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Pigot, A.L., Dyer, E.E., Redding, D.W. et al. (3 more authors) (2018) Species invasions and the phylogenetic signal in geographical range size. Global Ecology and Biogeography, 27 (9). pp. 1080-1092. ISSN 1466-822X

https://doi.org/10.1111/geb.12768

Received: 22 July 2017 | Revised: 6 February 2018 | Accepted: 14 March 2018

DOI: 10.1111/geb.12768

RESEARCH PAPER

WILEY Global Ecology and Biogeography A Journal of Macroecology

Species invasions and the phylogenetic signal in geographical range size

Alex L. Pigot[1] | Ellie E. Dyer[1] | David W. Redding[1] | Phillip Cassey[2] | Gavin H. Thomas[3] | Tim M. Blackburn[1,4]

[1] Department of Genetics, Evolution and Environment, Centre for Biodiversity and Environment Research, University College London, London, United Kingdom

[2] Centre for Conservation Science and Technology, School of Biological, Sciences, University of Adelaide, South Australia, Australia

[3] Department of Animal and Plant Sciences, University of Sheffield, Sheffield, United Kingdom

[4] Institute of Zoology, Zoological Society of London, London, United Kingdom

Correspondence
Alex L. Pigot, Centre for Biodiversity and Environment Research, Department of Genetics, Evolution and Environment, University College London, London, United Kingdom.
Email: alex.pigot1@gmail.com

Funding information
Leverhulme Trust, Grant/Award Number: RPG-2015-392.

Abstract

Aim: Accelerating rates of anthropogenic introductions are leading to a dramatic restructuring of species distributions globally. However, the extent to which invasions alter the imprint of evolutionary history in species geographical ranges remains unclear. Here, we provide a global assessment of how the introduction, establishment and spread of alien species alters the phylogenetic signal in geographical range size using birds as a model system.

Location: Global.

Time period: Contemporaneous.

Taxa: Birds.

Methods: We compare the phylogenetic signal in alien range size with that of native distributions of species globally (n = 9,993) and across different stages in the invasion pathway, from introduced (n = 965) to established species (n = 359). Using stochastic simulations, we test whether differences in phylogenetic signal arise from nonrandom patterns of species introduction, establishment or spread.

Results: Geographical range size in birds exhibits an intermediate phylogenetic signal, driven by the spatial clustering of closely related species. Nonrandom introductions, biased towards wide-ranging species from particular clades and regions, produce an anomalously strong phylogenetic signal in the native range size of introduced species. In contrast, the phylogenetic signal in alien range size is substantially weaker than for native distributions. This weak phylogenetic signal cannot be explained by a lack of time for dispersal but is instead regulated by phylogenetic correlations across species in the location and number of introduction events.

Main conclusions: We demonstrate that the effects of anthropogenic introductions on the phylogenetic signal in range size vary across different stages in the invasion pathway. The process of transport and introduction amplifies the phylogenetic signal in the pool of potential invaders, whereas the subsequent pattern of spread decouples variation in alien range size from phylogenetic ancestry. Together, our findings suggest that evolutionary relatedness is likely to be a relatively weak predictor of the spread of invasive species.

KEYWORDS
birds, geographical range size, invasive species, null model, phylogenetic signal, species introductions

1 | INTRODUCTION

The geographical distributions of species are shaped both by the current environment and by their evolutionary history (Gaston, 2003). Over recent centuries, the introduction of species to novel locations beyond their natural geographical range has become an increasingly important force shaping the distribution of life on Earth (Seebens et al., 2017). This anthropogenic dismantling of biogeographical barriers is leading to the mixing of previously distinct evolutionary biotas, driving some species to extinction (Bellard, Cassey, & Blackburn, 2016) and fundamentally altering the phylogenetic structure of species assemblages (Capinha, Essl, Seebens, Moser, & Pereira, 2015). Nonetheless, how and to what extent the signature of evolutionary history in the size and location of species geographical distributions is altered by anthropogenic introductions remains unclear.

The size of the geographical range of species often exhibits a moderate but detectable phylogenetic signal, whereby range sizes are more similar amongst closely related species than amongst distant relatives (Abellán & Ribera, 2011; Gaston, 1998; Hunt, Roy, & Jablonski, 2005; Machac, Zrzavý, & Storch, 2011; Webb & Gaston, 2005). This phylogenetic signal in range size is often explained as a result of heritable intrinsic traits, such as dispersal ability or niche breadth, that determine the potential geographical range that a species can maintain (Jablonski, 1987). In addition, range sizes are expected to vary predictably with evolutionary relatedness because closely related species tend to arise in the same geographical region and are thus subject to the same environmental and biogeographical barriers (Freckleton & Jetz, 2009). While heritable intrinsic traits and spatial location should promote phylogenetic signal in range size, random dispersal events and speciation may decouple variation in range size from evolutionary relatedness (Pigot, Phillimore, Owens, & Orme, 2010; Waldron, 2007). In particular, the isolation of peripheral populations during speciation can result in daughter species initially having very different range sizes (Pigot, Phillimore, et al., 2010). This asymmetry is expected to diminish over time, either as species with small geographical ranges go extinct or as species expand their distributions to reach the limits imposed by the environment and their intrinsic traits (Waldron, 2007). The finding that phylogenetic signal in range size is stronger than expected under null models of speciation (Waldron, 2007) supports the controversial idea that geographical range size might be a heritable property of species, with important implications for understanding the past and future dynamics of biodiversity (Jablonski, 1987).

How anthropogenic species invasions alter the phylogenetic signal in range size remains unclear because different aspects of the invasion process may have potentially contrasting effects on alien range size and how it varies with evolutionary relatedness. In the case of birds, there is evidence that the phylogenetic signal in alien range size may be substantially weaker than is typical of avian species in their native distributions (Dyer et al., 2016). Such a pattern may be expected, because the process of human introduction bears some resemblance (but see Wilson et al., 2016) to the natural process of speciation that tends to weaken phylogenetic signal in native range size. In particular, most invasions are initiated by small founding populations; therefore, a strong phylogenetic signal in alien range size might emerge only amongst species that were introduced long ago and that have had sufficient time to expand their distributions to the limits imposed by their intrinsic traits or the environment (Byers et al., 2015; Wilson et al., 2007). However, differences in species residence times or other aspects of the anthropogenic introduction process could also have a positive effect on phylogenetic signal depending on their relative phylogenetic patterning. The number of introduction attempts is known to be an important determinant of alien range size (Dyer et al., 2016; Lockwood, Cassey, & Blackburn, 2005; Williamson et al., 2009). To the extent that closely related species tend to share characteristics (e.g., life history traits) that make them more or less likely to be introduced (Allen, Street, & Capellini, 2017), a phylogenetic signal in introduction effort would act to promote a phylogenetic signal in the range size attained by alien species. Alternatively, if differences in range size are primarily determined by geographical location (Machac et al., 2011), then the consequences of invasion will depend on the phylogenetic clustering of species introductions in space. If the introduction of closely related species occurs to widely scattered regions across the globe, then this would further decouple variation in alien range size from evolutionary ancestry regardless of the time available for their dispersal.

The examination of how invasions alter the phylogenetic signal in species range size is complicated by the fact that invasion is a multistage process, and differences in phylogenetic patterns can therefore arise through a variety of different routes (Blackburn et al., 2011; Figure 1a). In particular, although differences in phylogenetic signal between the native and alien ranges of established species must reflect processes operating post-invasion, broader comparisons of patterns in phylogenetic signal (e.g., between alien and nonintroduced native species) require accounting for the fact that introduced species and/or those that successfully establish represent a nonrandom subset of species in terms of their traits, evolutionary history or geographical origin (Allen et al., 2017; Duncan, Blackburn, & Sol, 2003; van Kleunen et al., 2015; Figure 1a). For instance, in the case of birds, certain taxonomic families (e.g., pheasants, ducks) and geographical regions (e.g., Palearctic, Nearctic) have disproportionately been sources of introductions (Dyer, Cassey, et al., 2017), whereas successful establishment is known to depend on a variety of intrinsic life history traits (Sol et al., 2012), and thus is also nonrandom with respect to phylogeny. These biases in introduction and establishment could in theory either amplify or dampen differences in phylogenetic signal between alien and native species. Another potential source of bias is that introductions are more likely to involve widespread species than those that are geographically restricted (Blackburn & Duncan, 2001b; Blackburn, Lockwood, & Cassey, 2009; Pyšek et al., 2009). If small range size is a symptom of recent speciation, and speciation tends to decouple variation in range size from evolutionary relatedness (Pigot, Phillimore, et al., 2010), then by selecting more widespread species the process of human introductions may impart an anomalously strong phylogenetic signal to the range size of established species. Separating these alternative explanations is challenging because it

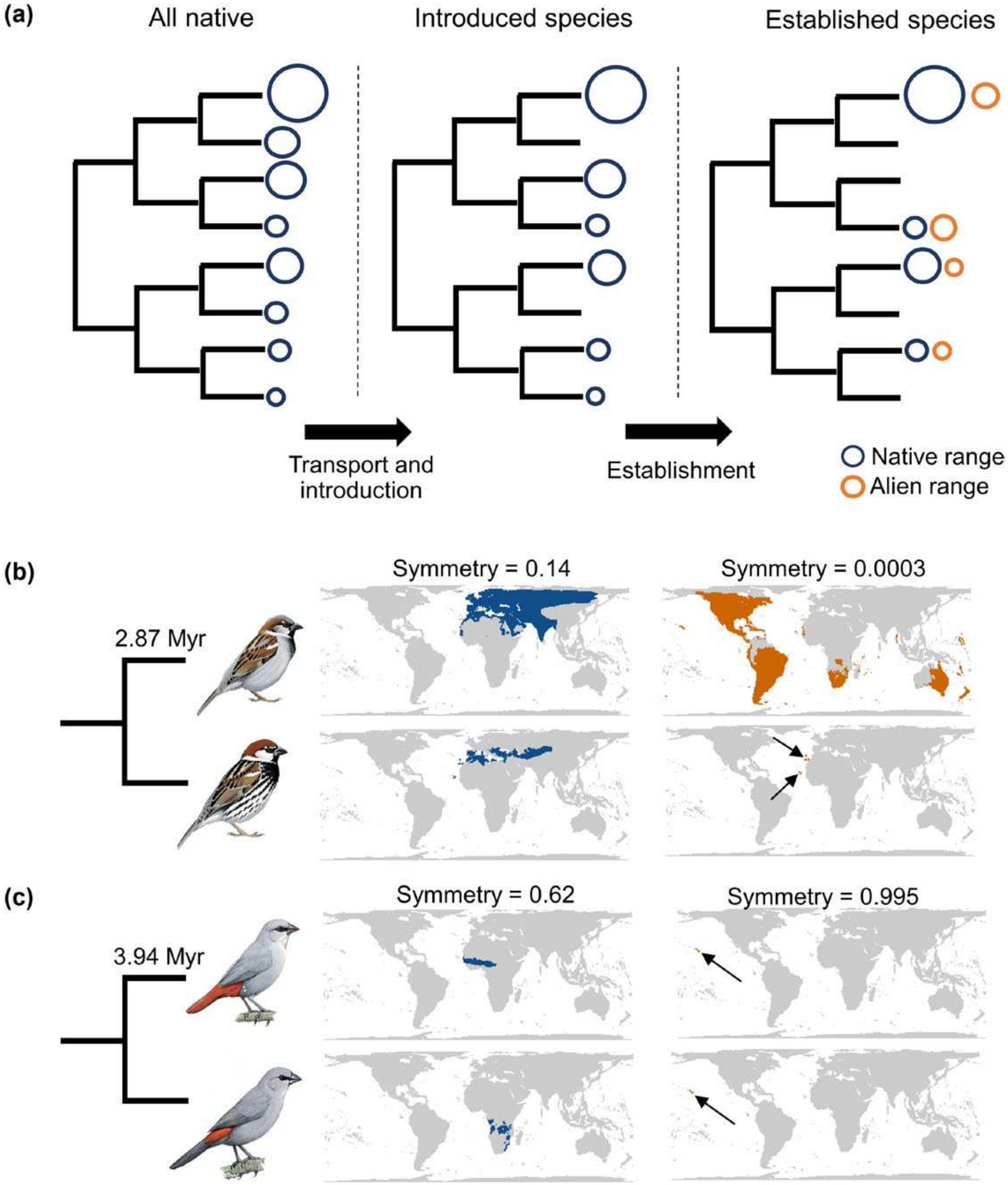

FIGURE 1 Phylogenetic signal in species geographical range size across the invasion pathway. (a) Cartoon phylogenies showing how evolutionary ancestry relates to the range size (circle size) of all species in a clade (all native), those species that have been introduced to new locations by human activity (introduced species) and those species that have established alien populations in these new locations (established species). Established species potentially have a distinct phylogenetic signal in their native (blue) and alien (orange) ranges. (b and c) Amongst established species, the symmetry in range size between sister pairs (i.e., species that are each other's closest relatives) may differ between native and alien distributions. Range size symmetry (area of smaller species range/area of larger species range) varies between zero and one, with higher values indicating ranges that are more similar in size. Shown are examples of where range size symmetry is either (b) lower [*Passer domesticus* (top) *and Passer hispaniolensis* (bottom)] or (c) higher [*Estrilda coerulescens* (top) and *Estrilda perreini* (bottom)] in alien compared with native distributions. Phylogenetic branching times are in millions of years. Bird illustrations are reproduced from *Handbook of the birds of the world* with the permission of Lynx Edicions (Del Hoyo et al. 2018) [Colour figure can be viewed at wileyonlinelibrary.com]

requires information not only on the range size of species that have successfully established, but also on the range size of those introduced species that failed to establish (Figure 1a). Unfortunately, information on these failed invasions is rarely available.

Here, we overcome this challenge by using a unique database, the Global Avian Invasion Atlas, which contains records of all known avian introductions and the geographical distributions of all established alien species (Dyer, Redding, & Blackburn, 2017). When combined with globally complete data on the native geographical distributions (Birdlife International, 2012) and phylogenetic relationships of birds (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012), this allows us to assess how the phylogenetic signal in range size changes across different stages in the invasion pathway (Figure 1a). We specifically address the following three key objectives. First, we compare the phylogenetic signal in the native and alien range size of species (*n* = 359) using two complementary metrics that variously quantify the symmetry in range sizes amongst the most closely related tips (Waldron, 2007) and the phylogenetic signal across the entire phylogeny (Pagel, 1999; Figure 1). Second, we test the hypothesis that different phylogenetic signals in native and alien range size are driven by the distinct processes influencing the spread of alien species after their introduction, including the spatial location, timing and number of introduction attempts. To do this, we examine how the spatial location of alien species relates to their phylogenetic similarity and quantify the effects of differences in propagule pressure and residence times on symmetry in range size. Third, we test the hypothesis that differences in phylogenetic signal between native and alien ranges are driven by nonrandom patterns of species introduction and establishment. We compare the phylogenetic signal in the native and alien ranges of established species with the native ranges of both introduced species (*n* = 965) and the entire global avifauna (*n* = 9,993) (Figure 1a). We then use stochastic simulations to identify the stage(s) in the invasion pathway at which significant differences in phylogenetic signal arise, and the taxonomic and geographical biases causing these differences. Overall, our results demonstrate that the process of species invasion decouples variation in range size from species evolutionary ancestry but that this phenomenon is detectable only after accounting for biases in the history of species introductions.

2 | METHODS

2.1 | Phylogenetic and geographical data

We quantified evolutionary relatedness using the time-calibrated phylogeny of Jetz et al. (2012) (https://birdtree.org) based on the backbone topology of Hackett et al. (2008). We incorporated phylogenetic uncertainty by conducting our analysis across 100 phylogenies drawn at random from the posterior distribution. Throughout, all reported values represent the mean across these trees. Estimates of range size (in km^2) for the native breeding distributions of species (*n* = 9,993) were calculated based on expert opinion extent of occurrence maps (Birdlife International, 2012). Information on the identity and distribution of introduced and established bird species was extracted from the Global Avian Invasions Atlas (GAVIA) database (Dyer, Redding, et al., 2017). This database comprises 27,723 distribution records across 965 species for which there is evidence of introduction outside their native range, based on almost 700 published references and substantial unpublished information derived from consultation with organizations and experts worldwide. Introduced species in GAVIA are categorized into six states indicating invasion status (established, breeding, unsuccessful, died out, extirpated and unknown). Here, we focused on established species (i.e., those with self-sustaining populations) for which information on their geographical distribution was available (*n* = 359). We overlaid species ranges onto a recent biogeographical regionalization for birds (Holt et al., 2013) and assigned species to the realm in which the majority of their distribution falls (*n* = 9 realms).

2.2 | Quantifying phylogenetic signal in range size

We quantified phylogenetic signal in range size using Pagel's λ (Pagel, 1999) estimated in the R package MOTMOT (Thomas & Freckleton, 2012). The parameter λ represents a multiplier applied to the off-diagonal elements of the phylogenetic variance–covariance matrix and varies from zero, where the trait is independent of phylogeny, to one, where variation is consistent with a Brownian motion model of evolution. We estimated λ separately for the native and alien ranges of established species ($\lambda_{\text{Established native}}$ and $\lambda_{\text{Established alien}}$, *n* = 359) and for the native ranges of all bird species ($\lambda_{\text{All native}}$, *n* = 9,993) and those that have been introduced ($\lambda_{\text{Introduced native}}$, *n* = 965). In the phylogeny of Jetz et al. (2012), species lacking genetic sequence data were inserted according to taxonomic constraints. Any resulting error in inferred evolutionary relationships may lead to biased estimates of λ. To test whether this influenced our results, we recalculated λ for only those species represented by genetic data: All species (*n* = 6,670), introduced species (*n* = 859) and established species (*n* = 329). Native and alien range sizes were strongly right skewed and were $\log_{10}$ transformed before analysis.

2.3 | Quantifying symmetry in range size

In addition to λ, we calculated the symmetry in range size within pairs of closely related established species (hereafter "sister species", *n* = 115 pairs; Waldron, 2007; Webb & Gaston, 2005; Figure 1b and c). Although not true sister species, these pairs represent lineages that are each other's closest relatives amongst the set of established species. Symmetry was calculated separately for native and alien ranges, as the area of the smaller species range divided by the area of the larger species range. According to this metric, a stronger phylogenetic signal should be reflected in sister species having more similar (i.e., symmetric) range sizes. Here, we compare range symmetry only between the native and alien ranges of established species, rather than across different stages in the invasion pathway. Estimates of range symmetry are not comparable across these different subsets because "sister species" would differ greatly in their average phylogenetic separation (all birds = 3.47 Myr, introduced species = 6.82 Myr, established species = 7.92 Myr).

2.4 | Testing for differences in phylogenetic signal and symmetry between native and alien ranges

To test whether there was a significant difference in λ between native and alien distributions of species, we compared the fit of a model in which the value of λ could differ between groups (n = 2 parameters) with a null model assuming a single global λ (n = 1 parameter). Relative model fit was assessed using the Akaike information criterion (AIC), where an AIC difference (ΔAIC) ≥ 2 indicates substantial support for the more complex model. In addition, we also report AIC weights (AICW), which quantify the relative probability that each model is correct given the set of models being compared.

We tested for a significant difference in range size symmetry (logit transformed) between the alien and native ranges of sister species using a mixed model including species pair as a random effect, enabling us also to examine possible factors driving differences in range size symmetry. In particular, the larger range size of species in their native distribution (Dyer et al., 2016) could potentially lead to differences in symmetry; therefore, we included the area of the larger species range ($\log_{10}$ transformed) within each pair as a predictor (as both a main effect and an interaction term) in the model. Models were fitted using the R package lme4 (Bates, Mächler, Bolker, & Walker, 2015). In addition, we aimed to test whether asymmetries in alien range size could arise from differences in the number of years since species were first introduced (i.e., residence time) or the total number of introduction attempts over this period (i.e., propagule number) (Dyer et al., 2016). To test this, we modelled symmetry in alien range size as a function of symmetry in residence time and propagule number. In each case, symmetry was calculated as the ratio of the smaller (e.g., residence time of the more recent introduction) to the larger (e.g., residence time of the older introduction) species value. Finally, we calculated the phylogenetic signal λ in residence time and propagule number after $\log_{10}$ transformation.

2.5 | Testing for differences in the spatial and phylogenetic components of native and alien ranges

In addition to the effects of phylogenetically conserved traits, a phylogenetic signal in native range size is expected because closely related species are generally clustered in space (Freckleton & Jetz, 2009). Consequently, if species are introduced to different locations at random with respect to phylogeny, this would weaken the phylogenetic signal in alien range size. We examined this possibility in two ways. First, we tested the hypothesis that introduction locations are random with respect to phylogeny by calculating the spatial overlap between sister species in both their native and alien distributions. For each group, we compared the frequency of spatial overlap with that expected under a null model in which species ranges were randomly reassigned to species (1,000 replicate simulations). Overlap scores were calculated as the area of overlap divided by the area of the smaller species range (Pigot, Tobias, & Jetz, 2016), as follows:

$$\text{Overlap}\,\% = \frac{A1 \cap A2}{\min(A1, A2)}$$

where $A1$ and $A2$ are the range sizes of the two species. Second, we jointly quantified the variation in range size that is uniquely structured according to either space (Φ) or phylogeny (λ') or that is independent of both components (γ), using the approach of Freckleton and Jetz (2009). Within this framework, Φ quantifies the proportion of the variance in range size attributable to spatial location (0 = no spatial effect, 1 = pure spatial effect). This spatial effect was modelled assuming that the variance in range size between species increases linearly with the great circle distance between species geographical range centroids. The parameter $\lambda' = (1 - \Phi)\,\lambda$, is a spatially corrected version of λ that quantifies the proportion of the variance in range size uniquely attributable to phylogenetic relatedness (0 = no phylogenetic effect, 1 = pure phylogenetic effect). Finally, $\gamma = (1 - \Phi)(1 - \lambda)$ describes the proportion of the variance in range size that is independent of either space or phylogeny. We used maximum likelihood simultaneously to estimate Φ and λ separately for both the native and the alien range size of introduced and established species. Code to fit this model was kindly provided by R. Freckleton. We predict that if spatial proximity is the primary determinant of phylogenetic signal in native range size then accounting for space should lead to a weaker phylogenetic signal in native range size (i.e., $\lambda' < \lambda$). In contrast, if spatial proximity is decoupled from phylogenetic similarity amongst species alien ranges, estimates of phylogenetic signal should be similar regardless of whether we account for space (λ') or not (λ).

2.6 | Testing for differences in phylogenetic signal across the invasion pathway

To test whether differences in phylogenetic signal arise from nonrandom patterns of introduction and establishment, we conducted a series of stochastic simulations. First, treating the global avifauna as the species pool (n = 9,993, "global pool"), we randomly sampled 965 species, equivalent to the number introduced (null model 1). Second, we randomly sampled 359 species from the global pool, equivalent to the number of established species (null model 2). This latter null model assumes that established species are a random sample of the global avifauna. However, species can establish only if they have first been introduced. We therefore implemented a third null model (null model 3) in which 359 species were randomly sampled from the pool of species that have been introduced (n = 965, "introduced pool"). For each null model, we performed 10,000 trials (i.e., 100 replicates for each of 100 phylogenetic trees). For each trial, we estimated λ for the simulated data and tested whether this differed significantly from the observed value of λ by comparing the AIC of a model with a single global λ (n = 1 parameter) with a model in which the value of λ could differ between groups (n = 2 parameters). Through these null models, we aimed to identify the stage(s) in the invasion pathway (global → introduced → established) during which any potential differences in phylogenetic patterns arise.

2.7 | Stochastic models of species introductions

The null models identified the transition from the global pool to introduced species as a key stage in the invasion pathway generating differences in phylogenetic patterns (i.e., null model 1). To test the causes of this finding, we compared the phylogenetic signal in the native ranges of introduced species with that expected under a suite of introduction scenarios, specifically testing the following hypotheses: Differences in λ arise from the tendency preferentially to introduce species: (a) With larger ranges ("range size-dependent scenario"), (b) from certain regions ("region-dependent scenario") and (c) from particular clades ("clade-dependent scenario"). We parameterized these models by fitting a series of generalized linear mixed effects models with a binomial error structure, predicting whether species from the global avifauna ($n = 9{,}993$) have been introduced (one) or not (zero). We variously included native range size as a fixed effect ("range size-dependent scenario"), and taxonomic family ("clade-dependent scenario", $n = 194$ families) and biogeographical realm ("region-dependent scenario", $n = 9$ realms) as random effects. We used the parameter estimates from these models to determine the probability of each species being selected for introduction in our stochastic models. As differences in λ may arise from a combination of factors, we additionally implemented three synthetic models combining the effects of range size and either avian family or biogeographical realm. For models including random effects, we compared a model including random slopes or random intercepts and used the model with the lower AIC. Finally, we fitted a model containing all three variables. In this case, a model with random slopes for both avian family and biogeographical realm could not be estimated; therefore, only models including random slopes for either family or realm were considered. For each scenario, we used the model-derived estimates of introduction probability to select 965 species from the global avifauna ($n = 9{,}993$) and repeated this 10,000 times (100 times for each of 100 phylogenetic trees) to generate expected distributions of λ.

3 | RESULTS

3.1 | Phylogenetic signal in native and alien range size

Phylogenetic signal in the native distributions of established species exhibits an intermediate value ($\lambda_{\text{Established native}} = 0.5$), rejecting both a model of Brownian motion model ($\lambda = 1$) and a model in which range size is independent of phylogeny ($\lambda = 0$) (Table 1). In contrast to the intermediate phylogenetic signal in native range size, the phylogenetic signal in alien range size is substantially weaker ($\lambda_{\text{Established alien}} = 0.26$). Phylogenetic error leads to large uncertainty in estimates of λ (Table 1), and a model with separate values of λ for native and alien ranges (AICW = 0.47) thus received equal support to a null model assuming that these groups are governed by the same λ ($\lambda_{\text{Established native and alien}} = 0.39$, AICW = 0.53). When we restricted our analysis to the highest-quality phylogenetic information (i.e., only those species represented by genetic data), support for a model where λ differs between native and alien ranges ($\lambda_{\text{Established native}} = 0.6$, $\lambda_{\text{Established alien}} = 0.23$, AICW = 0.72) exceeded that of the null model in which these groups share the same phylogenetic signal ($\lambda_{\text{Established native and alien}} = 0.43$, AICW = 0.28).

3.2 | Symmetry in native and alien range size

Amongst established species, range size symmetry differed dramatically both across sister pairs and between native and alien distributions. For instance, the native range size of the Spanish sparrow (*Passer hispaniolensis*) is only 14% of that of the house sparrow (*Passer domesticus*), and this pair thus exhibits a low-to-intermediate level of symmetry (Figure 1b). However, the range sizes of these species differ even more dramatically in their alien distributions; the house sparrow is now found across all continents except Antarctica, whereas the alien distribution of the Spanish sparrow is limited to the Canary and Cape Verde islands, and thus has an alien range only 0.3% the size of its sister lineage. The opposite pattern is evident in the lavender

TABLE 1 Phylogenetic signal in the native and alien range size of birds

	All species					Genetic only	
Group	Number of species	λ	Φ	λ'	γ	Number of species	λ
Established alien	359	0.26 (0.05, 0.51)	0.85	0.01	0.14	329	0.23 (0, 0.5)
Established native	359	0.5 (0.25, 0.69)	0.99	0.00	0.01	329	0.6 (0.35, 0.76)
Introduced native	965	0.61 (0.49, 0.71)	0.97	0.01	0.02	859	0.62 (0.5, 0.72)
Global avifauna	9,993	0.54 (0.51, 0.58)				6,670	0.64 (0.61, 0.68)

Note. Phylogenetic signal was estimated in isolation (λ) or having accounted for spatial effects (λ'). In the latter case, the unique components of range size variation attributable to phylogeny (λ'), space (Φ) or that is independent of either space or phylogeny (γ) are reported. Values of λ are shown for all species and those represented by genetic data. Values are maximum likelihood estimates (and 95% confidence interval). The parameters Φ, λ' and γ can each vary continuously between zero and one (summing to one), corresponding to scenarios in which none (zero) or all (one) of the variation is associated with space (Φ), phylogeny (λ') or neither space or phylogeny (γ).

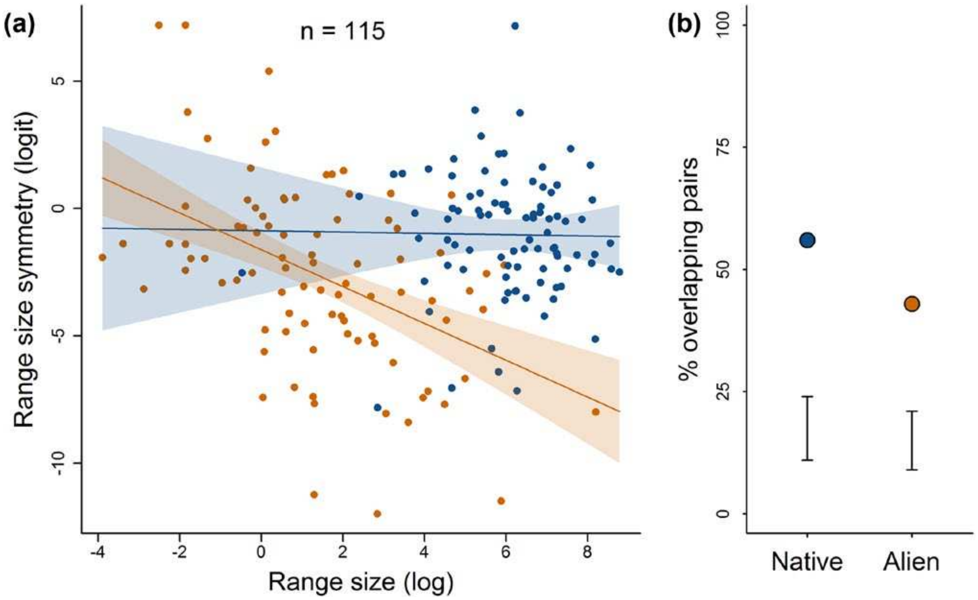

FIGURE 2 Symmetry and overlap of geographical ranges between "sister species" of established birds in their native (blue) and alien (orange) distributions (n = 115 pairs). (a) Range size symmetry (logit transformed) decreases with maximum range size ($\log_{10}$ transformed) across sister pairs in their alien (orange) but not native (blue) distributions. Fitted slopes (and 95% confidence interval) are from a linear mixed effects model, with sister pair as a random effect (Supporting Information Table S1). (b) The percentage of sister pairs with overlapping distributions in the native and alien ranges exceeds that expected under a null model (95% confidence interval in simulated values indicated by black bars) in which species distributions are independent of phylogeny [Colour figure can be viewed at wileyonlinelibrary.com]

waxbill (*Estrilda coerulescens*) and grey waxbill (*Estrilda perreini*), where the range size symmetry of their alien distributions greatly exceeds that of their native distributions (Figure 1c). In this case, the alien ranges are almost identical in size (symmetry = 0.995) because both species remain restricted to the island of Hawaii where they were first introduced.

In accordance with the patterns observed in λ, we found that overall range size symmetry was significantly higher for the native (mean symmetry = 0.34) compared with the alien (mean symmetry = 0.24) distributions of established species [effect = 1.06 ± 0.37 (*SE*), $p < 0.01$, $n = 115$ pairs; Supporting Information Table S1)]. There was a significant interaction between maximum range size and geographical origin (i.e., alien vs. native) in explaining range size symmetry (effect = 0.64 ± 0.17 *SE*, $p < 0.001$; Figure 2a; Supporting Information Table S1). Specifically, the symmetry in native range size was independent of maximum range size, whereas the symmetry in alien range size decreased strongly with maximum alien range size (Figure 2a). Furthermore, we found that although the symmetry in alien range size was unrelated to differences in species residence time (effect = 0.33 ± 1.07 *SE*, $p = 0.73$), it had a strong positive association with similarity in propagule number (effect = 4.24 ± 1.03 *SE*, $p < 0.001$; Supporting Information Table S1). Both residence time [$\lambda = 0.24$, 95% CI (0.09, 0.45)] and propagule number [$\lambda = 0.19$, 95% CI (0.05, 0.40)] exhibit weak but detectable phylogenetic signals, similar to that observed for alien range size ($\lambda_{\text{Established alien}} = 0.26$). All these results were qualitatively unchanged when restricting our analysis to only those pairs represented by genetic data ($n = 106$ pairs; Supporting Information Table S1).

3.3 | The effects of introduction location on the phylogenetic signal in range size

We found that 56% of established sister species co-occur across at least part of their native geographical range (mean overlap of co-occurring pairs = 52%; Supporting Information Figure S1a). The same trend is also evident across their alien distributions, where 43% of species pairs have partly overlapping distributions (mean overlap of co-occurring pairs = 66%; Figure 2b; Supporting Information Figure S1b). In both cases, the frequency of range overlap is significantly greater than expected under a null model in which species distributions are independent of phylogeny (Supporting Information Figure S2b). Thus, closely related species tend to co-occur not only in their native ranges but are also introduced and/or spread into the same geographical locations.

When we quantified the joint spatial and phylogenetic components of variation in the native range size of established species, we found that space accounts for almost all the variation, with no independent effect of phylogeny ($\Phi_{\text{Established native}} = 0.99$, $\lambda'_{\text{Established native}} = 0$, $\gamma_{\text{Established native}} = 0.01$; Table 1; Supporting Information Figure S2). These patterns observed in the native range size of established species mirror those for all introduced species (Table 1; Supporting Information Figure S2). Variation in alien range size was also largely explained by space but with moderate additional variation that was independent of both space and phylogeny ($\Phi_{\text{Established alien}} = 0.85$, $\lambda'_{\text{Established alien}} = 0.01$, $\gamma_{\text{Established alien}} = 0.14$). Thus, the phylogenetic signal in both native and alien range sizes appears to be driven largely by the tendency for closely related species to occur in the same geographical locations rather than because of phylogenetically conserved traits.

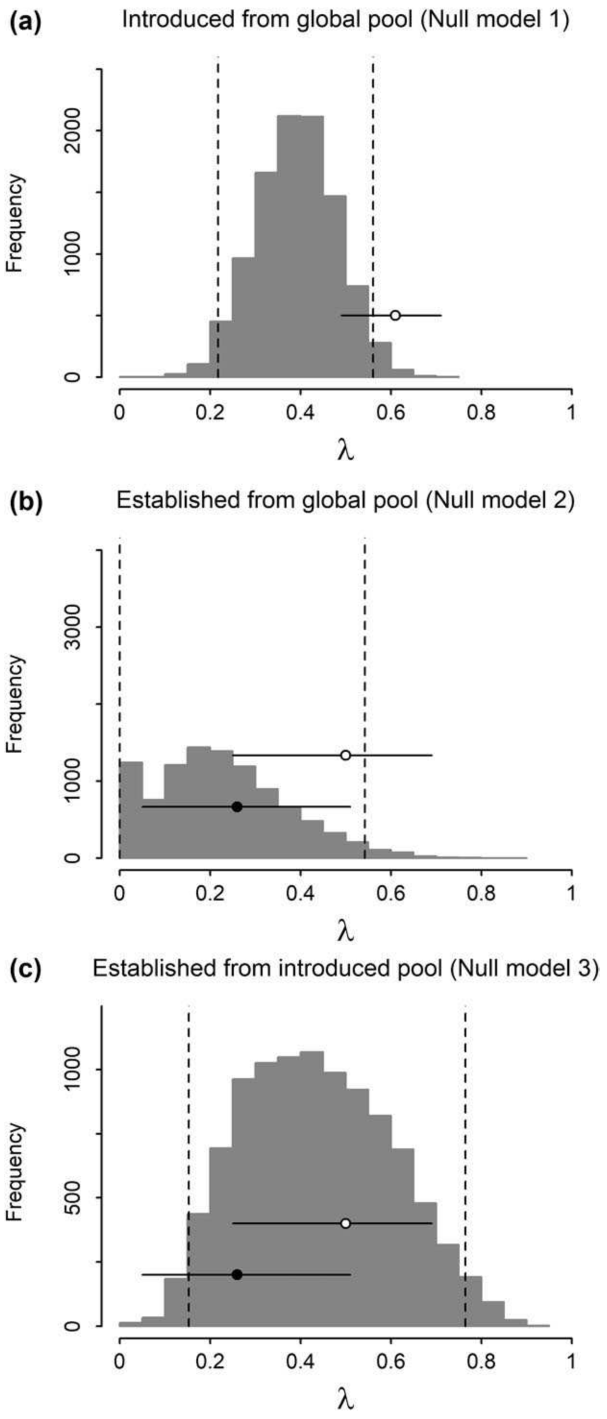

FIGURE 3 Phylogenetic signal (λ) in the range size of birds (points and 95% confidence interval) compared with a null model of random introduction and establishment (grey histograms). (a) Native range size of introduced species (n = 965) compared with a random sampling of the global pool (null model 1). (b) Native (open circle) and alien (filled circle) range size of established species (n = 359) compared with a random sampling of the global pool (null model 2). (c) Native (open circle) and alien (filled circle) range size of established species (n = 359) compared with a random sampling of the introduced pool (null model 3). Histograms (and 95% confidence interval, vertical dashed lines) indicate the expected λ from 10,000 replicate simulations

3.4 | Changes in phylogenetic signal across stages in the invasion pathway

The phylogenetic signal in the native range size of established species ($\lambda_{\text{Established native}}$ = 0.5, n = 359 species) is similar to that of introduced species ($\lambda_{\text{Introduced native}}$ = 0.61, n = 965 species), which in turn is similar to that of the global avifauna ($\lambda_{\text{All native}}$ = 0.54, n = 9,993 species). These similarities in λ are robust to whether estimates are made across all species or only those represented by genetic data (Table 1) and appear to suggest that as species pass through the various stages in the invasion pathway the phylogenetic signal in native range size remains largely unaltered. In accordance with this, we found that the phylogenetic signal in the native range size of established species ($\lambda_{\text{Established native}}$ = 0.5) was highly consistent with that expected from a random sampling of introduced species [null model 3, expected λ = 0.43 (95% CI: 0.15, 0.77); Figure 3c; Table 2]. However, the phylogenetic signal in the native range size of introduced species ($\lambda_{\text{Introduced native}}$ = 0.61) is significantly higher than expected given a random sampling of species from the global pool [null model 1, expected λ = 0.39 (95% CI: 0.22, 0.56); Figure 3a; Table 2]. These results demonstrate that robust comparisons of phylogenetic signal across the stages of the invasion pathway must account for the differences expected owing to the random sampling of species rather than relying on direct comparisons of λ. Conversely, our analysis also highlights that tests of differences in phylogenetic signal between native and alien range sizes should be based on comparisons between the same set of species. In particular, amongst established species, the phylogenetic signal in alien range size ($\lambda_{\text{Established alien}}$ = 0.26) is weaker than that of native range size ($\lambda_{\text{Established native}}$ = 0.5). This difference, however, is not statistically supported when comparing the phylogenetic signal in alien range size with a random sample of native species from the introduced [null model 3, expected λ = 0.43 (95% CI: 0.15, 0.77)] or global species pool [null model 2, expected λ = 0.22 (95% CI: 0, 0.54); Figure 3b and c; Table 2].

3.5 | The effects of biases in introductions on the phylogenetic signal in range size

Together, these results indicate that biases in introduction lead to a stronger than expected phylogenetic signal in the native range size of introduced species (Figure 3). Indeed, we confirmed that the probability of species introduction is highly nonrandom across species, varying significantly across biogeographical realms, taxonomic families and with native range size (Supporting Information Table S2). For example, the per-species probability (P) of introduction is highest for species from the Palearctic (P = 0.22) and Nearctic (P = 0.15) and lowest for species from the Neotropics (P = 0.06). Amongst taxonomic families, pelicans (Pelecanidae, P = 0.64) and ducks (Anatidae, P = 0.58) are the most likely to be introduced, whereas ovenbirds are the least (Furnariidae, P = 0.003). Finally, species with large ranges (fourth range size quartile, P = 0.18) are more likely to be introduced

TABLE 2 Tests of differences in phylogenetic signal (λ) in range size between native and alien distributions and across different stages of the invasion pathway

Group 1	Group 2	$\lambda1$	$\lambda2$	AIC	ΔAIC
Established native (*n* = 359)	Established alien (*n* = 359)	0.5	0.26	3,500.5	−0.22
Introduced native (*n* = 965)	Null model 1:965 species sampled from the global pool	0.61	0.39	9,037.06	4.13
Established native (*n* = 359)	Null model 2:359 species sampled from the global pool	0.5	0.22	3,400.78	1.37
Established alien (*n* = 359)	Null model 2:359 species sampled from the global pool	0.26	0.22	3,601.04	−1.13
Established native (*n* = 359)	Null model 3:359 species sampled from the introduced pool	0.5	0.44	3,293.09	−0.91
Established alien (*n* = 359)	Null model 3:359 species sampled from the introduced pool	0.26	0.44	3,493.45	−0.22

Note. In each comparison, $\lambda1$ and $\lambda2$ represent the estimates of λ for the two groups being compared ("group 1" and "group 2"). Model fit is assessed on the basis of the Akaike information criterion (AIC). The difference in AIC from a null model assuming that both groups are governed by the same value of λ is shown (ΔAIC). Values of ΔAIC ≥ 2 indicate substantial support for a model with distinct λ values in each group. Null models 1–3 were based on 10,000 random draws of species from the global (*n* = 9,993) or introduced (*n* = 965) pool of species (see Methods for more details).

than species with small ranges (first range size quartile, $P = 0.03$). Stochastic simulations reveal that when acting independently, these biases cannot explain the strong phylogenetic signal in the native range size of introduced species (Figure 4a–c). When these factors are combined, however, the simulated patterns converge on the observed value of λ (Figure 4d–f). A model combining all three factors fits the observed data best, accurately reproducing the strong phylogenetic signal in the native range size of introduced species (Figure 4f).

4 | DISCUSSION

We investigated the phylogenetic signal in the native and alien range sizes of birds and tested how these associations arose across different stages of the invasion process. Our results show that different stages in the invasion pathway have opposing effects on phylogenetic signal. First, we found that the phylogenetic signal in the native range size of introduced species is anomalously strong compared with that expected given a random sample of species from the global avifauna (Figure 3a). Second, we found that the phylogenetic signal in the alien range size of established species is relatively weak compared with the phylogenetic signal in their native distributions (Table 1). Thus, the process of introduction selects for species with a high phylogenetic signal in range size, whereas the process of establishment and spread appears subsequently to erase, albeit not entirely, the imprint of evolutionary history on species range size.

An important message of our paper is that robustly identifying these effects of invasion on phylogenetic signal relies crucially on the choice of species being compared (Blackburn & Duncan, 2001a; van Kleunen, Dawson, Schlaepfer, Jeschke, & Fischer, 2010). In particular, we found that the phylogenetic signal in alien range size of established species (*n* = 359) is remarkably consistent with the phylogenetic signal in native range size expected if an equivalent number of species are randomly sampled from the global avifauna (Figure 3b). This finding could be interpreted as evidence that human introductions do not fundamentally alter the rules governing species distributions. Direct comparison between the alien and native ranges of established species, however, clearly reveals the weaker phylogenetic signal in alien range size (Table 1). Likewise, although the phylogenetic signal in the native range sizes of introduced species appears similar to that of the global avifauna (Table 1), null model simulations revealed that this can be explained only by highly nonrandom patterns of species introduction (Figure 4). If introductions had occurred randomly with respect to species identity, then the phylogenetic signal in the native range size of introduced species would be expected to be significantly weaker than is observed (Figure 3a).

Why the phylogenetic signal in the native range size of introduced species should be particularly strong is unclear because, to our knowledge, this pattern has not previously been documented. Our results, however, suggest that this pattern can be explained by the nonrandom process of avian introductions, which has been biased towards a few geographical regions and taxonomic families, and species with large geographical ranges (Supporting Information Figure S3; Blackburn et al., 2009). The effects of these biases are consistent with the predictions from theoretical models of range size evolution. In particular, speciation is expected to lead to closely related species with highly asymmetric range sizes, and phylogenetic signal will thus increase over time as species with small ranges either expand their distributions or are "filtered out" by the process of extinction (Pigot, Phillimore, et al., 2010; Waldron, 2007). In a similar way, by preferentially selecting species with larger geographical ranges (Blackburn et al., 2009; Pyšek et al., 2009), the process of human introduction may impart a higher phylogenetic signal to the range size of introduced species than expected by chance. Furthermore, we found

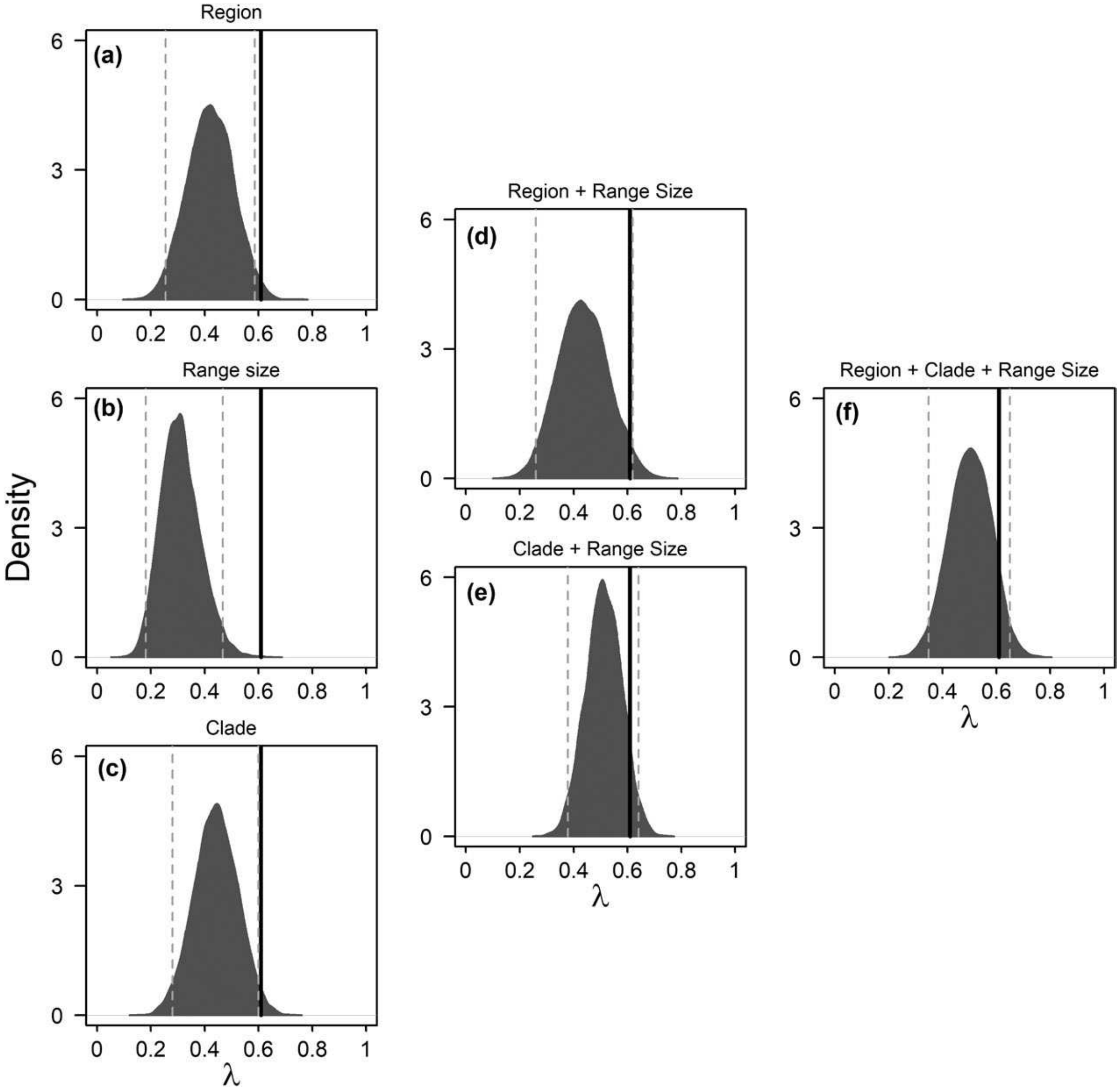

FIGURE 4 Stochastic models of species introductions explaining the phylogenetic signal (λ) in the native range size of introduced species (n = 965). Black lines indicate the observed λ, and grey probability distributions (and 95% confidence interval, vertical dashed lines) indicate the expected λ under different stochastic models in which introductions are: (a) region dependent, (b) range size dependent, (c) clade dependent, (d) region and range size dependent, (e) clade and range size dependent, and (f) region, clade and range size dependent. See Supporting Information Table S2 for the parameters used in each stochastic model

that the preferential sourcing of introduced species from a subset of geographical regions (particularly the Palearctic and Nearctic) also contributed to a higher phylogenetic signal in the range size of introduced species (Figure 4a). This makes sense because our results show that spatial proximity between closely related species is the major driver of phylogenetic signal in native range size, with no independent effect of evolutionary relatedness.

In contrast to the intermediate phylogenetic signal in the native range size of established birds, variation in alien range size exhibits a much weaker phylogenetic signal (Table 1). Indeed, even very closely related species often had highly asymmetric alien range sizes (Figure 2a). One explanation for this pattern is that, upon introduction, species will initially be uniformly rare, thus decoupling alien range size from phylogenetic ancestry. A stronger phylogenetic signal, comparable to that of native distributions, may only be expected to emerge over time, as alien range size expands to the limits imposed by species intrinsic traits (Byers et al., 2015). However, our results show that although the first introduction times of closely related alien species were in some cases separated by centuries, differences in range size were unrelated to differences in residence times. Thus, the phylogenetic signal in alien range size does not appear to be limited by a lack of time for dispersal.

An alternative possibility is that the weaker phylogenetic signal in alien range size is a consequence of the particular way in which humans have redistributed species across the planet. For native species, the phylogenetic signal in range size is almost entirely attributed to the tendency for closely related species to occur in close geographical proximity (Table 1; Freckleton & Jetz, 2009). This effect of space presumably arises because species occurring in the same region will be subject to the same environmental and geographical barriers to range expansion (Machac et al., 2011; Pigot, Owens, & Orme, 2010). As a result, if closely related species tend to be transported to widely scattered locations then this may decouple species phylogenetic relatedness from spatial proximity, thus eroding the key mechanism promoting the phylogenetic signal in range size. Our results, however, do not support this idea either. We found that closely related alien species tend to be introduced to the same locations more often than expected by chance (Figure 2b). Furthermore, as with native ranges, spatial proximity accounted for most of the variation in alien range size (Table 1). Thus, the positive association between phylogenetic and spatial distance observed in native species appears to be largely maintained in the alien distributions of species, despite the very different processes involved in determining the spatial location of their geographical ranges.

A lack of time for dispersal and the spatial patterns of species introduction therefore appear unlikely to explain the weak phylogenetic signal in alien range size. Alien range size in birds is strongly correlated with the number of locations to which species have been introduced (Dyer et al., 2016). Asymmetries in introduction effort could therefore provide another explanation for a weak phylogenetic signal in range size. In accordance with this hypothesis, here we found that variation in the number of introduction attempts exhibits a weak phylogenetic signal, similar to that observed in alien range size. Furthermore, those species with the greatest asymmetry in alien range size were also those with the largest asymmetry in the number of introduction attempts. Why the number of introduction attempts per species does not exhibit a stronger phylogenetic signal is unclear, given that we would expect closely related species to be similarly attractive as sources of intentional introductions and to have similar abilities to navigate the invasion pathway (Allen et al., 2017; Blackburn & Duncan, 2001b). One intriguing possibility is that there is a “priority effect” in species introductions, whereby species that, by chance, successfully establish and spread are more likely to become the source of future introductions compared with those alien species that, by chance, remained rare. This process would tend to re-enforce itself over time, leading to strong asymmetries in alien range size, even among phylogenetically and ecological similar species.

Our results suggest that these anthropogenic factors, interacting with the properties of the environment into which species are introduced, are the dominant cause of variation in alien range size, with little effect of strongly conserved aspects of life history or ecology. The weak phylogenetic signal in alien range size may have important implications for predicting the spread and future impact of invasive species (Blackburn et al., 2014). Specifically, our finding that closely related alien species often attain very different range sizes suggests that it will be difficult reliably to predict the spread of invasive species based on their phylogenetic relatedness. Furthermore, although predicting the traits of species that allow them to establish in new regions has had reasonable success (Allen et al., 2017; Blackburn & Duncan, 2001b; Sol et al., 2012), our results suggest that phylogenetically conserved traits may be unlikely to explain the subsequent extent of spread. This weak predictive ability of phylogeny is highlighted by the fact that alien range sizes are highly asymmetrical even amongst the most closely related species, and these asymmetries could not be explained by differences in the length of time available for dispersal. Where apparent associations exist between phylogenetic relatedness and the range size of invasive species, our results suggest that this is likely to be attibutable simply to closely related species being introduced to the same regions and with similar effort.

5 | CONCLUSIONS

Whether the geographical extent attained by alien species is predictable on the basis of their evolutionary ancestry has not previously been thoroughly explored. Here, we show, for an entire class of organisms, that the phylogenetic signal in alien range size is weak compared with native species distributions. This result implies that heritable intrinsic traits have relatively little effect on the range size of alien species and that phylogenetic relatedness is unlikely to provide a robust approach for predicting the spread of invaders. Importantly, we demonstrate that these patterns are detectable only when accounting for the taxonomic and geographical biases in species introductions and are not evident when using the naïve assumption that avian introductions represent a random sample of species. Predictions of the potential spread and impact of introduced species should therefore account for historical biases in species introductions.

ACKNOWLEDGEMENTS

We thank R. Freckleton for providing the code to quantify the phylogenetic and spatial component of variation in range size. We are grateful to A. Ordonez and three anonymous reviewers whose comments improved the manuscript. Funding for this study was provided by a grant from the Leverhulme Trust (RPG-2015-392).

CONFLICT OF INTEREST

The authors declare no conflict of interests.

DATA ACCESSIBILITY

Code and data analysed here are provided in Supporting Information Database S1. All raw data, including alien geographical range maps (https://dx.doi.org/10.6084/m9.figshare.4234850), native range maps (https://datazone.birdlife.org/home) and phylogenies (https://birdtree.org/), are freely available for download.

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BIOSKETCH

Alex L. Pigot is a macroecologist interested in the origin and distribution of biodiversity. His research interests concern the processes governing species geographical ranges, diversity gradients and the assembly of ecological communities.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Pigot AL, Dyer EE, Redding DW, Cassey P, Thomas GH, Blackburn TM. Species invasions and the phylogenetic signal in geographical range size. *Global Ecol Biogeogr.* 2018;27:1080–1092. https://doi.org/10.1111/geb.12768