# Location-level processes drive the establishment of alien bird populations worldwide

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**Human-mediated translocation of species to areas beyond their natural distribution (here termed aliens[1]) is a key signature of the Anthropocene[2] and a primary driver of global biodiversity loss and environmental change[3]. Stemming the tide of invasions requires understanding why some species fail to establish alien populations, while others succeed. To achieve this, we need to integrate the impact of features of the introduction site, the species introduced, and the specific introduction event. However, determining which, if any, location-level factors affect establishment success has proved difficult due to the multiple spatial, temporal and phylogenetic axes along which environmental variation may influence population survival. Here, we apply Bayesian hierarchical regression analysis to a global spatially and temporally explicit database of alien bird introduction events[4] to show that environmental conditions at the introduction location, climatic suitability, and the presence of other alien species groups are the primary determinants of establishment success. Species-level traits and founding population size (propagule pressure) exert secondary, but still important, effects on success. Thus, current trajectories of anthropogenic environmental change will most likely facilitate future incursions by alien species, but predicting future invasions will require integrating multiple location, species, and event-level characteristics.**

Globally, alien species are accumulating at ever-increasing rates[5], mainly driven by growing trade and transport connectivity[6]. Once an alien species is established (i.e. self-sustaining) in a new location, the economic and environmental costs of eradicating it or controlling its spread are often prohibitive[3]. Understanding the processes that facilitate or inhibit the initial establishment of alien species is therefore a critical step in limiting the future threat of biological invasions. Most early attempts to predict alien species establishment focussed on the characteristics of the introduced species or the introduction location[7], but with limited success[8], and did not consider the key role of idiosyncratic "event-level" factors, notably propagule pressure[9]. Some species-level traits (life history[10], behavioural[11] and ecological[12]) have subsequently been shown to explain variation in alien establishment success. However, determining which, if any, location-level factors affect success generally at a global level and across large taxonomic groups has proved challenging, for several reasons.

First, many different biotic (e.g. recipient assemblage composition[13]) and abiotic (e.g. climate[14], disturbance[15]) factors may be important. Second, these factors vary across both space and time, and drive differences in susceptibility at a range of levels of biological organisation – population (e.g. stochastic weather events), species (e.g. climatic affinity), community (e.g. native species richness), and landscape (e.g. habitat composition). Third, how a new environment interacts with a species is dependent on the evolutionary and adaptive history of the species introduced[16]: a harsh environment for a house sparrow (*Passer domesticus*) may or may not be harsh for the closely related Eurasian tree sparrow (*P. montanus*), and vice versa. Fourth, alien introductions happen in synergy with other major anthropogenic environmental changes such as increasing human population density, agricultural land conversion, and the presence of other alien species[17]. Yet, despite this apparent complexity, many previous analyses have treated location-level variables in a relatively simplistic way, considering either only coarse features of locations (e.g. latitude[18], island versus continent[19]) or gross differences between native and alien environments[20], and typically ignore spatial autocorrelation[21]. Therefore, we still await an integrated analysis of variation in alien establishment.

Here, we undertake a global analysis to identify both the absolute and relative contributions of location, species, and event-level processes in predicting alien establishment. Using birds as a model system, we interrogate data on the success or failure of 4,346 individual introduction events spanning 708 species and, crucially, include information on propagule pressure, the key event-level driver of establishment[9]. To assess the specific influence of location, we consider a wide array of abiotic, biotic and anthropogenic factors. These account for both the mean and temporal variability in the abiotic environment, the suitability of the environment in terms of its similarity to conditions experienced by a species in its native range (‘environmental match’), metrics of human disturbance, and the characteristics of recipient biological communities, including both their diversity and their phylogenetic similarity to each introduced species. Finally, we incorporate aspects of species’ life history, behaviour and ecology that have previously been hypothesised to explain establishment success in alien birds. Features of introduction events are not random with regard to the identity, relatedness and characteristics of the species introduced[16], their spatial location of origin and introduction[4], nor to propagule pressure[22], and so we undertake this analysis using Bayesian hierarchical regressions, inferred using Integrated Nested Laplace Approximation (INLA)[23]. This method provides efficient and accurate parameter estimation for complex inferences incorporating both random and fixed effects, allowing us to control for spatial and temporal non-independence in the abiotic and biotic features of locations, and for taxonomic non-independence in species traits.

At a global scale, combinations of location-, species- and event-level variables are selected as important terms across all fitted models, including the best fitting model of avian establishment success (Fig. 1, Extended Data Table 1, n = 1530, $_{w}$AIC = 892.96, AUC = 0.75 – for definitions see methods). This result was robust to the precise way in which introduction events were defined (Extended Data Fig. 1) and highlights that alien establishment cannot be adequately explained by characteristics of the environment, the species, or the specific introduction event in isolation. The most strongly supported individual determinant of establishment is the environment of the recipient location (Fig. 2a). Within this category, anthropogenic features, followed by climatic suitability, have the greatest influence on establishment success (Fig. 2b).

A strong anthropogenic determinant of establishment success is the number of alien taxonomic groups already established at a location at the time of introduction. The positive effect of the number of alien groups introduced is broadly consistent with the invasion meltdown hypothesis[17], whereby ecological disruptions caused by, or enabling, earlier invasions facilitate further successful introductions. This result is not simply indexing anthropogenic environmental disturbance; crop coverage and human population density, while included in the best fitting model, did not have a strong and consistent global signal for alien establishment success (Fig. 1, Extended Data Fig. 2). This may be due to historical patterns of introductions being mainly restricted to already disturbed areas[12]. In fact, our analysis shows that *less* disturbed areas have higher establishment success rates, with rapid agricultural land-conversion not only causing native species declines[2], but also negatively impacting alien species, at least in the early stages of the invasion process.

Previous evidence has suggested that species are more likely to establish when they are pre-adapted to local climatic conditions[16] and our analysis confirms this hypothesis. We found that alien establishment success is highest in locations where environmental conditions are more similar to those in the species' native range ('environmental match', Fig. 1-2), albeit with the proviso that average conditions across the range are relatively crude measures of climatic preferences. Our analysis also suggests a hump-shaped effect of mean annual temperature on establishment (Fig. 1). This relationship implies a "Goldilocks effect", such that locations with intermediate conditions are more amenable to establishment than those that are too hot or too cold, regardless of the conditions naturally experienced by each species. Environmental extremes are also important[24], with establishment success reduced by the occurrence of historical storm events in the period immediately following introduction. Anecdotal evidence had previously suggested extreme weather as a cause of specific establishment failures (e.g., the house crow (*Corvus splendens*) on Mauritius[25]), and our spatiotemporal analysis identifies this as a general effect in the global record of avian introductions.

The extent to which communities differ in their biotic resistance to introduced species has remained controversial, with studies variously reporting positive, negative or no effects of local species richness on patterns of establishment[26]. Overall, we found that the biotic environment had a relatively weak effect on establishment compared to the other location-, species- and event-level factors. Nevertheless, accounting for these other factors revealed a potential negative effect of native bird species richness on alien establishment success, with this switching to a hump-shaped relationship (Fig. 1) when considering only the most closely related and presumably ecologically similar species. These results help clarify previous contradictory findings, by showing that while overall native biodiversity may inhibit invasions, (i) this effect is relatively weak compared to other extrinsic and intrinsic factors, and (ii) it may be partially masked by the tendency for locations with many closely related species to be more environmentally suitable, and thus be more susceptible to establishment (i.e. biotic acceptance hypothesis[17]).

In addition to environmental factors, features of the species' life history and ecology are strongly supported as determinants of establishment success. In particular, larger brood sizes promote establishment, while lifespan showed a hump-shaped relationship with invasion success (Fig. 1, Extended Data Fig. 2), confirming previous evidence of a trade-off between the benefits of fast and slow life histories[10]. While species with fast life histories can gain a quick 'foothold' at a new location through rapid population growth, slower life histories give resilience against demographic and environmental variation, allowing alien populations to be better able to ride out extreme conditions[27,28]. In our model, there is also evidence that foraging specialism and habitat-use generalism may, taken together, increase establishment success. Life history variables are generally strongly phylogenetically conserved (e.g. brood size, $\lambda = 0.96$, Fig. 3), implying that related species could have similar rates of establishment success. However, globally, establishment success has a much weaker phylogenetic signal ($\lambda = 0.4$; Fig. 3), due to phylogenetically conserved traits being overwhelmed by the combined spatial effects of the local environment and propagule pressure, all of which tend to exhibit little phylogenetic signal. The inherently idiosyncratic nature of these effects with regard to the identity of the species introduced (Spearman $\rho$ between predictions based on life history and the final model is 0.64) explains why it has proven difficult to identify consistent life history predictors of establishment in isolation[29].

Lastly, we confirm the strong general role of propagule pressure which, in line with previous work on alien birds[30], is best represented by an asymptotic log-term (Fig. 1, Extended Data Fig. 2): small founding populations are likely to fail due to stochastic and Allee effects, while the success of larger populations[30] depends instead on the species- and location-level effects we identify here. Our analysis highlights the key role of the presence of other alien species groups, suggesting that locations that are already hotspots for introductions are especially susceptible to accumulating alien species**,** but also show that alien species are more likely to establish when they are pre-adapted to local climatic conditions. Growth in global trade means that an ever-growing number of species are being introduced to novel locations[4,31], and the environmental matches of ever more species are being tested against new environments. These trajectories will facilitate future incursions by alien species, exhibiting features of an invasion meltdown[32], which, as we show, could be further exacerbated depending on precise combinations of species and sites where the introductions are occurring. Our analyses confirm the urgent need for enhanced management programs to prevent or mitigate the negative impact of these invasions.

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**Supplementary Information** is available in the online version of the paper.

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**Fig. 1. Posterior distributions for fixed effects parameter estimates for the best fitting model of alien bird establishment success**. Boxplots summarise the posterior marginal distributions for all fixed-effects parameters ($\beta$) from a Bayesian regression of the most conservative data subset (n = 1530 introductions). Box widths show the interquartile range, the mean is represented as a bold vertical line within each box, and whiskers the 2.5th and 97.5th percentiles (i.e. the 95% credibility interval) of the distribution. Colours indicate the fixed effect category, and bold y-axis labels indicate that there is evidence for a non-zero slope for the described data variable. Further details are in Extended Data Table 1.

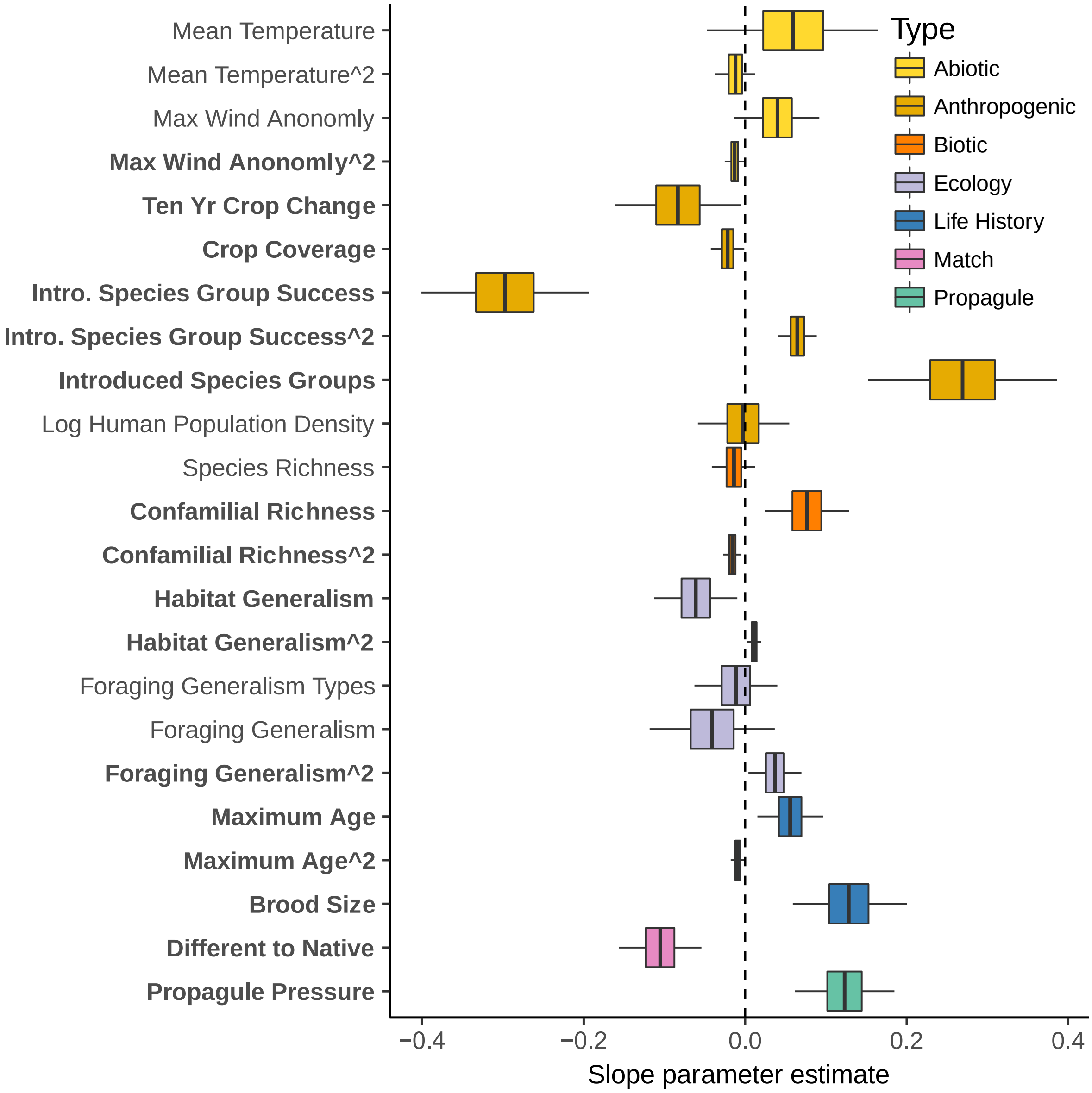

**Fig. 2. Relative effect size of different categories of predictors in the best fitting model of alien bird establishment success.** Each wedge represents the sum of the change in $_w$AIC for the fixed effects in each category when added to a Bayesian regression of establishment success versus failure (n = 1530 introductions). The left-hand panel (a) presents variables classified into location-, species- and event-level categories, while the right-hand panel (b) presents the sub-categories within those broad levels (n = 1530 introduction events).

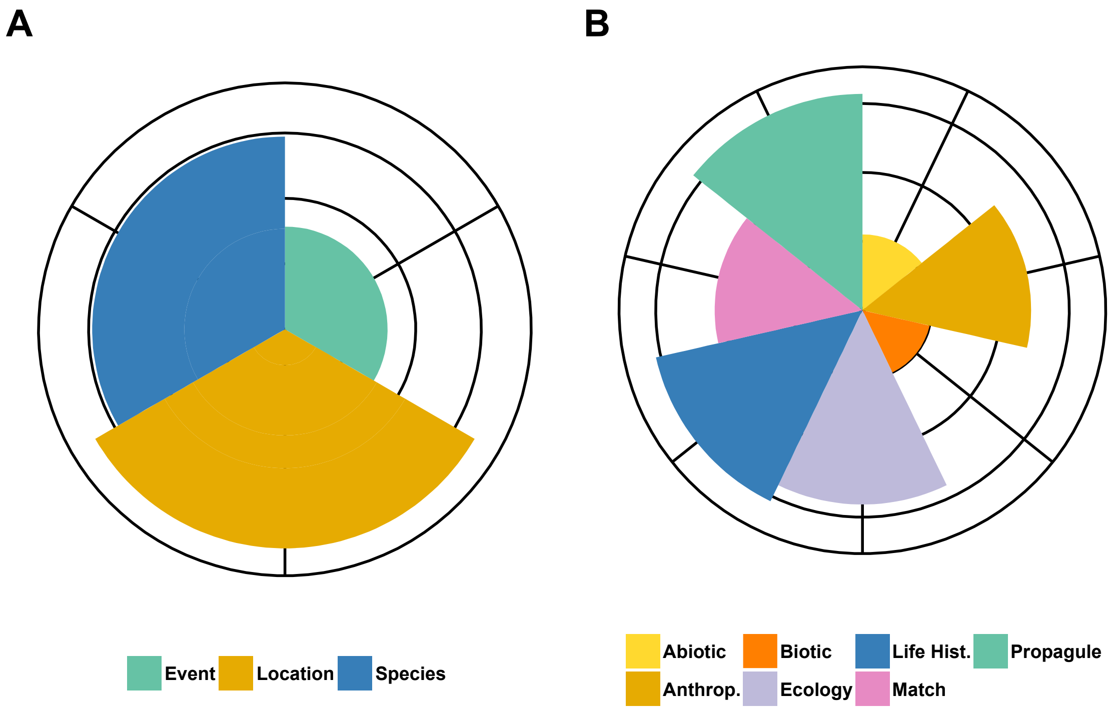

**Figure 3. Phylogenetic patterns of invasion probability across alien birds.** Shows 358 species with the highest quality information on introduction events. Blue-green-yellow outer bars show the mean establishment potential of a species across all 1-degree grid cells beyond its native range, with longer and yellower bars indicating that a species has greater potential to establish outside its native range. Phylogenetic branches are coloured according to brood size, with lighter colours indicating higher brood sizes, and darker colours lower brood sizes. Silhouettes (from http://phylopic.org/) show the approximate location of avian families.