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Ant interceptions reveal roles of transport and commodity in identifying biosecurity risk pathways into Australia

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Abstract

We obtained 14,140 interception records of ants arriving in Australia between 1986 and 2010 to examine taxonomic and biogeographic patterns of invasion. We also evaluated how trade and transport data influenced interception rates, the identity of species being transported, the commerce most associated with the transport of ants, and which countries are the primary sources for ants arriving in Australia. The majority of ant interceptions, accounting for 48% of interceptions, were from Asia and Oceania. The top commodities associated with ant interceptions were: (1) Live trees, plants, cut flowers; (2) Wood and wood products; (3) Edible vegetables; and (4) Edible fruit and nuts. The best fitting model for predicting ant interceptions included volumes for these four commodities, as well as total trade value, transport volume, and geographic distance (with increased distance decreasing predicted ant interceptions). Intercepted ants identified to species consisted of a combination of species native to Australia, introduced species already established in Australia, and species not yet known to be established. 82% of interceptions identified to species level were of species already known to be established in Australia with *Paratrechina longicornis* having the most records. These data provide key biogeographic insight into the overlooked transport stage of the invasion process. Given the difficult nature of eradication, once an ant species is firmly established, focusing on early detection and quarantine is key for reducing the establishment of new invasions.

Keywords
Anoplolepis gracilipes, biological invasions, interception records, introduced ants, *Iridomyrmex purpureus*, *Linepithema humile*, *Monomorium pharaonis*, *Pheidole megacephala*, ports of entry, *Tapinoma melanocephalum*

Introduction

Biological invasions are a global economic and ecological threat (Vitousek et al. 1996; Mack et al. 2000; Pimentel et al. 2005; Bellard et al. 2016). Insular environments are particularly vulnerable to invasion; due to their high levels of endemism the loss of beta diversity results in global biotic homogenization (Case 1996; McKinney and Lockwood 1999; Kier et al. 2009; Ricotta et al. 2014; Tershy et al. 2015; Moser et al. 2018). Given that invasive species are difficult to eradicate once established, prevention is key to minimizing their consequences (Simberloff et al 2013; Hoffmann et al. 2016). Risk assessment strategies for invasive species therefore often prioritize identifying sources and pathways of invasion (Anderson et al. 2004; Hulme et al. 2008). Identifying vectors, commerce, and regions that are sources of introduced species will provide additional benefits. For example, examining records of species intercepted during transport can provide information on how introduction effort (e.g., propagule supply) influences establishment success (Cassey et al. 2004; Lockwood et al. 2005), and identify biogeographic patterns of invasion providing key insight into mechanisms of their success (Cassey et al. 2005; Hulme et al. 2008; Brawley et al. 2009; Ricotta et al. 2014; Moser et al. 2018).

Ants are among the most widespread and costly invasive species (Holway et al. 2002, Rabitsch 2011). Over 150 ant species have become established outside their native range, and island ecosystems appear particularly susceptible (McGlynn 1999; Suarez et al. 2010). For example, many islands that historically maintained unique, depauperate or no native ant diversity, now harbor communities dominated by introduced species (Morrison 1996; O'Dowd et al. 2003; Krushelnycky et al. 2005; Smith and Fisher 2009; Ward 2009; Cerdá et al. 2012; Sarnat and Economo 2012; Hoffmann et al. 2017). Despite over a century of research on the consequences of ant invasions, we know relatively little about which taxa are transported by human commerce or the biogeographic patterns of ant introductions. However, recent efforts examining ant interception records have shed light on these issues (Lester 2005; Ward et al 2006; Suarez et al. 2010; Miravete et al. 2013; Bertelsmeier et al. 2018). For example, ants intercepted in quarantine in the United States suggest introductions do not follow a biogeographic pattern typical of other introduced insects in North America (Suarez et al. 2005; Bertelsmeier et al. 2018); while most insect invasions to the Nearctic region historically originated from the Palearctic (Sailer 1978) and most ants transported and introduced to the U.S. originate from the Neotropics (McGlynn 1999; Suarez et al. 2005). By contrast, most ant interceptions in New Zealand originate from the Pacific despite the species transported not being native to that region (Ward et al. 2006; Bertelsmeier et al. 2018). Taken together, these studies suggest that patterns of ant introduction, and subsequently risk assessment, may be regionally specific.

Australia is the world's largest continental island, and has biosecurity standards considered to be among the most stringent in the world (Meyerson and Reaser 2002; Wilson and Weber 2002). Over 100 ant species were intercepted at Australian ports from 1986–2002, with accelerated rates in the last five years accounting for 90% of all interceptions (Commonwealth of Australia 2006). Consequently, Australia provides an exceptional case study through which we can better understand patterns of ant invasions, providing valuable data to assist biosecurity managers and policy makers. We used a dataset of over 10,000 interception records of ants arriving in Australia via human commerce to examine biogeographic patterns of invasion. We compared these records to trade and transport data over the same time frame to examine how these factors influence interception rates and the identity of species being transported. We also determined what commerce is most associated with the transport of ants, and what countries are the primary sources for ants arriving in Australia. These data provide key biogeographic insight into the overlooked transport stage of the invasion process.

Methods

Interception data

Interception records were sourced from the Australian Government Department of Agriculture and Water Resources Pest & Disease Information database (PDI) (1986–2003), and the Incidents database (2003–2010), which replaced PDI. Interception data included information on the following: date, location (source country and arrival state in Australia), transport vector (air/sea), associated traded commodities that the ants were intercepted with, identification to the lowest taxonomic level possible (e.g. species/genera/subfamily), animal condition (alive/dead), life stage (egg/larva/pupa/adult), and caste (worker, alate or dealate queen).

For each record, which was identified to species or genera, the record was placed into one of four discrete categories describing its status in Australia:

endemic – if range of species or genus is only known to occur within Australia;
native – for species/genera whose native range includes Australia;
introduced – for species/genera established in Australia but whose native range is outside of Australia;
not established – for species/genera whose native range is outside of Australia and are not known to have yet established populations in Australia.

This information was determined using databases and literature of species and genera known to occur in Australia (e.g. Anderson 1991, 2000; Shattuck 1999; https://www.antweb.org, https://www.antwiki.org).

For most records, ants were only identified to genus. Exceptions included the most commonly intercepted introduced ant species for which diagnostic guides are available to staff (e.g., black crazy ant [*Paratrechina longicornis*], yellow crazy ant

[*Anoplolepis gracilipes*], coastal brown ants/big headed ant [*Pheidole megacephala*], Singapore ant [*Trichomyrmex destructor*], Pharoah's ant [*Monomorium pharaonis*], and Argentine ant [*Linepithema humile*]). Even for these species, expertise may be port specific. For example, the Argentine ant is well established and common around port areas in Melbourne while more tropical species like the black crazy ant are more commonly seen in Brisbane. Consequently, intercepted ants may be more likely to be identified to species in areas where they already occur. Common or easily recognized native species were also often identified to species or species group (e.g., *Iridomyrmex purpureus*). Finally, reproductive castes (e.g., winged alates and dealate queens) were often not identified beyond family level (A. Broadley Pers. Comm.).

Trade and transport data

We extracted the import value (US$) of merchandise trade (AG2 classification code) with Australia's trading partner countries from the United Nations Commodity Trade Statistics Database (UN Comtrade) for the years 1988–2015. Commodity descriptions associated with ant interceptions were standardized to match these AG2 classification codes. GDP per capita (current US$) data were obtained from the World Bank national accounts data, and OECD National Accounts data files available from 1960–2013 (http://data.worldbank.org/indicator/NY.GDP.PCAP.CD, accessed 29/09/2014). We used trade data from 2010 for all calculations. For physical international transport into Australia we obtained: (1) shipping data from the Australian Government Department of Agriculture and Water Resources; and (2) flight information data from OAG Aviation (http://www.oag.com), over the time period 1999–2012. Flight and shipping data were combined into an integrated physical transport metric by taking a weighted sum, $I = w_s \times$ number of ships + $w_p \times$ number of passenger flights + $w_c \times$ number of cargo flights (*sensu* Cope et al. (2016)), with weights (w_s, w_p, w_c) chosen so that the three transport pathways contributed in proportion to the total number of ant interceptions associated with that pathway.

Data analysis

We analyzed these data for summary statistics and general trends relating to ant interceptions into Australia over time. We also identified pathways and commodities associated with high levels of ant interceptions. We used Poisson regression to model the number of ant interception records, testing predictors including: integrated physical transport into Australia (flights and ships), and trade value into Australia (both total trade value, and trade associated with key commodities), to highlight high risk pathways and commodities. Geographic distance to Australia, and GDP per capita of source countries were also tested as possible predictors. Finally, we calculated the Shannon diversity index per year (using the `vegan' package in R: ; Okasanen et al. 2018) for ants from the introduced category that were identified to species, and the diversity per region of detected genera.

Model selection was performed using Akaike Information Criterion (AIC), with the model producing the minimal AIC being chosen (Akaike 1974). We report AIC and Akaike weights for competing models, and regression parameters (both raw, and with continuous parameters standardized to have mean zero and standard deviation 1) for the final model. Models with interaction terms were excluded to allow clear interpretation of parameters and avoid overfitting. A binary indicator for the presence of any physical transport from the source country to Australia was used as an additional predictor, as many countries had no recorded (direct) transport. All analysis was performed in R 3.5.1 (R Core Team 2018).

Results

Interception and identification summary

We obtained 14,140 interception records between 1986 and 2010. The number of recorded ant interceptions was relatively low from 1986–1997 (with a mean of 112 interceptions per year across this time period) before increasing to a peak of 1541 interceptions in 2002. The number of interceptions then levelled off to an average of 998 interceptions per year from 2002–2010 (Figure 1a). Most recorded ant interceptions included adult ants (92.5% of records), although substantial proportions of interceptions included eggs (15.5%), or larva / pupa (19.5%) (many records included different life stages). Most interceptions included live ants (90%). Castes were unknown for 86.6% of interceptions, but those interceptions for which they were recorded included a variety of forms including workers, and alate and dealate queens. Overall, 90 different genera and 104 species or species groups were identified from these samples (Suppl. material 1: Table S1). More than half (59%) of the interceptions were identified to genus, 27% to species, and 14% were unidentified (Figure 1b). There was relatively little variation through time in the status of intercepted species; most intercepted species were in the "introduced" category defined as being non-native but already established in Australia (Figure 1c).

There was considerable variation in interceptions among ports of entry and biogeographic region of origin (Figure 2). The smallest proportion of ant interception records identified to species level was in Sydney (5.2%), followed by Adelaide (15.0%) and Melbourne (16.3%). Records were most frequently identified to species level in Cairns (59.9%), and Darwin (53.5%). Brisbane had 44.1% of records identified to species level, despite having the second largest number of total interceptions, behind Sydney (Figure 2). The number of ants intercepted from each country was correlated with the number of genera that made up those interceptions (n = 209 countries, correlation coefficient 0.80; Figure 3), suggesting that generic diversity was primarily due to increased interceptions rather than some source or pathway-specific factor. The top 20 sources for ant interceptions accounted for approximately 48% of interceptions; all originated in Asia or Oceania (specifically Fiji), and the top 7 occurred in either Brisbane or Sydney (Table 1).

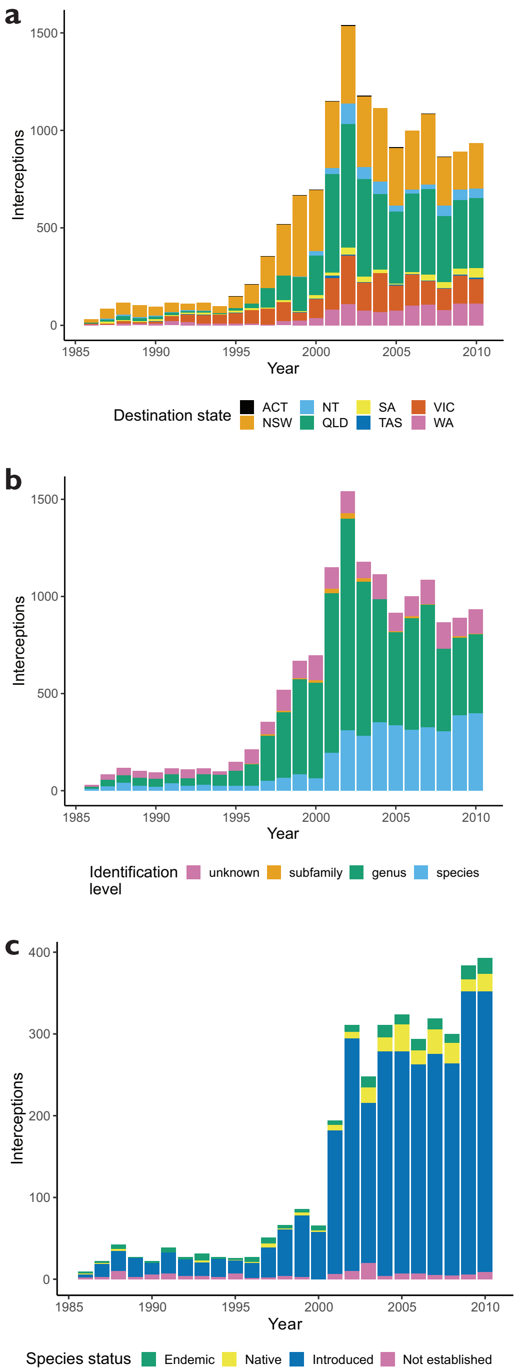

Figure 1. Ant interceptions into Australia by year and (**a**) State in which the interception occurred (ACT = Australian Capital Territory, NT = Northern Territory, SA = South Australia, VIC = Victoria, NSW = New South Wales, QLD = Queensland, TAS = Tasmania, WA = Western Australia), (**b**) taxonomic level the interception was identified to, and (**c**) species status for records that were identified to species level.

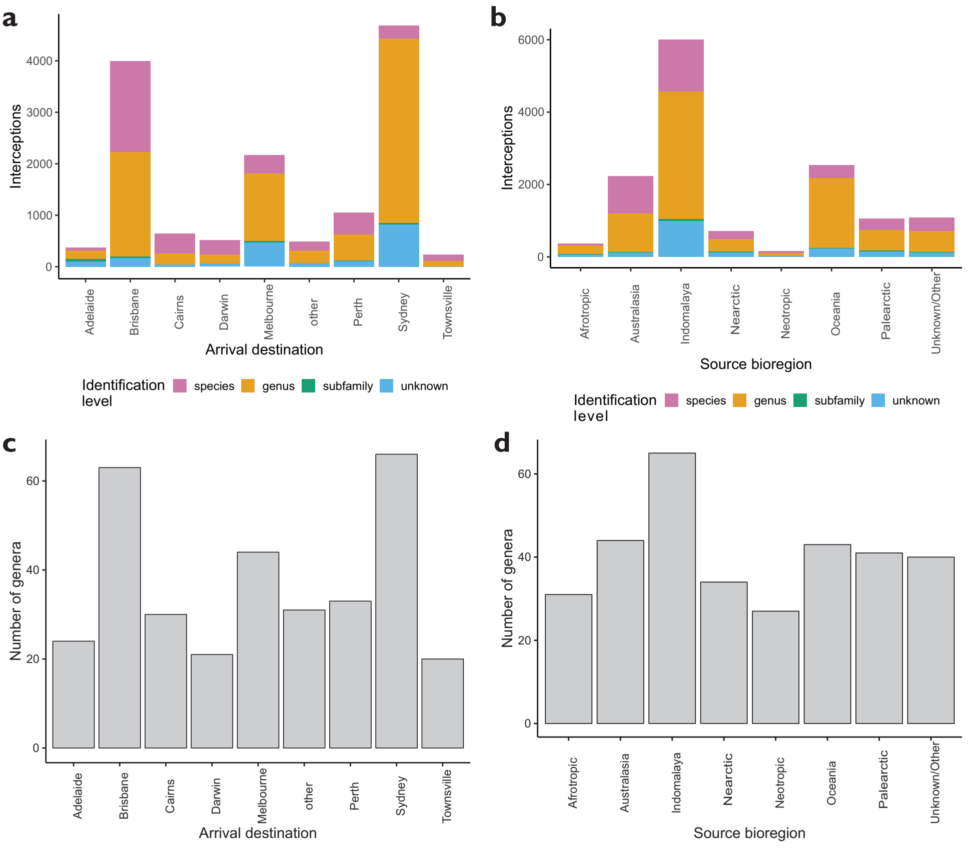

Figure 2. Taxonomic patterns of Australian ant interception data. Taxonomic level identified for interceptions separated by (**a**) city of arrival (e.g., port of entry) and (**b**) source biogeographic region. The number of genera identified in interceptions by (**c**) city of arrival and (**d**) source bioregion.

Trade and transport data

Over half (57%) of the ant interceptions were associated with air traffic, 40% were from seaborne traffic, and the remaining 3% were listed as 'other', including international mail and records with no listed vector. In contrast to the pattern in interceptions, which leveled off between 2005–2010, the amount of air and sea traffic into Australia continued to increase from 2003–2010 (Suppl. material 2: Figure S1). Most interceptions were from Asia (48%) or Oceania (33%) (Table 1; Figure 2). Interceptions from Asia and Oceania were more likely to be associated with air traffic than those from Europe or the Americas (Suppl. material 3: Figure S2). The number of interception events per country-of-export was positively correlated with both total weighted transport (correlation coefficient 0.40, Figure 4a) and total import value of traded commodities into Australia from that country (correlation coefficient 0.36; Figure 4b). The volumes of transport into Australia along each transport pathway (i.e.,

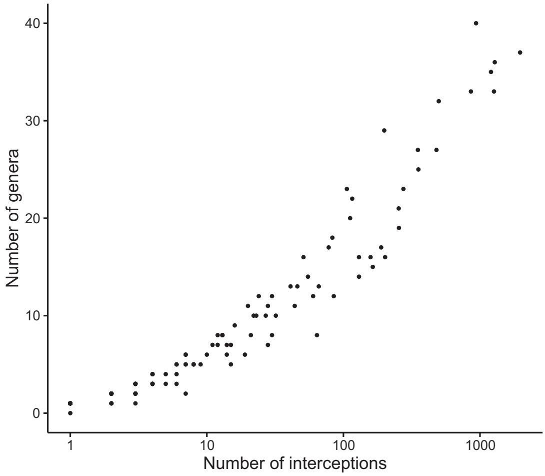

Figure 3. The number of genera observed within ant interceptions from a country of origin, correlated with the number of interceptions detected from that country (n = 209, correlation coefficient 0.80).

Table 1. Top 20 pathways for commerce on which ants were intercepted in Australia from 1986–2010. From a total of 14140 records, these top eight source countries account for approximately 48% of interceptions.

Source country	Port of entry	Interceptions
Fiji	Sydney	1528
Papua New Guinea	Brisbane	730
Thailand	Sydney	440
Singapore	Brisbane	413
Other	Brisbane	388
Fiji	Brisbane	316
Indonesia	Sydney	272
Singapore	Perth	265
Malaysia	Sydney	250
Papua New Guinea	Cairns	247
Singapore	Sydney	236
Singapore	Melbourne	235
Malaysia	Melbourne	221
Indonesia	Brisbane	201
Indonesia	Melbourne	192
Sri Lanka	Sydney	190
Thailand	Melbourne	189
Indonesia	Cairns	183
Vietnam	Melbourne	183
Malaysia	Brisbane	176

shipping, passenger flights, cargo flights) were also each positively correlated with ant interceptions: the number of ant interceptions per country-of-export had correlation coefficients of 0.33 with the number of ships originating in that country, 0.51 with the number of passenger flights, and 0.35 with the number of cargo flights.

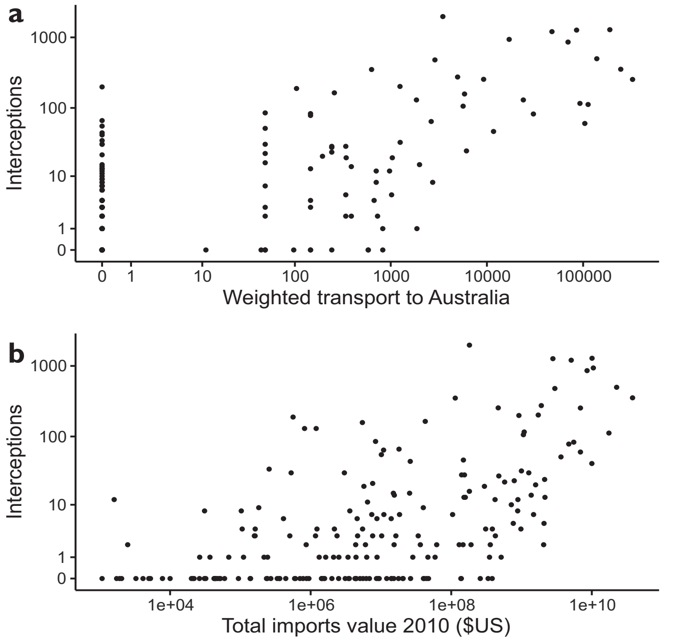

Figure 4. Ant interception counts correlated with (**a**) weighted transport volumes and (**b**) import value in 2010, by country. Correlation coefficients 0.36 for transport volume and 0.40 for import value.

Commodities

The top 10 commodities associated with the most interceptions covered 65% of all interceptions (Table 2). These 10 commodities accounted for 4.8% of total imports into Australia by value in 2010, and in general these commodities were not the imports of highest value. An additional 22% of ant interceptions were not associated with any of the listed commodities (e.g., goods unknown); these interceptions were rather associated with the transport mechanism itself, particularly shipping containers, vessels, air baggage, and personal luggage.

The majority of ant interceptions associated with plant and animal products were with products transported by air, except for those associated with timber products, which were mostly transported by sea. The four most common commodities in terms of ant interceptions were: (1) Live trees, plants, cut flowers; (2) Wood and wood products; (3) Edible vegetables; and (4) Edible fruit and nuts (Table 3). In some cases, high trade volumes of these commodities into Australia corresponded to high numbers of associated ant interceptions (e.g., Indonesia was the third largest source of wood products by value, and the highest source of ant interceptions associated with this commodity), but in other cases, countries with the highest trade volumes were not those with the most ant interceptions (e.g., the Netherlands was the greatest source of live trees and cut flowers, but had few associated ant interceptions).

Table 2. The top 20 commodity groups for ant interceptions in Australia from 1986 to 2010.

Commodity	Ant interceptions	Proportion of interceptions (%)
Live trees, plants, bulbs, roots, cut flowers, etc.	2599	19.3
Wood, and articles of wood, wood charcoal	1829	13.6
Edible vegetables and certain roots and tubers	1786	13.3
Edible fruit, nuts, peel of citrus, fruit melons	828	6.1
Vegetable plaiting materials, vegetable products	781	5.8
Residues: wastes of food, industry, animal fodder	422	3.1
Meat, fish, and seafood food preparations	333	2.5
Cereals	271	2.0
Vegetable, fruit, nut, etc. food preparations	187	1.4
Vehicles other than railway tramway	177	1.3
Plastics and articles thereof	171	1.2
Boilers, machinery, etc.	140	1.0
Fish, crustaceans, molluscs, aquatic invertebrates, etc.	137	1.0
Miscellaneous edible preparations	122	0.9
Products of animal origin	108	0.8
Coffee, tea, mate and spices	98	0.7
Salt, sulphur, earth, stone, plaster, lime and cement	73	0.5
Dairy products, eggs, honey, edible animal products	71	0.5
Ores, slag and ash	68	0.5
Miscellaneous manufactured articles	60	0.4
Unknown	3159	23.5

The trade value of these common commodities increased over time, but the relative proportions of each commodity remained consistent (Suppl. material 4: Figure S3). In contrast, ant interceptions associated with these commodities varied though time in both magnitude and relative proportion (Figure 5). For example, the proportion of interceptions associated with edible vegetables varied from 1% in 1991 to a peak of 37% in 1999, whereas edible fruit were more consistently between 2–14% of interceptions in every year.

Statistical model for ant interceptions by country

The best fitting model included each of the top four commodity volumes, along with total trade value ($US), transport volume (and an indicator variable for non-zero direct transport to Australia), GDP per capita, and geographic distance (Tables 4, 5). Geographic distance had the largest magnitude coefficient after standardization, with an increase in distance resulting in a decrease in predicted ant interceptions (Tables 4, 5). Total trade value, and the values of each commodity, also had large coefficients. However, the coefficient of 'Edible vegetables' was negative, likely because the greatest value source countries of this commodity do not correspond to the majority of ant interceptions associated with it (Table 3). GDP per capita had a small positive standardized coefficient. The indicator variable for having non-zero transport to Australia had a relatively large coefficient, whereas transport volume itself had a very small negative coefficient: indicating that direct transport from a country substantially increased the frequency of interceptions from that country (relative to

Table 3. For the four commodity groups associated with most ant interceptions into Australia, the top ten countries of origin ranked by number of ant interceptions (left column) or the overall value of the imported commodity (right column).

Commodity	Top countries (interceptions)	Number of interceptions	Top countries by trade value	Trade value US$
Live trees, plants, cut flowers, etc.	Singapore	834	Netherlands	18118004
	Thailand	345	Singapore	10148629
	Malaysia	331	Malaysia	4003579
	Sri Lanka	144	Kenya	3548410
	Indonesia	96	Colombia	2928767
	Fiji	80	India	1829210
	Vietnam	69	China	1757426
	Papua New Guinea	67	New Zealand	1721401
	United States of America	65	Thailand	1568278
	Kenya	53	Chile	1378043
Edible vegetables	Fiji	1407	New Zealand	79814617
	Thailand	90	China	67045088
	Tonga	56	USA	24352741
	Singapore	33	Canada	7452113
	China	22	Peru	6905847
	France	16	Turkey	6766208
	New Zealand	15	Mexico	6207453
	Indonesia	12	India	5854088
	Malaysia	12	Thailand	5682768
	Australia	9	Fiji	5394880
Edible fruit, nuts, etc.	Thailand	198	USA	135207706
	Fiji	96	New Zealand	87758680
	Papua New Guinea	59	Viet Nam	83315454
	Samoa	49	Areas not elsewhere specified	62127512
	United States of America	47	Turkey	44986111
	Tonga	42	China	44272718
	New Zealand	40	Chile	20272657
	Vietnam	28	Thailand	11017653
	American Samoa	26	Philippines	10908714
	Indonesia	25	Italy	9971842
Wood, and articles of wood	Indonesia	301	New Zealand	320834318
	Canada	181	China	217468391
	Papua New Guinea	164	Indonesia	202735959
	United States of America	148	Malaysia	147228707
	Malaysia	121	USA	92654945
	Other	114	Germany	47331442
	Singapore	92	Chile	45200210
	China	62	France	41276732
	Thailand	59	Canada	40821830
	India	54	Czech Rep.	34258319

countries with no transport), but that increasing transport volumes did not increase ant interception frequency, when accounting for the effect of trade volume and geographic distance (Tables 4, 5).

Species patterns

Intercepted ants identified to species or "species group" consisted of a combination of Native (n = 19), Endemic (37), Introduced (17), and not established (31) spe-

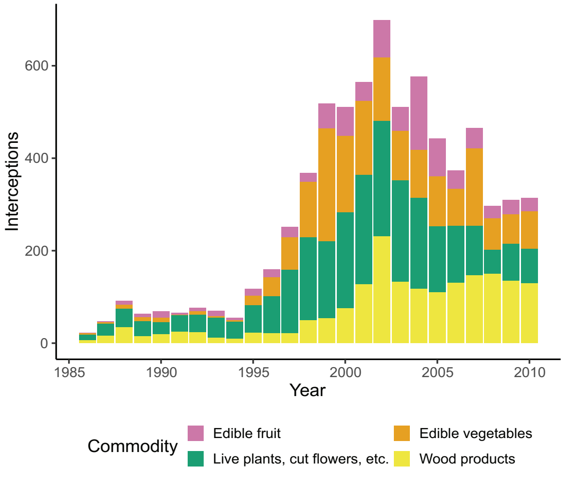

Figure 5. Ant interceptions into Australia by commodity group by year, for the top four commodity groups on which ants were found.

Table 4. AIC for 10 best candidate Poisson GLMs predicting total number of ant interceptions by country. All possible model combinations of these predictors were tested (512 total models): models not shown had higher AIC.

Regression formula	AIC	ΔAIC	Akaike weights
Ant interceptions from country ~ Trade value to Australia + Weighted transport to Australia + Non-zero transport to AU + GDPpc + geographic distance + com6 + com7 + com8 + com44	11960.77	0	1.00
Ant interceptions from country ~ Trade value to Australia + Non-zero transport to AU + GDPpc + geographic distance + com6 + com7 + com8 + com44	12018.95	58.18	10^{-13}
Ant interceptions from country ~ Trade value to Australia + Weighted transport to Australia + Non-zero transport to AU + GDPpc + geographic distance + com6 + com7 + com8	12138.72	177.94	10^{-39}
Ant interceptions from country ~ Trade value to Australia + Non-zero transport to AU + GDPpc + geographic distance+ com6 + com7 + com8	12169.69	208.92	10^{-46}
Ant interceptions from country ~ Trade value to Australia + Weighted transport to Australia + Non-zero transport to AU + GDPpc + geographic distance+ com6 + com8 + com44	12442.87	482.10	10^{-105}
Ant interceptions from country ~ Trade value to Australia + Weighted transport to Australia + Non-zero transport to AU + GDPpc + geographic distance+ com6 + com8	12489.41	528.63	10^{-115}
Ant interceptions from country ~ Trade value to Australia + Weighted transport to Australia + Non-zero transport to AU + GDPpc + geographic distance+ com7 + com8 + com44	12525.92	565.15	10^{-123}
Ant interceptions from country ~ Trade value to Australia + Non-zero transport to AU + GDPpc + geographic distance+ com7 + com8 + com44	12562.29	601.51	10^{-131}
Ant interceptions from country ~ Trade value to Australia + Weighted transport to Australia + Non-zero transport to AU + GDPpc + geographic distance+ com7 + com8	12694.84	734.06	10^{-160}
Ant interceptions from country ~ Trade value to Australia + Non-zero transport to AU + GDPpc + geographic distance+ com7 + com8	12767.64	806.86	10^{-176}

cies (Suppl. material 1: Table S1). Many identified species had only 1–3 interceptions however the species with the most records were those classified as introduced; 82% of interceptions identified to species level were of introduced species, with eight species having at least 100 interception records (Table 6). Most records were for the introduced *Paratrechina longicornis* (802 records). *Iridomyrmex purpureus* was the most

Table 5. Coefficients and standardized coefficients for the chosen model. Parameters com6, com7, com8, and com44 denote the total value of imports from the country into Australia of the given commodities: com6 for 'Live plants, cut flowers, etc.', com7 for 'Edible vegetables', com8 for 'Edible fruit', com44 for 'Wood products'.

Parameter	Coeffficient	Standardised coefficient	Standard error of standardised coefficient	95% confidence interval for standardised coefficient
(Intercept)	5.0668	1.3349	0.0440	(1.249, 1.421)
Trade value	6.9283×10^{-11}	0.2600	0.0062	(0.2478, 0.2722)
Weighted transport	-2.3064×10^{-6}	-0.0843	0.0108	(-0.1055, -0.06324)
Non-zero transport indicator*	2.0912	2.0912	0.0423	(2.008, 2.174)
GDP per capita	1.0379×10^{-7}	0.0019	0.0141	(-0.02569, 0.02949)
Geographic distance	-3.2222×10^{-7}	-1.3275	0.0142	(-1.355, -1.3)
Live trees, plants, etc. trade value (com6)	1.0563×10^{-7}	0.1650	0.0065	(0.1523, 0.1778)
Edible vegetables etc. trade value (com7)	-2.3888×10^{-8}	-0.1844	0.0086	(-0.2012, -0.1676)
Edible fruits, nuts, etc. trade value (com8)	1.3141×10^{-8}	0.1809	0.005	(0.171, 0.1907)
Wood and wood articles trade value (com44)	2.0587×10^{-9}	0.0699	0.0051	(0.06004, 0.07989)

[*] Note that this is a binary indicator variable, and is therefore not standardized.

Table 6. The number of records for the most commonly intercepted species separated by status (endemic, native, introduced, or not established) and whether the port of origin for the record was within ("yes") or outside ("no") the known range of the species.

Status	Port of origin within known range		
	yes	no	unknown
Endemic species			
Camponotus consobrinus	3	19	7
Iridomyrmex chasei	1	12	1
Iridomyrmex purpureus	40	80	14
Rhytidoponera metallica	2	13	6
Native Species			
Camponotus novaehollandiae	7	16	5
Nylanderia obscura	12	1	2
Ochetellus glaber	81	6	7
Oecophylla smaragdina	29	6	9
Introduced Species			
Anoplolepis gracilipes	161	73	33
Linepithema humile	19	139	13
Trichomyrmex destructor	249	0	14
Monomorium floricola	54	0	1
Monomorium pharaonis	497	0	27
Paratrechina longicornis	703	0	99
Pheidole megacephala	364	0	22
Solenopsis geminata	25	77	11
Tapinoma melanocephalum	327	0	32
Technomyrmex albipes	94	0	3
Tetramorium bicarinatum	24	0	5
Wasmannia auropunctata	20	2	1
Not Established Species			
Camponotus modoc	16	0	0
Camponotus pennsylvanicus	57	4	2

commonly intercepted species in either the native or endemic categories with more than 95 records.

Interceptions of species classified as introduced increased with time, not levelling off like overall interception records did (Figure 1c; Figure 6). This was primarily driven by increases in interceptions of *Tapinoma melanocephalum*, *Pheidole megacephala*, *Paratrechina longicornis*, *Monomorium pharaonis*, *Trichomyrmex destructor*, *Linepithema humile*, and *Anoplolepis gracilipes*, each of which had low levels of interceptions in the 1980s-1990s, increasing to higher levels through the 2000s (though interceptions of *Anoplolepis gracilipes* decreased 2008–2010)(Figure 6). Diversity had an initial peak around 1991, before decreasing until 1997. Diversity then increased until 2004, at which point it levelled off (Suppl. material 5: Figure S4).

The overall number of interceptions of not established species (those neither native to nor currently known to be established in Australia) remained low over time. Not established species were proportionally more likely to be detected on commerce originating from Africa or the Americas. For example, there were low levels of interceptions of the Nearctic species *Camponotus pennsylvanicus* throughout the whole range of years, and more sporadic low levels of other species. Records of endemic species (148 interceptions) are particularly remarkable, as these species are not found outside of Australia. Either these ants were transported away from Australia and then returned (unlikely), or the interception records are a product of at-border contamination (i.e., they were resident around the ports or airports in question, and moved on to cargo between arrival and quarantine processing). *Iridomyrmex purpureus* accounted for most endemic ant interception records, including almost all recorded endemic interceptions from 1986–1998 and more than half of total endemic interceptions from 2003–2006. Numerous other species were also detected solely or primarily in the 2001–2010 decade, including *Camponotus consobrinus*, and *Rhytidoponera metallica*

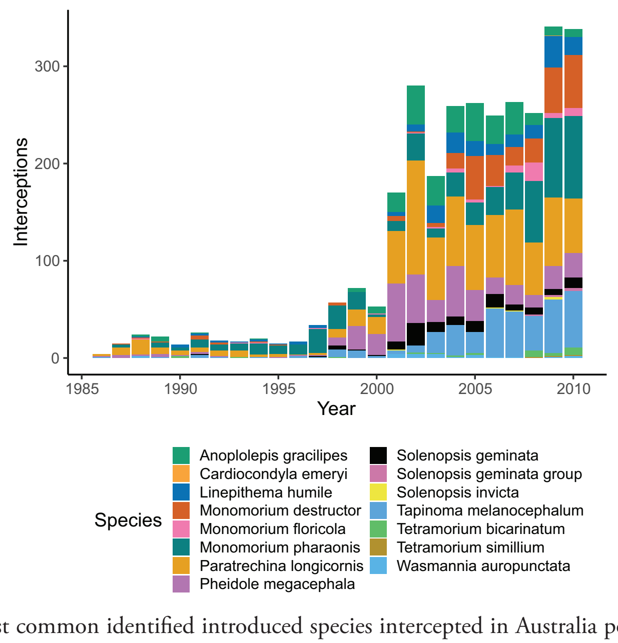

Figure 6. The most common identified introduced species intercepted in Australia ports of entry from 1986–2010.

with many interceptions over multiple years. These endemic species were generally detected at multiple locations.

For records identified to species, we also compared the source location for each record to bioregions in which the species is known to exist, i.e., to determine if ants are intercepted as coming directly from their known existing ranges, or via some intermediate location where they are not yet known to exist (Table 6). First, we excluded those records in which the interception was from the Australasian region; as for native, endemic, and introduced species these species will all be coming from a bioregion in which they are known to exist (because they are present in Australia). After excluding these Australasian interceptions, 2724 records remained (c. 73% of records with known species). Of the three categories (excluding endemic for reasons mentioned above), c. 11% of records were of unknown origin, 73% were recorded as coming from a bioregion within their known range, and the remaining 16% from bioregions outside currently known ranges.

Discussion

Ants inhabit a wide variety of ecosystems, acting as predators, scavengers and mutualists as well as playing important ecological roles as ecosystem engineers (Lach et al. 2010; Del Toro et al. 2012). As invasive species, ants therefore have the potential to be associated with considerable economic and environmental consequences. Attempts to eradicate introduced ants are accompanied by great costs and are rarely successful (Hoffmann et al. 2016). Strategies aimed at prevention, including identifying high risk pathways and sources for new invaders, are therefore a priority. In this study, we analyzed historic interceptions of ants entering Australia to uncover biogeographic patterns of arriving ants, and correlate these data to patterns of trade and commerce. Three main conclusions come from this analysis. First, that there is significant variation in the level of taxonomic identification of intercepted ants, both over time, by genera, and, most importantly, between different locations. Given that biosecurity is of national importance, variations in efficacy between different parts of the country should be of significant concern. Second, the number of ant interceptions from different countries are associated with total volumes of transport and trade, but are also associated with the transport of specific commodity groups. That is, the risk associated with different transport pathways is non-uniform. Finally, ant species are typically transported from locations where they are already established, but not necessarily from where they are native. This pattern suggests that introduced species are more likely to spread once established in key transportation hubs (Passera 1994; Bertelsmeier et al. 2018).

Most ant interceptions arrived from Asia and Oceania, consistent with transport patterns into Australia. The largest numbers of interceptions occurred in Sydney, Brisbane, and Melbourne, however, there were also substantial numbers of interceptions in other ports of entry. On a per-country level, the presence of direct transport to Australia and volume of total trade to Australia were positive predictors of the number of ant interceptions, with increases in geographic distance and per-capita GDP of the source country both decreasing the expected number of interceptions from a given country. All of these predictors make sense: high trade increases opportunities for transport events to occur, per capita GDP suggests that more affluent countries are less likely to transport ants, and distance suggests that increased journey time may decrease the likelihood of ant survival. Overall trends in ant interceptions did not increase along with trends of transport / trade into Australia through the same time period. This pattern suggests that either the number of ants being transported per voyage has changed, decreasing from 2004–2010, or that the proportion of ant transport events that are detected has changed (e.g., Eyre et al. 2018). There is some evidence for the latter; due to occurrence overseas of Bovine spongiform encephalopathy, there was an increase in biosecurity effort in 2000–2002 such that 100% of imported containers were checked externally (Adam Broadley pers. comm.). This may explain the increase in ant detections within this time period, and then a subsequent return to lower levels of container inspections (30%). However, it is not certain to what extent ant interceptions may also be increasing or decreasing beyond this effect due to biosecurity effort.

Ant interceptions into Australia were primarily associated with the transport of particular commodities, particularly plant and timber products, and edible vegetables and fruit. There was also a substantial number of interceptions associated with transport itself (e.g., on vessels, baggage, personal effects, or containers). The commodities with which ant interceptions were primarily associated were not those responsible for the greatest total volume of imports into Australia; as such, it is clear that some commodities are much more likely than others to be associated with the transport of ants. However, the transport of these commodities alone is insufficient to explain patterns of ant interception as there were examples of countries that export plant products to Australia but had few ant interceptions (e.g., the Netherlands and New Zealand). There are likely a number of contributing factors to this discrepancy. For example, countries vary in their biosecurity measures on exported goods, the diversity of their ant fauna, and the degree to which their ants are likely to associate with human commerce or tolerate variation in abiotic conditions. Any of these explanations would be plausible for why, for example, the Netherlands or New Zealand had large volumes of trade in live plants, cut flowers, or wood products, but few ant interceptions. The association of ant interceptions with plant and wood products is not unique to this study (see Suarez et al. 2005; Ward et al. 2006; Lee et al. 2019), and is also prevalent in other insect groups (Liebold et al. 2012). It is possible that the next wave of ant invaders will include species from genera that commonly nest in plants / wood (e.g., *Camponotus* and *Crematogaster*) (Lee et al. 2019). The number of transported, but not yet known to be established ant species, identified in this and other analyses of interception records suggest the potential number of future introduced species is likely very underestimated at present (Miravete et al. 2013).

The number of ant interceptions associated with the transport of edible vegetables from Fiji accounted for more than 15 times as many interceptions as the next county associated with edible vegetables (Thailand), and almost 10% of all ant interceptions in the data set. Many of the interceptions from Fiji were also associated with leaves, primarily Taro leaves but also Cassava, Roselle, Amaranth, and Bele. Taro leaves are a feature of Fijian cuisine, and Taro is one of Fiji's primary exports, with Australia a key destination (McGregor et al. 2011). However, it is not entirely clear why there are so many ant interceptions associated with these leaves, and further investigation of this phenomenon would be a valuable avenue for future work. One possibility is that Taro is known to have many honeydew producing insect associates, both on leaves and tubers (Palaniswani and Peter 2008). These aphids, scales and other insects might increase ant association and nesting and may explain why ants are more frequently intercepted when Taro is inspected.

The majority of interceptions identified to the species level were of known introduced species, and the number of these interceptions increased over time. It is not clear if the number being transported are actually increasing, or if they are just more effectively identified than other species due to improvement in the identification of ants generally, or of these known invasive species in particular, by biosecurity officers. This variation in identification also occurred among ports of entry with proportionally more interceptions identified to species in Queensland, Darwin, and Perth. One possible explanation for this is the detection of red imported fire ants, *Solenopsis invicta*, in south east Queensland in 2001, and subsequent concern over possible further incursions meaning extra effort was put in to identifying ant interceptions in Queensland. Overall, the proportion of interceptions not identified beyond "ant" decreased to a low level by the early 2000s, with the proportion of ants identified to species level rather than genus increasing through 2000–2010, suggesting a possible increase in overall expertise at identification, or at least an increase in confidence when identifying particular highly-invasive species, which were those most frequently identified to the species level.

However, it is also possible that many species are mis-identified or similar species incorrectly lumped into a single taxon (e.g. *Technomyrmrex*, *Ochetellus*, *Camponotus*). Mis-identifications could have significant biosecurity consequences including allowing species to enter without treatment if they are mistaken as either native to, or already established, in Australia.

Most of the native, introduced, and not established species interceptions originated from locations from within their known native range. However, ~16% of interceptions of non-native species originated from outside their native range including *Camponotus novaehollandiae*, *Linepithema humile*, and *Solenopsis geminata*. These three are widespread introduced species, and these interceptions are coming from previously established introduced populations, a process known as the bridgehead effect and likely very important in influencing the invasion dynamics of ants and other invasive species (Bertelsmeier et al. 2018). The tropical fire ant, *Solenopsis geminata*, provides an example of this process as genetic data revealed an initial invasion from Mexico to Manila followed by subsequent invasions throughout Southeast Asia from this port city (Gotzek et al. 2015). Identifying hub countries that act as sources of invasive species is essential for planning biosecurity management. However, for such planning to be effective, up to date information on the current range of invasive species is essential – requiring real-time international cooperation and data sharing.

Conclusions

In this study, we investigated historic records of ant interceptions to determine trends relating to potential ant invasions, to elucidate key pathways and hotspots, and to determine the commodities presenting the highest risk of future ant invasions in Australia. Given the difficult nature of eradication, once an ant species is firmly established (Hoffmann et al. 2016), focusing on early detection and quarantine is key for reducing the establishment of new invasions. In addition, these ant interceptions can be considered a model system from which more general conclusions about the global transport of invasive species can be drawn. Caley et al. (2015) argued that interception records may not provide an early warning system for insect incursions, as their study found that most successful incursions were not even intercepted by border quarantine in Australia (see also Eschen et al. 2015 for Europe). However, for species that were known to have been intercepted, incursion probability was higher for those with higher interception rates (Caley et al. 2015), indicating that the role of transport and commerce in facilitating higher propagule pressure/interception rates of species is key to informing biosecurity risk management. Whether the number of interceptions per species in this study equates/relates to establishment risk would require further study. Finally, in addition to inspection on arrival, more effort needs to be placed on inspection in high-risk ports of departure. Implementing port-of-departure biosecurity measures can be very effective at reducing contamination of goods as evidenced in New Zealand where ant presence in containers dropped from 17% to less than 1% (Nendick et al. 2006; Hoffmann et al. 2017).

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Supplementary material 1

Table S1. Ant species (or species group), number of records and status of ants identified from interception records to Australia from 1986–2010

Authors: Elissa L. Suhr, Dennis J. O'Dowd, Andrew V. Suarez, Phillip Cassey, Talia A. Wittmann, Joshua V. Ross, Robert C. Cope

Data type: species data

Link: https://doi.org/10.3897/neobiota.53.39463.suppl1

Supplementary material 2

Figure S1. Flights into Australia 1999–2012

Authors: Elissa L. Suhr, Dennis J. O'Dowd, Andrew V. Suarez, Phillip Cassey, Talia A. Wittmann, Joshua V. Ross, Robert C. Cope

Data type: measurement

Explanation note: Data from OAG Aviation (http://www.oag.com).

Link: https://doi.org/10.3897/neobiota.53.39463.suppl2

Supplementary material 3

Figure S2. Ant interception records into Australia separated by transportation type (aircraft, sea vessel or other) and source bioregion

Authors: Elissa L. Suhr, Dennis J. O'Dowd, Andrew V. Suarez, Phillip Cassey, Talia A. Wittmann, Joshua V. Ross, Robert C. Cope

Data type: biodiversity data

Link: https://doi.org/10.3897/neobiota.53.39463.suppl3

Supplementary material 4

Figure S3. Import value over time for the 4 commodities with the most associated ant interceptions

Authors: Elissa L. Suhr, Dennis J. O'Dowd, Andrew V. Suarez, Phillip Cassey, Talia A. Wittmann, Joshua V. Ross, Robert C. Cope

Data type: biodiversity data

Link: https://doi.org/10.3897/neobiota.53.39463.suppl4

Supplementary material 5

Figure S4. Shannon diversity index calculated annually for interceptions identified to species from the "introduced" species category

Authors: Elissa L. Suhr, Dennis J. O'Dowd, Andrew V. Suarez, Phillip Cassey, Talia A. Wittmann, Joshua V. Ross, Robert C. Cope

Data type: biodiversity data

Link: https://doi.org/10.3897/neobiota.53.39463.suppl5