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 indexes 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 the geographical origin in determining the likelihood of establishment after introduction. 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 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 the 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, whereas 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 population. 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 numbers 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,
variation of infrequent species, whereas Table 1. species that are estimated to be arriving in temperate regions America [12]. In other words, the potential number of ant regions is 11 species in New Zealand [10], 65 species in The species is three times higher (768 species) than observed 2.0 for established genera). The proportion of uniques over duplicates or triplicates is especially in the USA (see electronic supplementary material, by ‘uniques’ (see species found only in one sample), The samples considered in our study [4–7] are dominated We compiled data on the introduction and establishment of exotic ants in the USA [4,7], New Zealand [5] and The Netherlands [6] (see 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 jackknife and second-order jackknife) with SPADE [8]. 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 [6,9]. The estimators were evaluated based on the study of Brose et al. [9], 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 χ²-tests. The native range of species was determined based on the type locality (see electronic supplementary material, S2).

3. Results

The ants arriving in temperate regions do not draw randomly from the biogeographic regions of the world (figure 1). Most introduced species come from the Neotropical realm, while a lower proportion comes from the Palearctic, Indo-Malaysia and Australasia. The relative importance of the source biogeographic realms changes throughout the three study regions, both in terms of introduced species (χ² = 87.67, d.f. = 12, p < 0.001) and established species (χ² = 56.13, d.f. = 12, p < 0.001). Specifically, the majority of species introduced and established in the USA come from the Neotropical realm (52% and 43%, respectively), whereas in The Netherlands and New Zealand the majority of species come from their own realms (Palearctic (35 and 38%) and Australasia (33 and 43%).

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, whereas Mean estimated value is the mean value across the seven richness estimators.

<table>
<thead>
<tr>
<th></th>
<th>introduced species</th>
<th>established species</th>
<th>introduced genera</th>
<th>established genera</th>
</tr>
</thead>
<tbody>
<tr>
<td>observed value</td>
<td>252</td>
<td>145</td>
<td>65</td>
<td>46</td>
</tr>
<tr>
<td>CV infrequent</td>
<td>0.652 ± 0.560</td>
<td>0.523 ± 0.393</td>
<td></td>
<td></td>
</tr>
<tr>
<td>estimated values</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chao2</td>
<td>714.4 ± 108.5</td>
<td>485.7 ± 109</td>
<td>97.6 ± 14.9</td>
<td>63.3 ± 9.3</td>
</tr>
<tr>
<td>Model(h)</td>
<td>768.4 ± 14.0</td>
<td>529.4 ± 11.7</td>
<td>100.3 ± 4.6</td>
<td>65.6 ± 3.7</td>
</tr>
<tr>
<td>Model(h)-1</td>
<td>995.2 ± 20.8</td>
<td>656.7 ± 51.2</td>
<td>110 ± 4.9</td>
<td>69 ± 4.2</td>
</tr>
<tr>
<td>Model(th)</td>
<td>1019.7 ± 183.6</td>
<td>940.3 ± 297.9</td>
<td>109.7 ± 19.2</td>
<td>74.6 ± 15.5</td>
</tr>
<tr>
<td>Model(th)-1</td>
<td>1733.2 ± 452.6</td>
<td>2048.4 ± 962.7</td>
<td>128.9 ± 31.4</td>
<td>86 ± 24.9</td>
</tr>
<tr>
<td>first-order jackknife</td>
<td>388 ± 15.1</td>
<td>226.7 ± 11.7</td>
<td>89.7 ± 6.4</td>
<td>63.3 ± 5.4</td>
</tr>
<tr>
<td>second-order jackknife</td>
<td>451 ± 20.1</td>
<td>265.5 ± 15.7</td>
<td>99.7 ± 8.5</td>
<td>69.8 ± 7.1</td>
</tr>
<tr>
<td>mean estimated value</td>
<td>867.1</td>
<td>736.1</td>
<td>105.1</td>
<td>70.2</td>
</tr>
</tbody>
</table>

The estimated number of established species is smaller (657 species), but nearly four and half 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 (85% 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 (100 genera) and established genera (70 genera) are much more similar to the observed values than for species numbers. In other words, the numbers of known introduced and established ant genera in temperate regions are approaching the true number.

Figure 1. The percentage of introduced (grey bars; n = 253) and established (black bars; n = 145) species that have arrived in the USA [4,7], New Zealand [5] and The Netherlands [6] from each biogeographic realm.
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 times higher than the number so far detected, with most (85%) of these species established. These values suggest that at least one-sixth (16%) of the world myrmecofauna (i.e. 12 762 species [13]) have been shipped to new habitats. Clearly, many introduced species are living around us but are as yet undetected.

These estimates could be influenced by the high number of ‘uniques’ species 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’ species 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 (see electronic supplementary material S5).

Introduced and established ants might draw randomly from the biogeographic regions of the world [14]. 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 [15] 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 Paleartic 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 [16]. 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 [17]. The frequency of introduction is, in turn, likely 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 disproporionately derive from the same or nearby biogeographic regions as that into which they are introduced [8]. 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.

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Retraction

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Herewith, we retract our paper ‘How many and which ant species are being accidentally moved around the world?’ by Verónica Miravete et al., published online on 23 October 2013 (Biol. Lett. 9, 20130540; doi:10.1098/rsbl.2013.0540). After careful examination of the original data on introduced and established ants on regions worldwide, we realized that we used a wrong list of species and omitted to include a reference (Sarnat E. (2012) North America checklist. Antkey <http://antkey.org>. Extracted 3 June 2014) in the paper. Although the main arguments and conclusions remain the same after correcting these errors, the use of the wrong version of the data affected the magnitude of the analyses conducted at the country level (in the electronic supplementary material) and, to a lesser extent, when all countries were considered together (in the main text). Therefore, we wish to retract the article. We deeply apologize for any inconvenience this publication might have caused to the readers of Biology Letters.

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