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Cite this article: Miravete V, Roura-Pascual N, Dunn RR, Gómez C. 2014 How many and which ant species are being accidentally moved around the world? *Biol. Lett.* **10**: 20140518.
http://dx.doi.org/10.1098/rsbl.2014.0518

Received: 1 July 2014
Accepted: 30 July 2014

Subject Areas:
ecology, environmental science

Keywords:
biological invasions, exotic species, formicidae, richness estimator

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Electronic supplementary material is available at http://dx.doi.org/10.1098/rsbl.2014.0518 or via http://rsbl.royalsocietypublishing.org.

Royal Society Publishing

Global change biology

How many and which ant species are being accidentally moved around the world?

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Human transportation facilitates the dispersal of exotic ants, but few studies have quantified the magnitude and geography of these movements. We used several non-parametric indices to estimate the number of species successfully introduced to or established in new regions. We also compared their source biogeographic realms to assess the importance of geographical origin in determining the likelihood of establishment after introduction. Occurrence data on exotic ants derive from studies of three temperate regions. Our results suggest that the numbers of introduced or established ants may be much larger than the numbers so far documented. Ants introduced or established in new regions tend to arrive from the same or neighbouring realms, as would be expected if exotic species tend to match climates and if arrival/establishment is dependent upon higher trade rates from neighbouring countries.

1. Introduction

Global trade facilitates the dispersal and establishment of ant species in areas outside their biogeographic ranges. Established, introduced ants include many highly invasive species, five of which are considered among the world's top invaders [1]. Although a relatively small number of species are considered invasive, and no more than a few hundred have been recorded as exotics, the number of ant species that have successfully moved and established outside of their native range is almost certainly larger than the number recorded to date [2].

A voluminous literature attempts to understand the spread and ecology of exotic ants. However, no one has examined what proportion of the myrmecofauna on Earth has been shipped to new habitats. McGlynn [3] identified 147 ants as being accidentally transported to new regions, but three recent studies suggest that this number is an underestimate. Suarez *et al*. [4] showed that 232 species were intercepted in the USA, while Lester [5] intercepted 66 species in New Zealand and Boer & Vierbergen [6] 76 species in The Netherlands. Here, the term *introduced ants* refers to species that have arrived in new regions, whereas *established species* are those that establish temporary or permanent viable populations. We do not distinguish here between those ant species that establish temporarily and those that persist for decades. Although such differences are interesting, data on the persistence of established species are sparse except in the case of very abundant invasive species.

We use samples of exotic ants arriving and establishing at three different temperate regions to address the following questions: (i) what are the potential number of species (and genera) introduced and established to temperate regions? And (ii) how are introduction and establishment processes influenced by the geographical origin of exotic ants? In considering this second question,

Table 1. Observed and estimated values (±s.d.) for introduced and established ant species (and genera) worldwide. *CV infrequent* refers to the coefficient of variation of infrequent species, while *mean estimate value* is the mean value across the seven richness estimators. Best estimates are indicated in italics.

	introduced species	established species	introduced genera	established genera
observed value	235	115	66	42
CV infrequent	0.758	0.673	0.613	0.437
estimated values				
Chao2	844.8 ± 160.9	406.0 ± 107.0	116.9 ± 23.2	59.5 ± 9.8
Model(h)	*883.1 ± 26.4*	441.0 ± 10.9	*117.6 ± 5.3*	61.7 ± 3.6
Model(h)-1	1259.2 ± 15.6	*593.1 ± 25.6*	136.6 ± 6.0	*65.9 ± 4.0*
Model(th)	1123.3 ± 220.6	663.1 ± 213.3	128.3 ± 25.5	68.2 ± 14.5
Model(th)-1	2026.8 ± 566.9	1331.3 ± 624.0	160.1 ± 45.0	78.1 ± 22.8
first-order jack-knife	365.7 ± 14.8	180.3 ± 10.4	93.3 ± 6.7	58.0 ± 5.2
second-order jack-knife	427.5 ± 19.7	211.2 ± 13.9	105.2 ± 9.0	64.2 ± 6.8
mean estimated value	990.1	546.6	122.6	65.1

we seek to identify the biogeographic origin of introduced ants and also to understand whether established ants appear to be a biased or random sample with respect the biogeography of introduced species.

2. Material and methods

We compiled data on the introduction and establishment of exotic ants in the USA [4,7,8], New Zealand [5] and The Netherlands [6] (electronic supplementary material, S1). Based on these records, we estimated the potential number of introduced and established ant species (and genera) by means of the richness estimators (Chao2, Model(h), Model(h)-1, Model(th), Model(th)-1, first-order jack-knife and second-order jack-knife) with SPADE [9]. All these estimators rely on presence/absence data but differ in how they treat the number of species found in one or two samples and their detection probabilities [9,10]. The estimators were evaluated based on the study of Brose *et al*. [10], which calculates the mean of all estimators and chooses the one with the closest value to the mean. To assess the importance of geographical origin in determining the likelihood of establishment after introduction, we compared the region of origin of both introduced and established species by means of χ^2 tests. The native range of species was determined based on the type locality (electronic supplementary material, S2).

3. Results

The samples considered in our study [4–8] are dominated by 'uniques' (see species found only in one sample), especially in the USA (electronic supplementary material, S3). The proportion of uniques over duplicates or triplicates is high in introduced and established species (5 and 5.7, respectively), but lower in genera (1.6 for introduced and 1.3 for established genera).

Richness estimators suggest that the number of introduced species is three and half times higher (883 species) than observed (table 1). For comparison, the number of natives to these regions is 11 species in New Zealand [11], 65 species in The Netherlands [12] and approximately 1000 species in North America [13]. In other words, the potential number of ant species that are estimated to be arriving in temperate regions is comparable with the number of native species. The estimated number of established species is smaller (593

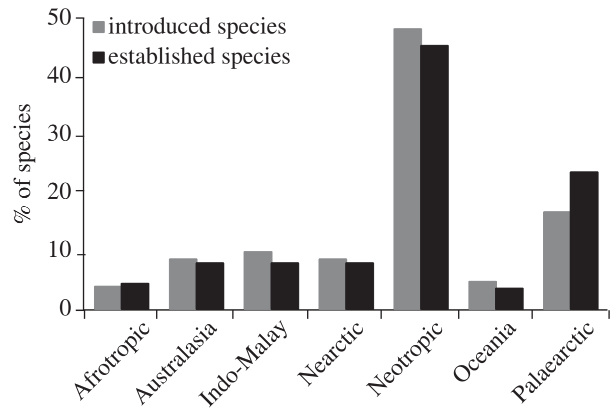

Figure 1. The percentage of introduced ($n = 235$) and established ($n = 115$) species that have arrived in the USA [4,7], New Zealand [5] and The Netherlands [6] from each biogeographic realm. Grey bars represent introduced species, and black bars represent established species.

species), but nearly five times higher than observed (table 1). Also, the number of arriving species is enormous and the proportion able to establish appears greater than we would expect (67% of estimated introduced species).

There was a much smaller disparity between the numbers of genera recorded and estimated to occur. Although somewhat higher, the estimated numbers for introduced (117 genera) and established genera (66 genera) are much more similar to the observed values than for species numbers. In other words, the number of known introduced and established ant genera in temperate regions are approaching the true number.

The ants arriving in temperate regions are not drawn randomly from the biogeographic regions of the world (figure 1). Most introduced species come from the Neotropic realm, whereas a lower proportion comes from the Palaearctic, Indo-Malay and Australasia. The relative importance of the source biogeographic realms changes throughout the three study regions, both in terms of introduced species ($\chi^2 = 84.44$, d.f. = 12, $p < 0.001$) and established species ($\chi^2 = 32.89$, d.f. = 12, $p < 0.001$). Specifically, the majority of species introduced to and established in the USA come from the Neotropic realm (58% and 51%, respectively), whereas in The Netherlands and New Zealand the majority of species come from their own realms (Palaearctic (33% and 43%) and Australasia (26% and

35%), respectively) (electronic supplementary material, S4). However, there were not significant differences between the source biogeographic realms of introduced and established within each study region (USA: $\chi^2 = 1.94$, d.f. = 6, $p > 0.05$; The Netherlands: $\chi^2 = 2.29$, d.f. = 5, $p > 0.05$; New Zealand: $\chi^2 = 3.25$, d.f. = 6, $p > 0.05$).

4. Discussion

Assessing rates of introduction and establishment of exotic ants is a critical first step towards understanding the dynamics of ant invasions. However, our results suggest that the number of ants introduced and established outside their native range is much greater than the number documented [3,4]. At the global scale, the number of introduced species in temperate regions could be three and half times higher than the number so far detected, with most (67%) of these species established. These values suggest that at least 1/14th (7%) of the world myrmecofauna (i.e. 12 953 species [14]) has been shipped to new habitats. Clearly, many introduced species are living around us and as of yet undetected.

These estimates could be influenced by the high number of 'uniques' introduced and established in the USA in contrast with the other two samples. The USA is a larger geographical area than New Zealand or The Netherlands and, as such, presents both more opportunities for introductions and more area and more varied climatic conditions in which introduced species can establish. The difference in the geographical area and climatic diversity of the focal regions could influence our estimates of the total number of introduced and established species, though the direction of bias is hard to anticipate. It is possible that were the USA to be compared with larger regions (e.g. Europe or Australia) fewer 'uniques' would be found (and hence our estimates might need to be revised downward). On the other hand, it appears (based on faunal lists) that very few of the 'uniques' from North America have yet been observed in Europe, such that expanding the scale of our European sample to all of Europe might increase the number of species. Including additional regions in our analyses (where data on established species are more preliminary) produces estimates of the number of established species in line with our estimates from three regions, suggesting that our results are not simply an artefact of the regions about which we know the most (electronic supplementary material, S5).

Introduced and established ants might be drawn randomly from the biogeographic regions of the world [15]. We did not find this to be the case. The vast majority of introduced and established species appear to come from the Neotropics. These results are in line with previous studies [2] and perhaps not surprising given that the Neotropics account for the largest number of ant genera and species, and the greatest number of endemic genera [16] and that our list of introduced and established species was dominated by species found or intercepted in the USA. Most species established in The Netherlands have a Palaearctic origin (the same biogeographic region as the study region) and most established in New Zealand come from Australasia (the neighbouring biogeographic region).

There are two possible explanations for the apparent tendency of neighbouring regions to contribute disproportionately to establishment. Exotic species tend to establish in regions with similar climatic conditions to their region of origin, a phenomenon termed climate matching [17]. Regions in similar latitudes or in the same biogeographic realm are more likely to have similar climates and habitats which might increase the odds of the success of introduced species. In addition, species are more likely to be noted as introductions if they arrive more than once [18]. The frequency of introduction is, in turn, probably linked to shipping frequency and the most frequent shipping routes tend to originate in nearby regions. Combined, these two effects, climate matching and shipping frequency, seem sufficient to account for the observed pattern that introduced species tend to disproportionately derive from the same or nearby biogeographic as that into which they are introduced. If the regional effect were due primarily to climate matching, we might expect that the biogeographic regions of introduced and established species might differ (since the arrival of a non-introduced species does not guarantee that it has found a suitable climate). However, in our study, there were no significant differences between the source biogeographic realms of introduced and established species within each country, such that the biogeographic region of origin of introduced and established species may have as much to do with shipping routes (propagule pressure) as biology (e.g. climate matching).

To reduce the chances of establishment of exotic ants in new regions, it is necessary to prevent their accidental entry, but our results make clear that most such accidental entries are missed. Only one-third of the potential number of introduced species has been recorded so far. Because the introductions of ants seem biogeographically non-random, it might be fruitful to observe more carefully the shipping routes from those regions (e.g. the Neotropics) with the highest probability of leading to introductions. The identification of donor regions is useful for the management of invertebrates—such as ants—that arrive inconspicuously and so are difficult to intercept. Better identification of donor regions will require more studies of introduced and established ants in regions other than those considered here.

Acknowledgements. Thanks to Amy Savage, Jes Pedersen, Phil Lester, Eli Sarnat, James Wetterer and one anonymous reviewer.

Funding statement. V.M. and C.G. received support from MICINN (CGL2010-16451), N.R-P. from MICINN (CSD2008-00040) and R.R.D. from US DOE PER (DE-FG02-08ER64510), NASA Biodiversity (ROSES-NNX09AK22G) and NSF Career (0953390) grants.

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