. Thirty species were identified and 18 generic-level identifications were made. Five taxa were recorded in this period that had previously not been identified in POE records (Appendix).

There was strong overlap between the historical POE records and AAAP records. For example, 18 of the 20 most frequently intercepted species were present in both sets of records. Absent from AAAP records were *Camponotus pennsylvanicus* and *Monomorium monomorium*. In the AAAP records *Monomorium pharaonis* was the most recorded species (54 records), whereas *P. megacephala* was second (47 records).

Maritime cargo made up the largest proportion of AAAP records (42.6%), but air passengers (34.4%) were also a significant source, with air cargo (16.0%) and mail (4.6%) making smaller contributions. Worker ants made up the majority of the life stages of ants that were intercepted (75.9%). However, reproductive castes, including queens, males, alates, and combinations of these reproductive stages with workers, contributed 24.1% of intercepts.

Table 3 The number of records and number of exotic ant species intercepted from different commodities ('All Ants, All Pathways' records 2004–2005)

Commodity	Number of records	Percentage of records	Number of species
Fresh produce	156	46.7	26
Air/maritime containers	75	22.4	18
Personal items	53	15.8	17
Vehicle	37	11.1	15
Timber	13	3.9	11

The majority of the AAAP records (64.4%) originate from countries in the Pacific region. Fiji, Tonga, and Samoa contribute > 70% of Pacific records, but ant species were intercepted from a total of 12 Pacific nations. Countries in Asia contribute 22.2% and Australia 8.8% of AAAP records. These data also parallel POE records from 1983 to 2003, which show a high proportion (> 65%) of POE records that originate from countries in the Pacific region. Fiji, Tonga, and Samoa also contribute > 85% of all records from 1983 to 2003. Overall, 21 species were intercepted from the Pacific (Appendix). Fifteen (71.4%) of these are exotic to the Pacific islands, and these are also all considered invasive species (Holway *et al.*, 2002). The remaining six species (28.6%) are wide ranging species native to the Pacific. No endemic species from the Pacific were intercepted.

The main commodity on which ant species arrived was fresh produce (46.7%) (Table 3). The number of species detected from each commodity type was very strongly correlated with the number of AAAP records ($y = 0.0995x + 10.755$, $R^2 = 0.98$).

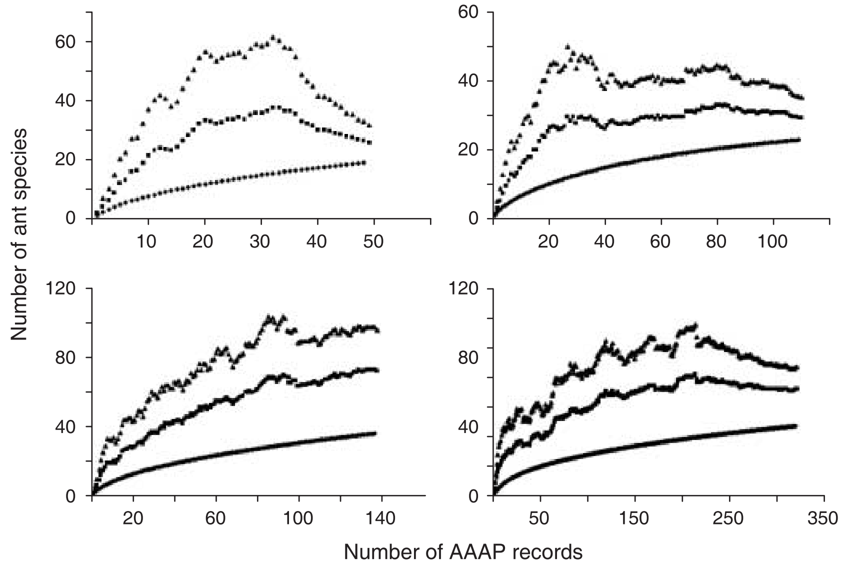

Figure 1 Observed rarefaction curves ('best-case' scenario, bottom curve), 'probable case' estimates (Chao 2 estimator, middle curve), and 'worst case' estimates (Chao 2 estimator ± 1 SD, top curve) of the total number of exotic ant species arriving into New Zealand (December 2004–June 2005) by (a) air cargo, (b) air passenger, (c) maritime cargo, and (d) total 'All Ants, All Pathways' (AAAP) records.

Table 4 The number of records, observed number of exotic ant species, proportion of records that originate from the Pacific, and predominant countries and commodities for different trade pathways ('All Ants, All Pathways' records 2004–2005)

Trade pathway	Number of records	Number of species	Pacific records (%)	Predominant country, % of total records	Number of countries	Predominant commodities, % of total records
Air cargo	49	19	89.1	Fiji, 67.3	8	Fresh produce, 89.1; personal items, 5.4
Air passenger	110	23	64.4	Samoa, 25.4	20	Fresh produce, 26.3; personal items, 22.0
Maritime cargo	137	36	47.3	Japan, 14.4	26	Container, 43.8; used vehicles, 19.2
Total cargo	319	48	64.4	Fiji, 22.2	36	Fresh produce, 46.7; container, 22.4

There was some variation in the importance of different commodities and origins for each specific trade pathway (Table 4). For example, fresh produce was an important source of exotic species from air cargo and air passengers, which arrived predominantly from the Pacific (Table 4). For maritime cargo, containers and used vehicles were the major source of exotic species, predominantly from Asia.

For each trade pathway the number of exotic ant species detected increased as the number of records increased, but, asymptotes were never reached (Fig. 1). This indicates that a number of other species remained undetected in these pathways. Projected estimates of the total number of exotic species for the 'probable-case' scenario, suggested that species asymptotes were reached for air cargo, air passengers, and total cargo (Fig. 1). Efficiency of detection was 78% for air passengers, 73% for air cargo, 66% for total cargo, but only 48% for maritime cargo. However, a species asymptote was not reached for maritime cargo, so this estimate needs to be treated with caution.

DISCUSSION

Diversity of species, commodities, and origins

Over a 50-year period (1955–2005), at least 114 species of ants from 52 genera and nine subfamilies were intercepted at the New Zealand border. McGlynn (1999) listed 147 species of ants that had been transported to new regions around the globe, but only 45% of the species in this study were also recorded by McGlynn (1999). Suarez *et al.* (2005) also documented the ant species entering the USA through human trade. Their results showed that over a 60-year period, 232 species (58 genera) were intercepted from 394 samples. Taken together, these studies illustrate the remarkable diversity of ant species that have been, and are being, transported by global trade.

The data also show that there can be considerable diversity of exotic species arriving at the borders of a relatively small trading country. For example, the land area of the USA is 35 times larger, the population 75 times larger, and the quantity of goods imported into the USA is 750 times larger than for New Zealand (CIA, 2005). The exotic ant data sets of both countries are based on border authorities collecting information on positive interceptions of species, yet almost the same number of genera, and half the number of species were intercepted from New Zealand in comparison to the USA (Suarez *et al.*, 2005). Furthermore, the USA samples generally contained many species with few records (e.g. a high number of singletons, 68%), while interceptions into New Zealand were dominated by a few species with many records (e.g. twenty species contained > 90% of all records).

We are unsure why such a high number of taxa have been recorded from New Zealand (or a low number from the USA).

New Zealand is regarded as having very strict border control procedures that may have meant that a higher proportion of species has been detected. However, the number of POE records/samples may also account for part of the 'disported comparison' between the New Zealand (> 4000) and the USA (394). If more records were available from the USA, the number of taxa recorded there would probably increase. However, this would only add to the already high diversity of ant species being transported around the globe.

Suarez *et al*. (2005) found that the exotic ant species intercepted in the USA most commonly originated from the Neotropics. However, these data are in stark contrast to our study where the majority of exotic ant species were intercepted on commodities originating from the Pacific islands. Trade volumes do not account for the relationship between the Pacific and New Zealand. Trade and immigration of people from the Pacific into New Zealand represent an extremely small proportion of New Zealand's overall trade and immigration (total imported cargo NZ$ million is < 1%; human immigration *c*. 3.5% from the Pacific; David Bateman Ltd, 2002). Furthermore, imported goods into New Zealand from South and Central America (Neotropics) is two to three times larger than between New Zealand and the Pacific (David Bateman Ltd, 2002). In addition, many of the species being transported to New Zealand from the Pacific are known invasive species (McGlynn, 1999; Holway *et al*., 2002). McGlynn (1999) has previously shown that while the majority (> 55%) of intercepted exotic ant species originate from Neotropical and oriental regions, the Pacific region is the recipient of most of these species.

Another major difference between the present study and Suarez *et al*. (2005) is in the taxonomic composition of species at the subfamily level. While POE records from Suarez *et al*. (2005) represented a subset of global ants and established species were also a subset of POE records, this was not the case for New Zealand. POE records from New Zealand had proportionally more species of Dolichoderinae but fewer Myrmicinae than expected based on the taxonomic composition of global ants. However, fewer Formicinae species but more Myrmicinae have become established in New Zealand. A number of factors will combine to influence the taxonomic composition of POE records. One of the most important is the regional pool of species. For example, several subfamilies of ants are not present in the Pacific (Ward & Wetterer, 2006) and so would not be expected in POE records from that region. Sampling procedures at the border may also bias detection and records, for example, in the New Zealand data, a number of species may be hidden within generic only records.

Recommendations for quarantine authorities

Although valuable, historical POE records provide imperfect information and need careful interpretation. There is often a multitude of information collected from trade-related activities at the border of a country, mostly for economic reasons. However, for biosecurity purposes this information is often inadequate, inconsistent, and difficult to utilize for the purposes of generating comparable statistical data. For example, quantifying the effort put into detecting exotic ant species from the POE records in New Zealand is not possible, and how this effort changes over long periods of time is uncertain (e.g. because of government policies). The ability to quantify sampling and detection procedures to estimate arrival rates of exotic species and to develop risk assessments remains a key challenge. However, greater interaction between quarantine authorities and researchers would greatly assist in defining the information needed to obtain such data.

Results from the AAAP pilot study showed that current levels of border inspection in New Zealand remain inadequate to detect all exotic ant species. The effectiveness of detecting exotic ant species at the New Zealand border was estimated at 66–78% for different trade pathways, indicating a number of species remain undetected. For maritime cargo, a species asymptote was not reached, indicating that detection of exotic ant species from this pathway was the least effective.

Detection rates of ant species will vary depending on an array of factors, including the trade pathways and commodities that border authorities focus on, the traits of the taxa (e.g. cryptic behaviour, nesting habit, body size), and importantly, the sampling protocols in place for detecting species (Venette *et al*., 2002). Despite strict quarantine standards in New Zealand, exotic ants species remain undetected from several trade pathways. Although these undetected species undoubtedly occur in low numbers or are of a low occurrence, several authors have shown that invasive ant species can establish with either no, or very few, POE records (Lester, 2005; Suarez *et al*., 2005). Thus, there is a clear need for post-border monitoring to, at least, document and quantify these occurrences.

Implications for New Zealand

Border control remains the major line of defence of preventing the establishment of exotic species (Hayden & White, 2003). However, the arrival of exotic ant species should be particularly worrying for a country with a near absence of native social insects (New Zealand has only 11 species of ants, three species of termites, and no social wasps or bees). Communities with a near absence of a taxonomic or functional group may be comparatively vulnerable to invasion by species of those groups (Drake *et al*., 1989; Mooney & Drake, 1989; Moller, 1996; Sandland *et al*., 1999).

Despite the overriding importance of the Pacific in terms of border interceptions of ant species to New Zealand, a question remains over whether ant species from tropical regions can actually establish and become invasive in New Zealand. Lester (2005) has recently modelled the establishment probability of exotic ant species in New Zealand using a range of historical, life-history, and climatic factors. Lester's list of exotic species that are most likely to establish in New Zealand include 19 of the 21 species intercepted from the Pacific in the POE records (see his supplementary material). However, only four of these intercepted species had a probability > 0.5 of successful establishment, of which two have already established in New Zealand, *Technomyrmex albipes* and *Tetramorium bicarinatum*.

Should New Zealand biosecurity authorities continue to be concerned about invasive ants of tropical origins? We suggest that exotic ant species from Australia potentially represent a greater ecological risk than exotic species from the tropics, for several reasons. Australia represents a very large trading partner to New Zealand, it is geographically close, a large part of the flora and fauna of New Zealand shares a related evolutionary history — particularly from cool temperate forests — and Australia has an extremely large and diverse ant fauna (Majer *et al*., 2004). Furthermore, the majority (64%) of the exotic ant species that are presently established in New Zealand are of Australian origin (Ward, 2005), including many of the ant species that have established most recently (Harris & Berry, 2001). These factors indicate that trade pathways with Australia should be given increased scrutiny at the New Zealand border.

The unintentional dispersal of insect taxa by humans remains largely understudied (Kolar & Lodge, 2001; Suarez *et al*., 2005; Work *et al*., 2005). However, trade pathways represent a major filter for the arrival of exotic species. Trade associated with specific geographical regions will limit the available pool of species that can be dispersed. Identification of potential donor regions and dispersal pathways is a key step in predicting future invasive species and mitigating their effects (Ricciardi & Rasmussen, 1998). Despite limitations associated with historical records, we agree with Suarez *et al*. (2005) that they represent a valuable resource, not only to test hypotheses concerning biological invasions, but to also provide practical information on the dispersal of exotic species and to prioritize trade pathways and commodities for the detection of unwanted organisms.

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REFERENCES

Bolton, B. (1995) *A new general catalogue of the ants of the world*. Harvard University Press, Cambridge, USA.

Bolton, B. (2003) Synopsis and classification of Formicidae. *Memoirs of the American Entomological Institute*, **71**, 1–370.

Central Intelligence Agency (2005) *The world factbook*. http://www.odci.gov/cia/publications/factbook/index.html. Accessed 15/12/05.

Christian, C.E. (2001) Consequences of a biological invasion reveal the importance of mutualism for plant communities. *Nature*, **413**, 635–638.

Colwell, R.K. (2005) *EstimateS: statistical estimation of species richness and shared species from samples*, Version 7.5. User's guide and application published at http://purl.oclc.org/estimates. Accessed 23 August 2005.

Colwell, R.K. & Coddington, J.A. (1994) Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, **345**, 101–118.

David Bateman Ltd. (2002) *New Zealand official yearbook*. David Bateman Ltd, Auckland, New Zealand.

Deyrup, M., Davis, L. & Cover, S. (2000) Exotic ants in Florida. *Transactions of the American Entomological Society*, **126**, 293–326.

Drake, J.A., Mooney, H.A., di Castri, F., Groves, R.H., Kruger, F.J., Rejmánek, M. & Williamson, M., eds (1989) *Biological invasions: a global perspective*. John Wiley & Sons, New York.

Floerl, O. & Inglis, G.J. (2004) Starting the invasion pathway: the interaction between source populations and human transport vectors. *Biological Invasions*, **7**, 589–606.

Harris, R., Abbott, K., Barton, K., Berry, J., Don, W., Gunawardana, D., Lester, P., Rees, J., Stanley, M., Sutherland, A. & Toft, R. (2005) *Invasive ant pest risk assessment project for New Zealand*. Available at http://www.landcareresearch.co.nz/research/biosecurity/stowaways/Ants/ant_pest_risk.asp. Accessed 4 July 2005.

Harris, R.J. & Berry, J.A. (2001) Confirmation of the establishment of three adventive ants (Hymenoptera: Formicidae) in New Zealand. *New Zealand Entomologist*, **24**, 53–56.

Hartley, S. & Lester, P.J. (2003) Temperature-dependent development of the Argentine ant, *Linepithema humile* (Mayr) (Hymenoptera: Formicidae): a degree-day model with implications for range limits in New Zealand. *New Zealand Entomologist*, **26**, 91–100.

Hayden, B.J. & White, C. (2003) Invasive species management in New Zealand. *Invasive species: vectors and management strategies* (ed. by G.M. Ruiz and J.T. Carlton), pp. 270–291. Island Press, Washington, D.C.

Hayes, K.R. (2003) Biosecurity and the role of risk assessment. *Invasive species: vectors and management strategies* (ed. by G.M. Ruiz and J.T. Carlton), pp. 382–414. Island Press, Washington, D.C.

Heger, T. & Trepl, L. (2003) Predicting biological invasions. *Biological Invasions*, **5**, 301–309.

Hölldobler, B. & Wilson, E.O. (1990) *The ants*. Harvard University Press, Cambridge, MA.

Holway, D.A., Lach, L., Suarez, A.V., Tsutsui, N.D. & Case, T.J. (2002) The causes and consequences of ant invasions. *Annual Review of Ecology and Systematics*, **33**, 181–233.

Keall, J.B. (1980) Some ants recently intercepted entering New Zealand (Hymenoptera: Formicidae). *New Zealand Entomologist*, **7**, 119–122.

Keall, J.B. (1981) *Interceptions of insects, mites, and other animals entering New Zealand 1973–1978*. Plant Health Diagnostic Station, Ministry of Agriculture and Fisheries, Wellington, New Zealand.

Kolar, C.S. & Lodge, D.M. (2001) Progress in invasion biology: predicting invaders. *Trends in Ecology & Evolution*, **16**, 199–204.

Lester, P.J. (2005) Determinants for the successful establishment of exotic ants in New Zealand. *Diversity and Distributions*, **11**, 279–288.

Lester, P.J., Baring, C.W., Longson, C.G. & Hartley, S. (2003) Argentine and other ants (Hymenoptera: Formicidae) in New

Zealand horticultural ecosystems: distribution, hemipteran hosts, and review. *New Zealand Entomologist*, **26**, 79–90.

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M.N. & Bazzaz, F.A. (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications*, **10**, 689–710.

Majer, J.D., Shattuck, S.O., Andersen, A.N. & Beattie, A.J. (2004) Australian ant research: fabulous fauna, functional groups, pharmaceuticals, and the Fatherhood. *Australian Journal of Entomology*, **43**, 235–247.

Manson, D.C.M. & Ward, A. (1968) *Interceptions of insects, mites, and other animals entering New Zealand 1955–1965*. Plant Health Diagnostic Station, Ministry of Agriculture and Fisheries, Wellington, New Zealand.

McGlynn, T.P. (1999) The worldwide transfer of ants: geographical distribution and ecological invasions. *Journal of Biogeography*, **26**, 535–548.

Moller, H. (1996) Lessons for invasion theory from social insects. *Biological Conservation*, **78**, 125–142.

Mooney, H.A. & Drake, J.A. (1989) Biological invasions: a SCOPE program overview. *Biological invasions: a global perspective* (ed. by J.A. Drake, H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmánek and M. Williamson), pp. 491–508. John Wiley & Sons, New York.

O'Dowd, D.J., Green, P.T. & Lake, P.S. (2003) Invasional 'meltdown' on an oceanic island. *Ecology Letters*, **6**, 812–817.

Puth, L.M. & Post, D.M. (2005) Studying invasion: have we missed the boat? *Ecology Letters*, **8**, 715–721.

Ricciardi, A. & Rasmussen, J.B. (1998) Predicting the identity and impact of future biological invaders: a priority for aquatic resource management. *Canadian Journal of Fisheries and Aquatic Science*, **55**, 1759–1765.

Richardson, C.A. (1979) *Interceptions of insects, mites, and other animals entering New Zealand 1966–1972*. Plant Health Diagnostic Station, Ministry of Agriculture and Fisheries, Wellington, New Zealand.

Sandland, O.T., Schei, P.J. & Viken, A., eds (1999) *Invasive species and biodiversity management*. Kluwer Academic Publishers, Dordrecht, the Netherlands.

Stanaway, M.A., Zalucki, M.P., Gillespie, P.S., Rodriguez, C.M. & Maynard, G.V. (2001) Pest risk assessment of insects in sea cargo containers. *Australian Journal of Entomology*, **40**, 180–192.

Suarez, A.V., Holway, D.A. & Case, T.J. (2001) Patterns of spread in biological invasions dominated by long-distance jump dispersal. *Insights from Argentine ants. Proceedings of the National Academy of Sciences of the United States of America*, **98**, 1095–1100.

Suarez, A.V., Holway, D.A. & Ward, P.S. (2005) The role of opportunity in the unintentional introduction of non-native species. *Proceedings of the National Academy of Sciences USA*, **102**, 17032–17035.

Townsend, J.I. (1984) *Interceptions of insects, mites, and other animals entering New Zealand 1979–1982*. Plant Health Diagnostic Station, Ministry of Agriculture and Fisheries, Wellington, New Zealand.

Venette, R.C., Moon, R.D. & Hutchison, W.D. (2002) Strategies and statistics of sampling for rare individuals. *Annual Review of Entomology*, **47**, 143–174.

Vermeij, G.J. (1996) An agenda for invasion biology. *Biological Conservation*, **78**, 3–9.

Ward, D.F. (2005) Changes to the classification of ants (Hymenoptera: Formicidae). *The Weta*, **30**, 16–18.

Ward, D.F. & Harris, R.J. (2005) Invasibility of native habitats by Argentine ants, *Linepithema humile*, in New Zealand. *New Zealand Journal of Ecology*, **29**, 215–219.

Ward, D.F., Harris, R.J. & Stanley, M.C. (2005) Human-mediated range expansion of Argentine ants *Linepithema humile* (Hymenoptera: Formicidae) in New Zealand. *Sociobiology*, **45**, 401–407.

Ward, D.F. & Wetterer, J.K. (2006) Checklist of the ants of Fiji (Hymenoptera: Formicidae). *Fiji Arthropod* Series 3 (ed. by N.L. Evenhuis and D.J. Bickel). *Bishop Museum Occasional Papers 85*: 23–47.

Williams, D.F. (1994) *Exotic ants: biology, impact, and control of introduced species*. Westview Press, Boulder, Colorado.

Work, T.T., McCullough, D.G., Cavey, J.F. & Komsa, R. (2005) Arrival rate of nonindigenous insect species into the United States through foreign trade. *Biological Invasions*, **7**, 323–332.

Appendix A list of species intercepted and the number of records for the period 1955–2005. * denotes the species is established in New Zealand. Interceptions from the Pacific ('All Ants, All Pathways' records) are indicated as ^{PE} = species that is exotic in the Pacific, ^{PN} = species that is native in the Pacific.

Top 20 species (by number of records): *Pheidole megacephala**^{PE} (Fabricius) (890), *Paratrechina longicornis*^{PE} (Latreille) (294), *Pheidole fervens*^{PE} Roger (235), *Tapinoma melanocephalum*^{PE} (Fabricius) (211), *Tetramorium bicarinatum**^{PE} (Nylander) (196), *Technomyrmex albipes**^{PN} (Smith) (173), *Monomorium pharaonis**^{PE} (Linnaeus) (170), *Paratrechina vaga*^{PE} (Forel) (94), *Anoplolepis gracilipes*^{PE} (F. Smith) (90), *Camponotus pennsylvanicus* (De Geer) (73), *Solenopsis geminata*^{PE} (Fabricius) (67), *Monomorium floricole*^{PE} (Jerdon) (64), *Monomorium destructor*^{PE} (Jerdon) (59), *Ochetellus glaber** (Mayr) (54), *Tetramorium pacificum*^{PN} Mayr (51), *Monomorium monomorium* Bolton (45), *Linepithema humile** (Mayr) (42), *Paratrechina bourbonica*^{PE} (Forel) (37), *Tetramorium simillimum*^{PE} (Smith) (32), *Iridomyrmex anceps* (Roger) (31).

Species with > 5 records: *Camponotus chloroticus* Emery, *Camponotus herculeanus* (Linnaeus), *Camponotus irritans* (Smith), *Cardiocondyla emeryi* Forel, *Hypoponera eduardi** (Forel), *Hypoponera punctatissima** (Roger), *Iridomyrmex purpureus* (Smith), *Iridomyrmex rufoniger* (Lowne), *Lasius niger* (Linnaeus), *Notoncus ectatommoides* (Forel), *Ochetellus itoi* (Forel), *Odontomachus simillimus* Smith, *Oecophylla smaragdina* (Fabricius), *Paratrechina minutula* (Forel), *Pheidole oceanica*^{PN} Mayr, *Pheidole umbonata* Mayr, *Plagiolepis alluaudi* Emery, *Polyrhachis femorata* Smith, *Rhytidoponera aspera* (Roger), *Rhytidoponera chalybaea** Emery, *Rhytidoponera metallica** (Smith), *Rogeria sublevinodis* Emery, *Solenopsis invicta* Buren, *Solenopsis papuana* Emery, *Strumigenys godeffroyi* Mayr, *Strumigenys rogeri* Emery, *Tetramorium grassii** Emery, *Tetramorium lanuginosum* Mayr, *Tetramorium tonganum*^{PN} Mayr.

Species with two records: *Brachymyrmex obscurior* Forel, *Camponotus chromaiodes* Bolton, *Camponotus tortuganus* Emery, *Camponotus variegatus* (F. Smith), *Cardiocondyla nuda*^{PN} (Mayr), *Dolichoderus thoracicus* (Smith), *Iridomyrmex emeryi* Crawley, *Lasius flavus* (Fabricius), *Myrmica rubra* (Linnaeus), *Polyrhachis ammon* (Fabricius), *Pristomyrmex pungens* Mayr, *Wasmannia auropunctata*^{PE} (Roger).

Species with one record: *Amblyopone australis** Erichson, *Anonychomyrma itinerans* (Lowne), *Camponotus compressus* (Fabricius), *Camponotus nearcticus* Emery, *Camponotus novaehollandiae* Mayr, *Camponotus maculatus* (Fabricius), *Camponotus truncatus* (Spinola), *Cardiocondyla minutior** Forel, *Diacamma rugosum* (Le Guillou), *Doleromyrma darwiniana* (Forel), *Formica fusca* Linnaeus, *Hypoponera confinis* (Roger), *Hypoponera opaciceps* (Mayr), *Iridomyrmex chasei* Forel, *Leptomyrmex wiburdi* Wheeler, *Liometopum microcephalum* (Panzer), *Mayriella spinosior* Wheeler, *Melophorus hirsutus* Forel, *Meranoplus bicolor* (Guérin-Méneville), *Monomorium australicum* Forel, *Monomorium sechellense* Emery, *Myrmica ruginodis* Nylander, *Myrmecia gulosa* (Fabricius), *Myrmecia nigrocincta* Smith, *Orectognathus antennatus* Smith, *Pachycondyla stigma* (Fabricius), *Pheidole indica* Mayr, *Pheidole rugosula** Forel, *Pheidole sexspinosa* Mayr, *Platythyrea parallela* (Smith), *Polyrchachis atropos* Smith, *Polyrhachis erato* Forel, *Polyrhachis hector* Smith, *Polyrhachis semiaurata* Mayr, *Polyrhachis trapezoidea* Mayr, *Ponera swezeyi* (Wheeler), *Prenolepis imparis* (Say), *Prionopelta kraepelini* Forel, *Rogeria exsulans* Wilson & Taylor, *Solenopsis aurea* Wheeler, *Solenopsis molesta* (Say), *Strumigenys perplexa** (Smith), *Tapinoma minutum*^{PN} Mayr, *Tetraponera rufonigra* (Jerdon).

Genera with only one record: *Azteca*, *Dorylus*, *Lepisiota*, *Pheidologeton*, *Prolasius*.

Additional taxa recorded from AAAP sampling: *Camponotus nigroaeneus* (Smith), *Cardiocondyla wroughtonii*^{PN} (Forel), *Iridomyrmex cyaneus* Wheeler, and *Tapinoma sessile* (Say), *Heteroponera* spp.