Title: A global analysis of the determinants of alien geographic range size in birds

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ABSTRACT

Aim Determining the causes of range size variation in alien species' distributions is important for understanding the spread of invasive species. Factors influencing alien range size have been explored for some species at a regional level, but to date there has been no global analysis of an entire class. Here, we present such an analysis for birds, testing for the effects of introduction event, location and species-level variables on alien range sizes.

Location Global.

Methods We used a novel dataset on the global distributions of alien bird species to test for relationships between alien range size and colonisation pressure, residence time, extent of the global climatic niche, native range size, body mass and specialisation, using a statistical approach based on phylogenetic generalised least squares models. We performed this analysis globally, and for separate biogeographic realms.

Results Approximately half of the variation in alien bird range size is explained by colonisation pressure in univariate analysis. We identified consistent effects of higher colonisation pressure at global and realm levels, as well as support for effects of native range size and residence time. We found less support for effects of body mass, specialisation, or extent of the global climatic niche on alien range size.

Main Conclusions Alien bird range sizes are generally small relative to their native range sizes, and many are continuing to expand. Nevertheless, current variation is predictable, most strongly by the event-level factor colonisation pressure. Whether a species is widespread is a better predictor of alien range size than whether a species could be widespread (estimated by global climatic niche extent), while we also find effects of residence time on alien range size. These relationships may help to identify those alien species more likely to spread, and hence have greater environmental an economic impacts where they have been introduced.

INTRODUCTION

The on-going influences of human settlement, acclimatization, recreation and commerce have led to repeated introductions of bird species into areas to which they are not native (Long 1981). Substantial progress in invasion biology has come from studying these alien birds (Blackburn *et al.* 2009), but significant gaps in our understanding remain. Most notably, aside from a few case studies (e.g. Liversidge 1962, Silva *et al.* 2002), the processes determining the geographic spread of alien bird species, and their resulting geographic range sizes, have largely been ignored (Mack *et al.* 2000, Blackburn *et al.* 2009). Geographic range size is one of the fundamental ecological and evolutionary characteristics of a species. It is a strong predictor of extinction risk (Gaston 2003) and, with regards to an alien species, the potential for impact (Parker *et al.* 1999). Range expansions are inextricably linked to global environmental and economic issues of increasing importance: climate change, habitat fragmentation, declining biodiversity, and genetic introgression (Vitousek *et al.* 1997, Kolar & Lodge 2001). An obvious question, therefore, is whether it is possible to identify the factors that are associated with the variation in geographic range sizes of alien bird species?

The establishment success of alien bird species relates to characteristics of the species introduced, of the location of introduction, and of the introduction event itself (Duncan *et al.* 2003). The same categories of factors have also been hypothesised to influence the extent of spread following establishment. Event-level factors are those that vary independently of the species and location concerned. In terms of alien geographic range size, important event-level variables are likely to be the number of times that a species has been introduced (colonisation pressure, *sensu* Lockwood *et al.* 2009), and the length of time since introduction (residence time, *sensu* Wilson *et al.* 2007). As far as we are aware, only two global scale analyses have considered the effects that these event level factors have on alien range size. These studies found that pine tree species (Proçhes *et al*. 2012) and reptiles and amphibians (Li *et al.* 2014) that have been introduced more often have larger alien ranges. Regional studies find similar relationships for bird species introduced to New Zealand (Duncan *et al.* 1999), and Australia

(Long & Mawson 1991, Duncan *et al.* 2001), and reportedly also in North America (Johnston & Garrett 1994). Regional studies have also demonstrated that residence time is positively related to alien range size (Williamson *et al.* 2009), total latitudinal extent (Guo *et al.* 2012), and likelihood of invasion and spread (Pyšek *et al.* 2009a). Conversely, Duncan *et al.* (1999) found no relationship between residence time and range size for bird species introduced to New Zealand.

The outcome of introduction events is likely to be constrained by characteristics of the environment at the location of introduction, and of the species introduced. In particular, the availability of suitable habitat or climate is likely to be important (Capinha *et al.* 2015), and therefore species for which greater land areas are environmentally suitable should be able to attain larger alien geographic ranges. It is likely that generalist species, which can tolerate a wider range of climatic, habitat and dietary variables (Brown 1984), or species that utilise more commonly encountered environments or resources, are likely to be more widespread as a result (Long & Mawson 1991, Gaston 2003). Duncan *et al.* (1999, 2001) showed that the range sizes of alien bird species in New Zealand and Australia were determined in part by the area of suitable habitat, while Forsyth *et al.* (2004) showed the same for alien mammals in Australia. Several studies have also investigated the relationship between alien range size and native geographic range size, a possible proxy for the availability of suitable environmental conditions. There is as yet little consensus on the factors that determine native range sizes (Gaston 2003), but if the same characteristics that enable a species to become widespread in its native location also allow it to become widespread in its alien range, a positive correlation would be expected between the two. Indeed, native range size has been demonstrated to be an indicator of probability of invasiveness in plant species (Pyšek *et al.* 2009b), and global native and alien range sizes have been shown to be correlated in introduced tree species in the genus *Pinus* (Proçhes *et al.* 2012), and for a limited sample of alien bird species (Guo *et al.* 2012). Alien geographic ranges may be constrained by the presence of barriers to range expansion such as oceans or mountain ranges. In a global study, Orme *et al.* (2006) showed that the geographic range sizes of native bird species are smaller on islands, and on mountain ranges in the tropics and sub-tropics.

Life history traits have also been shown to influence the extent to which established species can spread. For example, there is a relationship between the sizes of alien bird ranges in New Zealand and Australia and life history traits associated with higher rates of population growth (Duncan *et al.* 1999, Duncan *et al.* 2001). Small body mass and high reproductive rate influenced the spread of alien birds in Florida (Allen *et al.* 2013), and adult survival has been found to impact upon the potential of alien birds to succeed and spread in the Mediterranean (Blondel 1991). Species with faster growth rates may be less vulnerable to local extinction when their population is small, and able to colonize new sites more quickly following establishment (Duncan *et al.* 2001).

To date, tests of determinants of alien geographic range sizes have generally considered variation in relatively few taxa (e.g. a single genus: Proçhes *et al.* 2012) or restricted regional assemblages (e.g. New Zealand, Australia: Duncan *et al.* 1999, Duncan *et al.* 2001, Forsyth *et al.* 2004). Here, we present the first global-scale analysis of spatial variation in the geographic range sizes of extant alien species with a known established population for a major taxon, birds. We simultaneously explore event-, species- and location-level predictors of alien range size. Notably, we use an ecological niche modeling method, range bagging (Drake 2015), to estimate the global extent of climatic zones that are suitable for each alien bird species (i.e. an estimate of its potential geographic range size), to test whether species with larger global climatic niches also have larger alien geographic range sizes. We also contrast potential and native geographic range sizes as predictors of alien range extent. We do this while controlling for the number of times, and the length of time, that species have been introduced. Specifically, we test the hypotheses that bird species will achieve larger alien geographic range sizes when (i) they have been introduced more times, (ii) they have longer residence times, (iii) they have larger global climatic niches, (iv) they have larger native geographic range sizes,

(v) they have faster life histories, (vi) they are diet and habitat generalists, and (vii) they have been introduced to larger geographic regions.

METHODS

Data

We based our analyses on the list of bird species with established alien populations from the Global Avian Invasions Atlas (GAVIA) database (Dyer *et al*. in revision). GAVIA comprises 27,737 distribution records for 972 alien bird species (following the taxonomy of the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species, downloaded August 2010), based on 693 published references and substantial unpublished information derived from consultation with over 600 organisations and experts worldwide. A total of 419 bird species have established alien populations, but we limited our analysis to the 319 species for which data were available for all variables.

The total alien geographic range size for these 319 bird species was extracted from GAVIA. For this study, alien geographic range size was calculated as the total size in km^2 of the global alien range for each species, based on extent-of-occurrence polygon maps of the most recent data for populations. The frequency distribution of natural log-transformed alien range sizes for the 319 species is shown in figure 1 (Shapiro-Wilk test for normality: W = 0.99, p = 0.12).

Estimates of colonisation pressure, or the number of times that a species has been introduced to different locations, were extracted from the GAVIA database, and include only those records which explicitly refer to actual releases or escapes of species at a given location. Colonisation pressure varied from 1 to 110 separate introduction events (mean = 13.78; median = 6).

Residence times were calculated as the number of years from the earliest GAVIA record for that species to the year 2013, when the database was completed. Where there was no information available on the first date recorded, residence time was calculated from the date of the earliest published reference in which that species was mentioned. The longest recorded residence time of an established species was 1513 years (*Gallus gallus*, earliest record 500AD), and the shortest 7 years (*Polyplectron napoleonis*, earliest record 2006) (mean = 140.4; median = 98 years).

Native range sizes were extracted from the database of extent-of-occurrence avian range maps used by Orme *et al.* (2005), and were calculated as the total global breeding range size. The native range sizes of the species in the dataset showed similar variation to the alien ranges, from 219.67km^2 (*Megapodius pritchardii*) to 58.19 x 10^6 km^2 (*Tyto alba*), but with higher mean (6.06 x 10^6 km^2) and median (3.02 x 10^6 km^2).

Range bagging, an ecological niche modeling method (Drake 2015), was used to predict the extent of the global climatic niche for each established species at a global scale, based on climatic match to the species native range. Range bagging is a machine-learning based method that seeks to estimate the boundary of a species niche within multi-dimensional environmental space, as represented by a convex hull. Calculating a full convex hull from the typical range of climatic variables is computationally infeasible. Instead, range bagging approximates the full convex hull by constructing a series of ‘marginal’ convex hulls, based on subsets of the climate variables. Range bagging appears to be an effective method for the prediction of species potential ranges in an invasion context (Cope *et al*. submitted).

We obtained WORLDCLIM global climate data (Hijmans 2005), consisting of 19 climate variables at a 5 arc minute resolution (for a total of 2,287,341 points). We chose, uniformly at random, a subset of one million of these points to test against each species native range, for increased computational tractability. For each species, we calculated a range bagging score to the species native range for each of these one million test points, i.e., we calculated the proportion of marginal niches for which each test point was within the species marginal niche, determined from its native range. We used v=100 votes, two dimensional marginal niches, and built marginal niches from a proportion p of points within the native range, with p=1.0 for species with small native ranges (<200 points), p=0.5 for species with native range <10,000 points, and p=0.25 for species with large ranges (>10,000 points). These parameters were chosen to be within the range of good performance indicated by Drake (2015), and to balance marginal niche coverage with computational efficiency. It is not possible to construct convex hulls around fewer than three unique points (in two dimensions), as the result is just a line or a point. When there are small numbers of points beyond this minimal threshold, and those points are similar in climate (as may be the case when they originate from a continuous geographic range) the points may be identical in some covariates, creating a situation where some marginal niches are unable to be constructed. For this reason, range bagging scores could not be estimated for 6 established alien species with small native ranges.

The locations with a range bagging score of at least 0.8 (i.e., v = 80, or 80% of marginal niches matching the species native range) were deemed to be within the species potential invasive range due to climatic similarity to the native range. We calculated the proportion of the full set of test points that were suitable by this metric, as a measure of the proportion of total global landmass forming a species potential climatic niche extent. This proportion (estimating the potential range size of bird species with established alien populations) ranged from 0.000001 (*Collocalia bartschi*) to 0.87 (*Passer montanus*).

Body mass was used as a proxy for life history variation, as it is known to be highly correlated with many other reproductive, timing, physiological and ecological traits (Peters 1983), and relationships have been found between body mass and both native and alien range size (Gaston & Blackburn 1996, Duncan *et al.* 2001). Body masses were taken from the database used by Olson *et al.* (2009), and were calculated as the geometric mean body mass in grams. Body masses in the sample varied from 0.0062 kg (*Collocalia bartschi*) to 109.65 kg (*Struthio camelus*) (mean = 1.1 kg; median = 0.12 kg).

In order to address the effect of the level of specialism (or inversely, generalism) of a species, a specialisation index was calculated using the number of food types (diets) that a species is known to consume, and the number of habitats that it is known to utilise, where specialisation index = ln[100/(number of diets x number of habitats)] (after Sekercioglu 2011). Bird habitat and diet data were obtained from a global bird ecology database covering all the bird species of the world (see Sekercioglu 2012). The specialisation index in the sample varied from 0.87 (*Alectura lathami* and *Corvus frugilegus*) to 4.6 (*Agapornis personatus* and *Polyplectron napoleonis*) (mean = 2.3; median = 2.4). A low specialisation index indicates that a species is more of a generalist in terms of its diet and habitat preferences, whereas a high specialisation index indicates that a species is a specialist and utilises fewer habitats and dietary resources.

Species ranges were assigned to biogeographic realms (Afrotropical, Australasian, Indo-Malayan, Nearctic, Neotropical, Oceanic and Palearctic) following Olson *et al*. (2001). A spatial layer depicting the biogeographic realms was created using ESRI ArcGIS version 9.3 (2008), and realm-level alien range sizes, residence time, and colonisation pressure were extracted from GAVIA, as was the total land area of each realm. We also calculated the proportion of test points within each biogeographic realm that was suitable for each species using range bagging, as above. The Antarctic realm was excluded from the analysis due to a small sample size.

Statistical analyses

The parameters were tested to see if they were phylogenetically correlated using Pagel's λ calculated using function *phylosig* from the *R* package *phytools* (Revell 2012). To account for uncertainty in the avian phylogeny, these tests were repeated for a random selection of 100 bird trees for the 319 species in our analysis, downloaded from www.birdtree.org (Jetz *et al.* 2012; Hackett backbone, downloaded 19/5/16). Alien range size showed a low phylogenetic correlation (mean λ [2.5th percentile, 97.5th percentile]: 7×10^{-5}, [5×10^{-5}, 7×10^{-5}]), as did colonisation pressure (0.06, [0.05, 0.07]), whereas phylogenetic correlations were higher for global climatic niche extent (0.59 [0.54, 0.64]), native range size (0.69 [0.61, 0.77]), residence time

(0.13 [0.11, 0.16]), body mass (1.00 [1.00, 1.00]) and specialisation index (0.60 [0.56, 0.64]). Therefore, in order to account for any phylogenetic autocorrelation in our analyses, the tests of the determinants of alien range size were based on phylogenetic generalised least squares models (PGLS) applied by the function *pgls* from the *R* package *caper* (Orme *et al.* 2013).

Tests of collinearity between the predictor variables using *R* functions *cor* and *corr.p* found these to be generally only weakly correlated (table S1). The one exception was a strong correlation between global climatic niche extent and native range size. As we were interested in the effects of both these variables, we retained both, and therefore all variables were used in subsequent analyses. We initially examined the relationships between alien range size and each variable, using univariate PGLS models. We tested for the significance of squared terms for all variables, and retained these terms for the multivariate analysis where there was evidence that they improved model fit based on the Akaike Information Criterion corrected for small sample sizes (AICc), such that ΔAICc > 4.

We then examined the relationship between alien range size and the variables in a multivariate PGLS model. We used the *dredge* and *model.avg* functions from the package *MuMIn* (Barton 2014) to fit all possible models. We then calculated the full (i.e. including models from which a variable is absent) model-averaged coefficients (± standard error) for each variable, and the variable importance (the sum of the Akaike weights across all models) based on the Akaike Information Criterion corrected for small sample sizes (AICc), for all models with ΔAICc within 4 of the most likely model. Because of the strong correlation between global climatic niche extent and native range size, we also repeated the multivariate analysis without native range size.

A species with alien population(s) can attain its global alien range size in a variety of ways. For example, a species may have been introduced to a single area and spread out to attain a range size of 1000 km^2, or to five different locations, each time spreading to 200 km^2. The global model treats these two hypothetical species as the same, as the global alien range size is the sum of the ranges' overall alien populations, regardless of the number of separate areas to which a species has been introduced. We addressed the effect of multiple introductions by including colonisation pressure (total number of introductions) for each species with at least one alien population. However, we additionally explored the effect of different routes to an overall alien range size by dividing the global data into realm level ranges, and repeating the univariate and multivariate models separately on the data for each realm. This tested the robustness of our global model and the extent to which global patterns are driven by species introduced to multiple realms. ANOVA was used to test for differences in the mean alien range sizes between realms, and also to test whether the land area of the realm influenced the mean alien range size.

All analyses were conducted in R version 3.2.5 (R Core Team 2016). Alien range size, native range size, colonisation pressure, residence time and body mass were logarithmically transformed, and global climatic niche extent square root transformed, for analysis.

RESULTS

Native range sizes were significantly larger than alien range sizes for the species in our dataset (paired t-test: $t = -32.3$, d.f. = 318, $p < 0.001$). Univariate PGLS models showed that colonisation pressure, global climatic niche extent, native range size, residence time, and the specialisation index were related to alien range size, whereas body mass was not (figure 2). The relationship for colonisation pressure was improved by the addition of a squared term. All the significant relationships were positive except that for specialisation index, with the negative relationship for this last variable meaning that more generalist species have larger alien range sizes.

Out of all possible multivariate PGLS models from the variables in our analysis, 12 were well supported, in that they had ΔAICc < 4 relative to the most likely model. Full model averaging showed that colonisation pressure was the only variable significantly related to alien range size in birds, and this variable (and its squared term) were present in all the most likely models (variable importance = 1; Table 1): species introduced more times have larger alien range sizes. Residence time and native range size also attained high variable importance values, but the PGLS coefficients for these variables did not differ significantly from zero. Bird species have larger alien ranges if they were introduced more recently, and have larger native range sizes (Table 1).

There was less evidence for effects of global climatic niche extent, body mass or specialisation index on alien range size in birds: the highest variable importance value across these three variables was 0.51 for global climatic niche extent, and none of the coefficients for these variables differed significantly from zero (Table 1). However, re-running the model in Table 1 without native range size (which was strongly correlated with global climatic niche extent; Table S1) resulted in a strong and significant positive effect of global climatic niche extent on alien range size (estimate ± s.e. = 2.27 ± 0.56, $z = 4.04$, $p < 0.001$; importance = 1), but no qualitative changes to the effects of the other variables in the model.

Mean log-transformed alien range size differed between realms ($F_{6,583} = 4.94$, $p < 0.001$), but was not related to land area within each realm ($F_{1,5} = 0.44$, $p = 0.54$). Univariate PGLS models at the realm level showed that the colonisation pressure was always positively related to alien range size, while residence time and native range size were positively related to alien range size in most realms (Table S2, Figure S1). In contrast, body mass showed no relationship to alien range size in any realm, while specialisation index was negatively related to alien range size only in two realms, and global climatic niche extent in three (Table S2). Full model averaging based on all possible multivariate PGLS models for each realm found that the relative influence of different variables varied between realms (Table S3), but were generally congruent with the results from the global model (Table 1): colonisation pressure was present in all the most likely models for every realm, while native range size and residence time were the next two highest ranked variables in terms of importance, and were present in all the most likely models for two realms (Table 2).

DISCUSSION

Birds possess some of the greatest dispersal abilities of animals in the terrestrial environment (Wernham *et al.* 2002). Nevertheless, in the majority of cases, alien distributions actually tend to be relatively small, and most aliens have not reached the distributional extent observed in their native range (Guo *et al.* 2012). Indeed, the median non-native range size of the 319 established alien bird species is just 0.3% of the median for the native geographic ranges of those same species (10,457 km^2 vs 3,014,856 km^2, respectively). Therefore, despite being able to maintain a self-sustaining population in a new environment, in most instances alien bird species have not (yet) spread far from their point of introduction (Blackburn *et al.* 2009). There are, of course, exceptions to this rule, with species such as the common pheasant (*Phasianus colchicus*), common starling (*S. vulgaris*), mute swan (*Cygnus olor*), and house sparrow (*Passer domesticus*) having alien range sizes more than one million km^2 larger than their native geographic ranges. Our aim here was to take the first steps towards understanding the causes of this large variation.

Characteristics of the introduction event best explain current variation in alien geographic range size in birds. In particular, colonisation pressure was the most consistent predictor, explaining 53% of the global variation in alien range size in univariate analyses (Table S2, Figure 2), and being present in all the most likely models for both global and realm analyses (Tables 1, 2, S3). This is consistent with relationships found in regional studies (Long & Mawson 1991, Johnston & Garrett 1994, Duncan *et al.* 1999, Duncan *et al.* 2001), and suggests that this effect is general and global. Species with more introduction events are likely to have been introduced to a larger number of areas, and are therefore likely to attain a larger alien range. Multiple introductions also tend to involve larger overall propagule pressures (Blackburn *et al.* 2015) which increase the likelihood of successful establishment (Lockwood *et al.* 2005), and may also encompass greater genetic variation, enabling the population better to adapt (or to include genotypes pre-adapted) to local conditions and to realise a broader geographic range (Blackburn *et al.* 2009, Blackburn *et al.* 2015).

Native range size was also a relatively consistent predictor of alien range size: it explained 13% of the variance in alien range size in univariate analyses (Figure 2), and was present in most of the likely global models (Table 1) and all of the most likely models for two of the seven realms (Tables 2, S3). Even with the effect of colonisation pressure taken into account, species with larger native ranges were more likely to achieve larger alien ranges. It is generally observed that closely related species tend not to have similar geographic range sizes (Gaston 2003), and the lack of phylogenetic correlation in alien range sizes adheres to this pattern. Surprisingly, however, our results revealed a reasonably strong phylogenetic correlation in the native range sizes of established alien bird species, with $\lambda = 0.69$. Waldron (2007) reviewed published λ values for native range sizes, finding a mean of 0.38. Why the species in our sample show such a high lambda value is unclear, although it may be the result of phylogenetic clustering evident in introduced species (Blackburn *et al*. 2009).

This positive relationship between alien and native range sizes suggests that whatever factor(s) allow a species to attain a large native range also enable a species to achieve a large alien range. The causes of variation in native range size are still debated (Gaston 2003), but niche position (i.e. how typical of the environment are a species' favoured resources) is a likely determinant. For alien ranges, an effect of niche position is suggested by studies showing that climate matching increases both establishment success (Blackburn & Duncan 2001) and the extent of alien range sizes at the regional level (Duncan *et al.* 1999, Duncan *et al.* 2001, Forsyth *et al.* 2004). Consistent with this, we found that global climatic niche extent has the second strongest univariate relationship with alien range size after colonisation pressure (Figure 2), and is highly correlated with native range size (Table S1, Figure S2). Nevertheless, native range size is a more consistent predictor of alien range size than is global climatic niche extent, being more likely to be present in the best global and realm models (Tables 1, 2, S3). Species with a given native range vary considerably in global climatic niche: for example, species with native ranges c.20,000km^2 have niche extents spanning from about 0.2 to 0.6 of the land area of the world (Figure S2). Yet, whether a species *is* widespread is a better predictor of alien range size than whether a species *could be* widespread. Why this is the case is unclear, although one possibility may be a general bias towards introducing bird species to and from higher latitudes (Blackburn *et al*. 2009). Tropical species may have large areas that are potentially climatically suitable, yet be constrained in their native and alien ranges by other factors, such as biotic interactions. Global climatic niche extent is a consistent predictor of alien range size in a multivariate global model from which native range size is excluded.

The relationship between alien and native range sizes does not seem to be a consequence of generalist species (those with greater niche breadth; Gaston 2003) being able to attain larger range sizes. Species that can tolerate a wider range of conditions have been hypothesised to be able to have larger range sizes as a result, and in native bird assemblages the degree of habitat specialism has been found to correlate with range size (e.g. Davies *et al.* 2009), with specialist species usually occupying narrow ranges (Belmaker *et al.* 2011). However, the specialisation index was a generally weak predictor of alien range size in the multivariate analyses (Figure 2, Tables 1, 2, S2, S3). Thus, the relationship between alien and native range size persists when accounting for the degree of specialism.

Alien range sizes were not correlated with the extent of land in a realm (c.f. Orme *et al.* 2006). The alien range sizes of most species are still small relative to their native range sizes (Figure 2), suggesting that it may be too early in the process of range expansion for geographic limits to have been reached for most species. Range sizes will tend to be smaller for all species in the period immediately following introduction, while species with longer residence times will have had longer to adapt to and spread across the recipient environment, and univariate analyses show a general positive relationship between residence time and alien range size in birds (Table S2, Figures 2, S1). Nevertheless, evidence for an effect of residence time on alien range size to date has been mixed (c.f. Duncan *et al.* 1999 with Pyšek *et al.* 2009a, Williamson *et al.* 2009), and we actually found a negative effect of residence time in the global multivariate model (Table 1), and in four of the seven realm-level multivariate models that included this variable (Table S3). This result was unexpected. One possibility is that it is a consequence of changing drivers of bird introductions. Historical introductions (those with a longer residence time) were more likely to be deliberate, and to be targeted to specific regions through the efforts of acclimatisation societies (Blackburn *et al.* 2009). More recent introductions are more likely to be a result of unintentional and untargeted releases from the pet trade (Dyer *et al*. in revision), and may therefore be more likely to occur over a larger area for a given number of introductions.

Body mass was included as a proxy for life history variation, as previous studies have shown that species with fast life histories (smaller body size, shorter development times, higher fecundity) tend to have larger alien range sizes (e.g. Duncan *et al.* 1999, Duncan *et al.* 2001, Allen *et al.* 2013). However, body mass was not related to alien range size in univariate models (Table S2), and was not consistently related to alien range size in multivariate models (Tables 1, S3).

The data used in this study are the best currently available for an entire major taxon, but nonetheless come with caveats. The maps of alien ranges on which these analyses are based represent Extents of Occurrence, rather than Areas of Occupancy (Gaston & Fuller 2009), and species are unlikely to be extant in every part of their total recorded alien range (as is the case with most commonly used native species range maps). The species analysed are likely to be at different stages in their alien range expansion (Blackburn *et al.* 2009), and many (or most) therefore may still be spreading from their point of introduction. Others may yet die out in the future. The measure of colonisation pressure may be influenced by higher or lower recording effort in certain regions. All of these issues add noise into our analyses, although we do not believe that they will have generated any of the results we present here as artefacts. The general consistency of our results across different biogeographic realms also suggests that these analyses are robust. The variables included within the best models for alien range size varied across realms (Table S3), but in general there was good consistency in the global (Table 1) and realm-level predictors of alien range size.

In conclusion, we have shown that of the seven hypotheses laid out in the Introduction, the only one to receive consistent and unequivocal support from our analyses is that bird species achieve larger alien geographic range sizes when they have been introduced more times. We also find strong support for the idea that whatever it is that causes native geographic range sizes to be larger also feeds through into larger alien range sizes. There is some evidence that alien geographic range size is related to residence time, but the expected positive effect is only recovered in univariate analyses (c.f. Table S2 with Tables 1, S3). We find little consistent evidence that alien range sizes are related to global climatic niche extent, body mass, specialism, or the size of the realm into which a bird species is introduced, although the effect of global climatic niche extent may be intertwined with that of native geographic range size. This information can be combined with studies concerning predictors of the impact of alien birds in order to identify those species that have the potential to have a high impact on native ecosystems. It is important that we understand the structure and mechanisms behind alien geographic ranges, so that we can more readily identify those alien species likely to spread. This will help to inform policy and conservation action by highlighting which species pose the greatest overall threat (Parker *et al.* 1999), and therefore where limited management funds should be targeted.

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Biosketch

Ellie Dyer is a macroecologist investigating the determinants of global patterns in alien bird assemblages. Her research interests concern topics in biodiversity, macroecology and conservation, including the biology and impacts of introduced and invasive species, but also large-scale patterns in the abundance and distribution of species more generally.

Table 1. The relationship between alien range size (km^2) and the predictor variable in the first column at the global scale, from full model averaging based on all possible multivariate PGLS models. Squared terms (^2) were included if they improved the fit of the univariate model as described in Figure 2. Estimate = the coefficient of the relationship between the predictor and response variables; s.e. = standard error; Importance = the sum of the Akaike weights across all models with ∆AICc < 4 of the best model; N = 319.

Variable	Estimate	s. e	Z value	P	Importance
Intercept	4.63	1.64	2.82	< 0.01	
Colonisation pressure	1.10	0.29	3.78	< 0.001	1
Colonisation pressure ^2	0.17	0.07	2.46	< 0.05	1
Global climatic niche extent	0.79	1.07	0.74	0.46	0.51
Native range size	0.17	0.12	1.41	0.16	0.78
Residence time	-0.29	0.20	1.49	0.14	0.85
Body mass	-0.002	0.03	0.07	0.94	0.18
Specialisation index	-0.002	0.08	0.03	0.98	0.17

Table 2. Variable importance (the sum of the Akaike weights across all models with ∆AICc < 4 of the best model) for the relationship between alien range size (km^2) and the predictor variable in the first column for each biogeographic realm separately, from full model averaging based on all possible multivariate PGLS models for each realm. Full details of the model for each realm is provided in Table S3.

Variable	Neotropical	Nearctic	Palearctic	Afrotropical	Indo-Malayan	Australasia	Oceania
Colonisation pressure	1	1	1	1	1	1	1
Native range size	0.56	0.52	0.18	0.15	0.84	1	1
Residence time	0.22	0.38	1	0.28	1	0.31	0.38
Body mass	0.17	0.22	0.88	0.73	0.17	0.25	0.32
Global climatic niche extent	0.27	0.38	0.34	0.30	0.26	0.41	0.51
Specialisation index	0.40	0.54	0.20	0.15	0.13	0.15	0.29

Figure 1. The frequency distribution of log-transformed total alien range sizes (km^2) for the 319 species included in the analysis. Total alien range size varied from 0.48 km^2 (*Cacatua sanguinea* on Saint John's Island, Singapore) to 36.49 x 10^6 km^2 (*Passer domesticus*) (mean = 0.38 x 10^6 km^2; median 10,460 km^2).

Figure 2*.* The relationship between log total alien range size (km^2) and **a)** log colonisation pressure (linear term slope estimate ± s.e. = 0.96 ± 0.29, *p*CI = 7.9 x 10^{-4}; squared term slope estimate ± s.e. = 0.21 ± 0.07, *p*CI = 1.7 x 10^{-4}); R^2 = 0.53, p <0.001; **b)** log residence time (years) (slope estimate ± s.e. = 1.39 ± 0.19, R^2 = 0.15, p <0.001, *p*CI = 0.002); **c)** sqrt global climatic niche extent (slope estimate ± s.e. = 5.83 ± 0.76, R^2 = 0.15, p <0.001, *p*CI = 0.007); **d)** log total native range size (km^2) (slope estimate ± s.e. = 0.57 ± 0.08; R^2 = 0.13, p <0.001, *p*CI = 0.002); **e)** log body mass (grammes) (slope estimate ± s.e. = 0.16 ± 0.15; R^2 = 0.00, p = 0.29, *p*CI = 0.02); and **f)** specialisation index (slope estimate ± s.e. = -1.01 ± 0.26; R^2 = 0.04, p <0.001, *p*CI = 0.002). The solid lines represent the univariate phylogenetic generalised least squares models (slope estimate), the dashed lines the models with a squared term, and the thin black line in **(d)** is the 1:1 line (alien range size = native range). s.e. = standard error. *p*CI = phylogenetic confidence interval. N = 319 for all standard errors and estimates.

Figure 1.

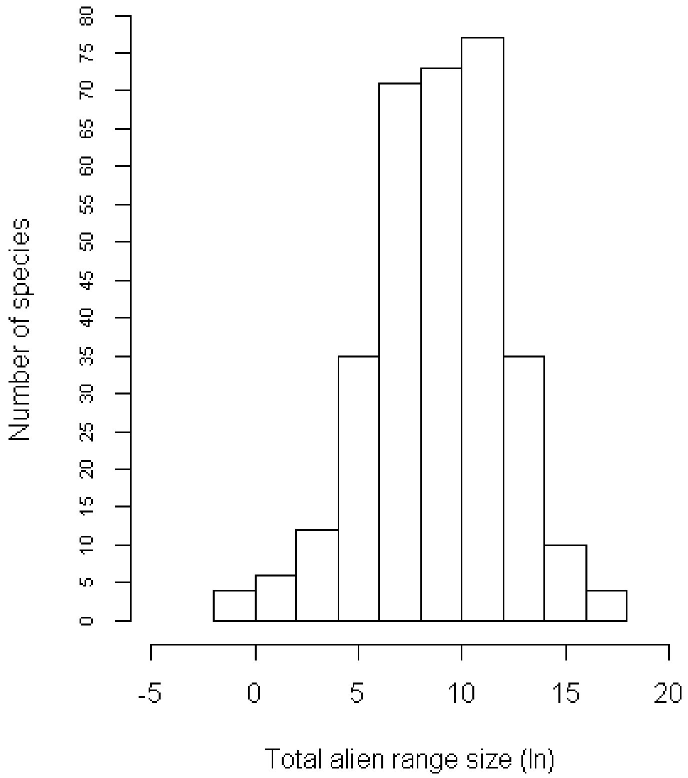

Number of species
0
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
80
-5
0
5
10
15
20
Total alien range size (ln)

Figure 2.

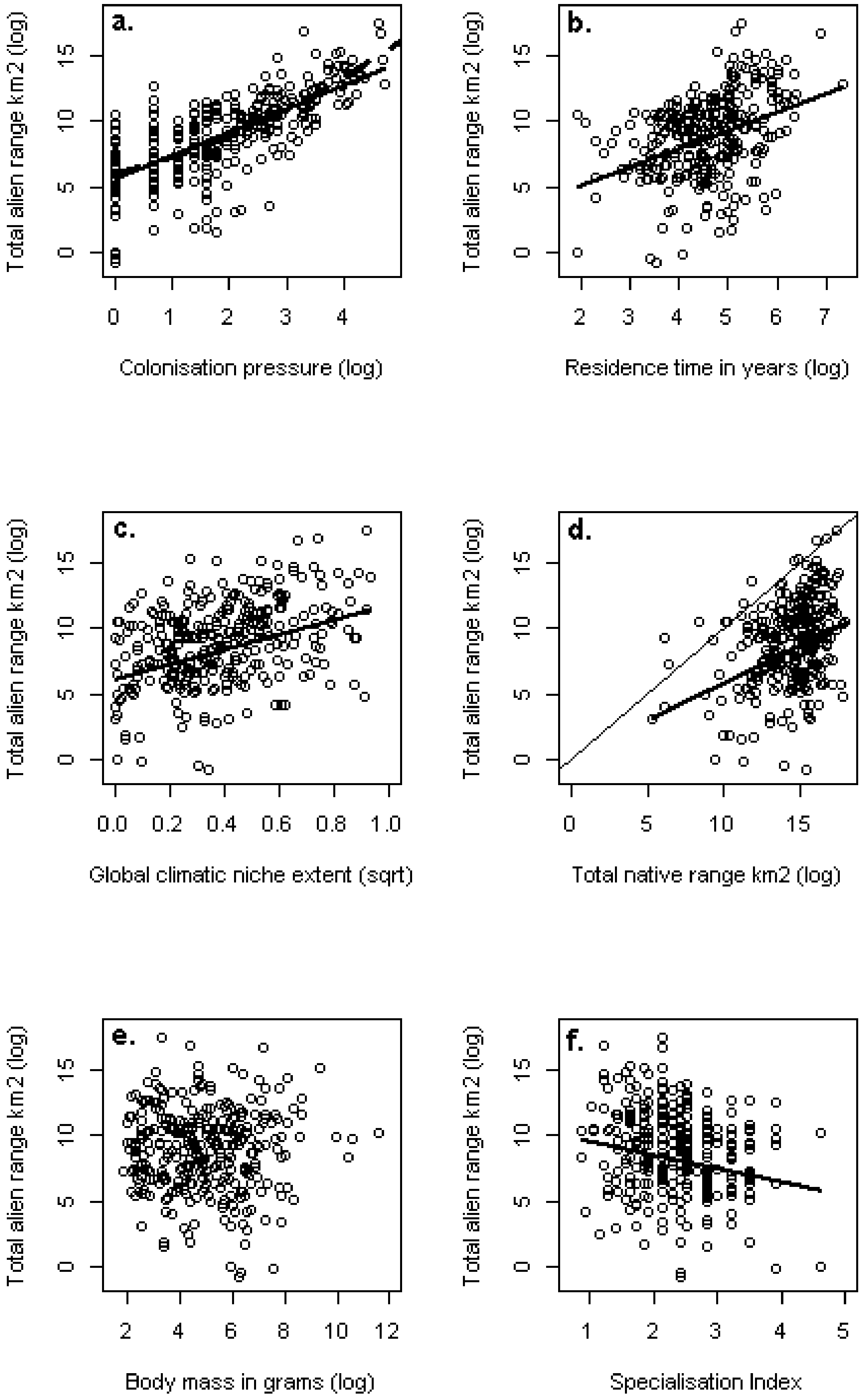

a.
Total alien range km2 (log)
0
5
10
15
0
1
2
3
4
Colonisation pressure (log)
b.
Total alien range km2 (log)
0
5
10
15
2
3
4
5
6
7
Residence time in years (log)
c.
Total alien range km2 (log)
0
5
10
15
0.0
0.2
0.4
0.6
0.8
1.0
Global climatic niche extent (sqrt)
d.
Total alien range km2 (log)
0
5
10
15
0
5
10
15
Total native range km2 (log)
e.
Total alien range km2 (log)
0
5
10
15
2
4
6
8
10
12
Body mass in grams (log)
f.
Total alien range km2 (log)
0
5
10
15
1
2
3
4
5
Specialisation Index

Table S1. Correlation matrix of all transformed predictor variables. Numbers above the diagonal are correlation coefficients (r); numbers below the diagonal are associated *P* values. N = 319 in all cases.

	Native range size	**Global climatic niche extent**	**Colonisation pressure**	**Residence time**	**Body mass**	**Specialisation index**
Native range size		0.84	0.26	0.21	0.00	-0.35
Global climatic niche extent	<0.001		0.30	0.25	0.04	-0.38
Colonisation pressure	0.12	0.08		0.60	0.00	-0.21
Residence time	0.22	0.15	0.00		0.06	-0.30
Body mass	0.98	0.84	0.98	0.71		-0.25
Specialisation index	0.04	0.02	0.21	0.07	0.13	

Table S2. Univariate PGLS relationships log between alien range size (km^2) and the predictor variable in the first column, at the global scale, and for bird species established in each biogeographic realm separately. Squared terms (^2) are reported if including them improved the fit for the model such that AICc is decreased by > 4 relative to a linear term alone. Estimate = the coefficient of the relationship between the predictor and response variables; s.e. = standard error. Sample sizes for each realm are as given in Table S3.

		Estimate ± s.e.	***P***	***R2***
Colonisation pressure (log)				
GLOBAL	linear squared	0.96 ± 0.29 0.21 ± 0.07	<0.01 <0.01	0.53
Afrotropical		1.63 ± 0.32	<0.001	0.28
Australasian		2.01 ± 0.27	<0.001	0.40
IndoMalay		1.65 ± 0.31	<0.001	0.24
Nearctic		2.21 ± 0.32	<0.001	0.38
Neotropical		1.56 ± 0.21	<0.001	0.39
Oceanic		1.07 ± 0.19	<0.001	0.23
Palearctic		1.64 ± 0.22	<0.001	0.39
Residence time (log)				
GLOBAL		1.39 ± 0.19	<0.001	0.15
Afrotropical		0.67 ± 0.31	<0.05	0.05
Australasian	linear squared	-13.59 ± 5.60 1.91 ± 0.67	<0.05 <0.01	0.27
IndoMalay	linear squared	-3.88 ± 1.46 0.56 ± 0.19	<0.01 <0.01	0.08
Nearctic		1.77 ± 0.47	<0.001	0.14
Neotropical		0.88 ± 0.25	<0.001	0.12
Oceanic		0.33 ± 0.30	0.27	0.00
Palearctic		1.18 ± 0.21	<0.001	0.26

Native range size (log)			
GLOBAL	0.57 ± 0.08	<0.001	0.13
Afrotropical	0.12 ± 0.22	0.59	0.00
Australasian	1.03 ± 0.15	<0.001	0.36
IndoMalay	0.29 ± 0.16	<0.1	0.03
Nearctic	0.52 ± 0.21	<0.05	0.06
Neotropical	0.58 ± 0.15	<0.001	0.15
Oceanic	0.28 ± 0.08	<0.001	0.10
Palearctic	0.20 ± 0.19	0.31	0.00
Global climatic niche extent (sqrt)			
GLOBAL	5.83 ± 0.76	<0.001	0.15
Afrotropical	1.73 ± 1.09	0.12	0.02
Australasian	3.02 ± 1.19	<0.05	0.06
IndoMalay	1.99 ± 1.01	<0.1	0.03
Nearctic	4.27 ± 1.28	<0.01	0.12
Neotropical	2.32 ± 1.04	<0.05	0.05
Oceanic	0.75 ± 0.61	0.23	0.00
Palearctic	0.29 ± 0.88	0.74	0.00
Body mass (log)			
GLOBAL	0.16 ± 0.15	0.29	0.00
Afrotropical	-0.38 ± 0.19	<0.1	0.04
Australasian	-0.10 ± 0.27	0.71	0.00
IndoMalay	-0.08 ± 0.19	0.69	0.00
Nearctic	0.17 ± 0.26	0.52	0.00
Neotropical	-0.18 ± 0.16	0.28	0.00
Oceanic	0.08 ± 0.11	0.46	0.00
Palearctic	0.14 ± 0.15	0.33	0.00
Specialisation index			
GLOBAL	-1.01 ± 0.26	<0.001	0.04
Afrotropical	-0.37 ± 0.53	0.49	0.00
Australasian	-0.79 ± 0.57	0.17	0.01
IndoMalay	-0.59 ± 0.42	0.16	0.01
Nearctic	-1.01 ± 0.64	0.12	0.02
Neotropical	-1.12 ± 0.47	<0.05	0.05
Oceanic	-0.36 ± 0.29	0.21	0.01
Palearctic	-1.39 ± 0.45	<0.01	0.09

Table S3. The relationship between alien range size (km^2) and the predictor variable in the first column for each biogeographic realm separately, from full model averaging based on all possible multivariate PGLS models for each realm. Squared terms (^2) are reported if including them improved the fit of the univariate model as described in Table S2. Estimate = the coefficient of the relationship between the predictor and response variables; s.e. = standard error; Importance = the sum of the Akaike weights across all models with ΔAICc <4 of the best model. N = sample size for each realm.

Neotropical (N = 86)	Estimate	s.e.	Z value	P	Importance
Intercept	5.46	2.73	2.01	< 0.05	
Colonisation pressure	1.44	0.25	5.83	< 0.001	1
Global climatic niche extent	-0.24	0.77	0.31	0.76	0.27
Native range size	0.14	0.18	0.79	0.43	0.56
Residence time	0.04	0.13	0.28	0.78	0.22
Body mass	-0.01	0.07	0.11	0.91	0.17
Specialisation index	-0.20	0.35	0.56	0.57	0.40

Nearctic (N = 78)	Estimate	s.e.	Z value	P	Importance
Intercept	3.63	3.89	0.94	0.35	
Colonisation pressure	2.10	0.34	6.19	< 0.001	1
Global climatic niche extent	0.62	1.18	0.53	0.60	0.38
Native range size	0.16	0.21	0.75	0.45	0.52
Residence time	0.20	0.38	0.53	0.60	0.38
Body mass	0.01	0.09	0.16	0.87	0.22
Specialisation index	-0.46	0.58	0.79	0.43	0.54

Palearctic (N = 87)	Estimate	s.e.	Z value	P	Importance
Intercept	4.39	1.69	2.60	< 0.01	
Colonisation pressure	1.32	0.23	5.81	< 0.001	1
Global climatic niche extent	-0.26	0.60	0.43	0.67	0.34
Native range size	0.01	0.09	0.14	0.89	0.18
Residence time	0.93	0.21	4.35	< 0.001	1
Body mass	-0.22	0.13	1.66	< 0.1	0.88
Specialisation index	-0.05	0.20	0.23	0.82	0.20

Afrotropical (N = 64)	Estimate	s.e.	Z value	P	Importance
Intercept	6.11	1.83	3.33	< 0.001	
Colonisation pressure	1.66	0.36	4.57	< 0.001	1
Global climatic niche extent	0.27	0.67	0.40	0.69	0.30
Native range size	0.01	0.08	0.10	0.92	0.15
Residence time	-0.09	0.23	0.38	0.70	0.28
Body mass	-0.23	0.20	1.15	0.25	0.73
Specialisation index	0.02	0.21	0.09	0.93	0.15

Indo-Malayan (N = 85)	Estimate	s.e.	Z value	P	Importance
Intercept	6.11	3.67	1.67	< 0.1	
Colonisation pressure	2.05	0.36	5.63	< 0.001	1
Global climatic niche extent	0.30	0.84	0.35	0.72	0.26
Native range size	0.31	0.20	1.57	0.12	0.84
Residence time	-1.50	1.24	1.21	0.23	1
Residence time ^2	0.11	0.17	0.65	0.51	0.46
Body mass	-0.02	0.08	0.23	0.82	0.17
Specialisation index	0.001	0.15	0.01	0.99	0.13

Australasia (N = 81)	Estimate	s.e.	Z value	P	Importance
Intercept	-2.59	6.78	0.38	0.70	
Colonisation pressure	1.40	0.30	4.69	< 0.001	1
Global climatic niche extent	-0.66	1.13	0.59	0.56	0.41
Native range size	0.78	0.20	3.95	< 0.001	1
Residence time	-0.87	3.02	0.29	0.77	0.31
Residence time ^2	0.12	0.37	0.31	0.76	0.13
Body mass	0.03	0.08	0.36	0.72	0.25
Specialisation index	-0.01	0.17	0.04	0.97	0.15

Oceania (N = 109)	Estimate	s.e.	Z value	P	Importance
Intercept	3.50	1.66	2.11	< 0.05	
Colonisation pressure	1.04	0.19	5.38	< 0.001	1
Global climatic niche extent	-0.48	0.65	0.74	0.46	0.51
Native range size	0.26	0.08	3.04	< 0.01	1
Residence time	-0.12	0.23	0.51	0.61	0.38
Body mass	0.03	0.07	0.41	0.68	0.32
Specialisation index	0.06	0.18	0.34	0.73	0.29

Figure S1. The relationship, where significant, between log total alien range size (km^2) and **a)** log colonisation pressure; **b)** log total native range size (km^2); **c)** square root global climatic niche extent **d)** log residence time (years); **e)** log body mass (g); and **f)** specialisation index, for each realm separately. The coloured lines represent the fitted realm-level univariate PGLS models (with a squared term where significant): Afrotropical = red; Australasian = orange; Indo-Malayan = pink; Nearctic = blue; Neotropical = green; Oceanic = purple; Palearctic = navy.

Figure S2. The relationship between global climatic niche extent (proportion of total global landmass) and native geographic range size (km^2) for the 319 bird species with established alien populations in our analysis.

Figure S1.

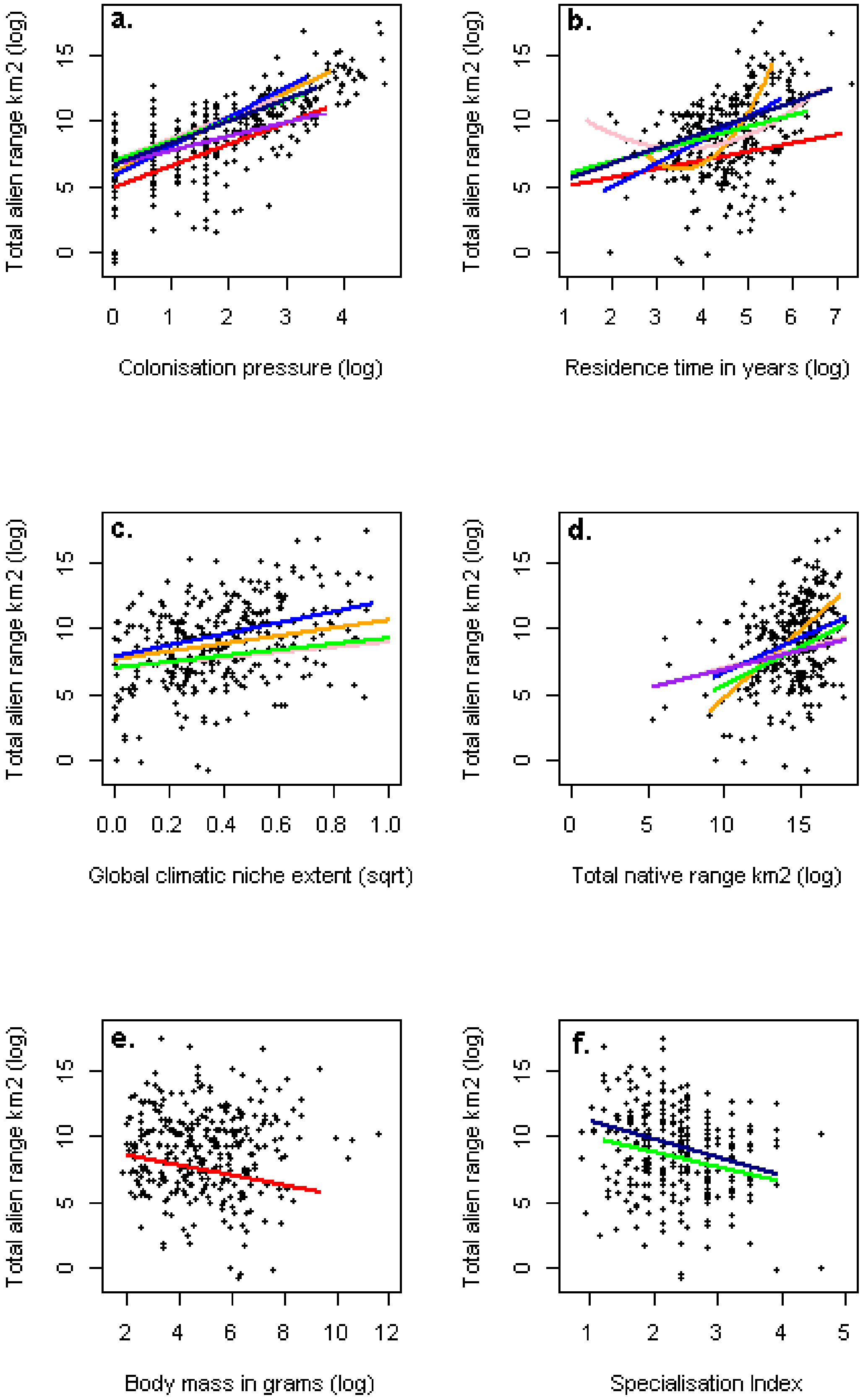
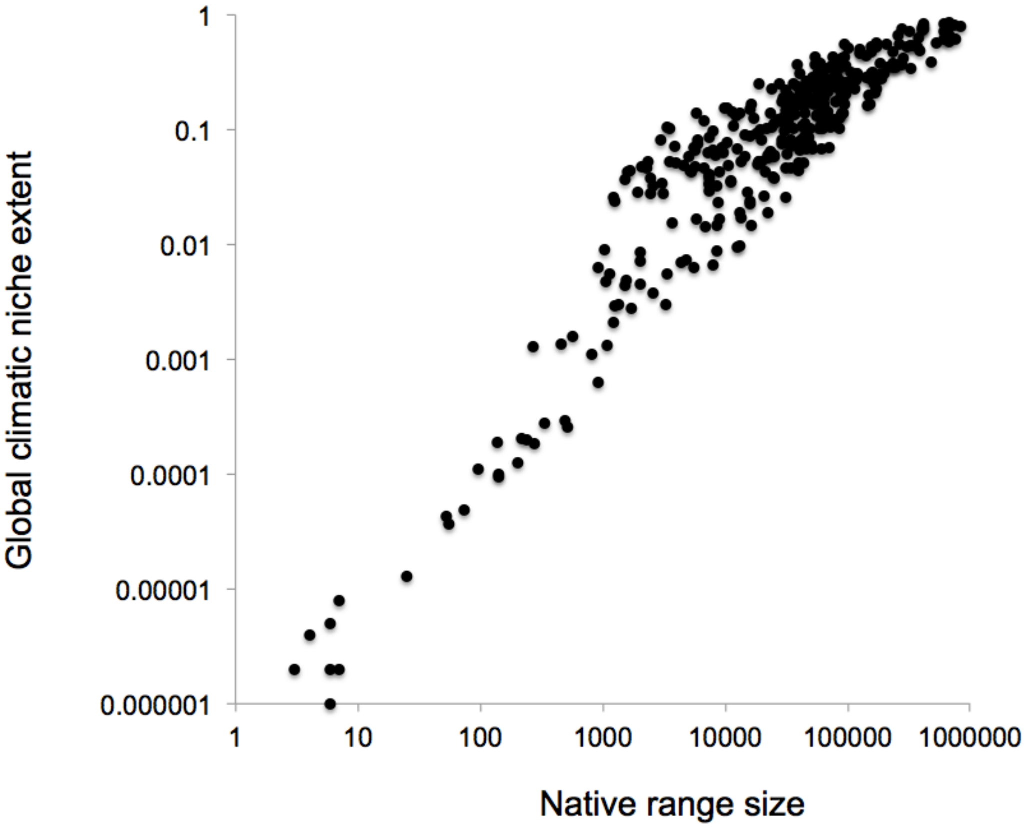

a.
Total alien range km2 (log)
0
5
10
15
0
1
2
3
4
Colonisation pressure (log)
b.
Total alien range km2 (log)
0
5
10
15
1
2
3
4
5
6
7
Residence time in years (log)
c.
Total alien range km2 (log)
0
5
10
15
0.0
0.2
0.4
0.6
0.8
1.0
Global climatic niche extent (sqrt)
d.
Total alien range km2 (log)
0
5
10
15
0
5
10
15
Total native range km2 (log)
e.
Total alien range km2 (log)
0
5
10
15
2
4
6
8
10
12
Body mass in grams (log)
f.
Total alien range km2 (log)
0
5
10
15
1
2
3
4
5
Specialisation Index

Figure S2.



1
0.1
0.01
0.001
0.0001
0.00001
0.000001
Global climatic niche extent
1
10
100
1000
10000
100000
1000000
Native range size