Patterns of bird invasion are consistent with environmental filtering

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Predicting invasion potential has global significance for managing ecosystems as well as important theoretical implications for understanding community assembly. Phylogenetic relationships of introduced species to the extant community may be predictive of establishment success because of the opposing forces of competition/shared enemies (which should limit invasions by close relatives) versus environmental filtering (which should allow invasions by close relatives). We examine here the association between establishment success of introduced birds and their phylogenetic relatedness to the extant avifauna within three highly invaded regions (Florida, New Zealand, and Hawaii). Published information on both successful and failed introductions, as well as native species, was compiled for all three regions. We created a phylogeny for each avifauna including all native and introduced bird species. From the estimated branch lengths on these phylogenies, we calculated multiple measurements of relatedness between each introduced species and the extant avifauna. We used generalized linear models to test for an association between relatedness and establishment success. We found that close relatedness to the extant avifauna was significantly associated with increased establishment success for exotic birds both at the regional (Florida, Hawaii, New Zealand) and sub-regional (islands within Hawaii) levels. Our results suggest that habitat filtering may be more important than interspecific competition in avian communities assembled under high rates of anthropogenic species introductions. This work also supports the utility of community phylogenetic methods in the study of vertebrate invasions.

Modern biological invasions pose an increasingly important threat to ecosystems globally (Hulme 2009) through their effects on native biodiversity (reviewed by Mcgeoch et al. 2010), ecosystem processes (Dunham and Mikheyev 2010), and community structure (Hejda et al. 2009). Predicting which exotic species are likely to establish in a given environment has thus become a central challenge in ecology and conservation biology because of its relevance for managing invasive species and for understanding community assembly (Whitney and Gabler 2008).

Darwin (1859) considered the argument that successfully established exotics are likely to be congeneric with native species because congenerics may share adaptations to particular local conditions. However, he did not observe such environmental filtering for naturalized plants of the United States, instead finding that established exotics were unlikely to be congeneric with native species. Darwin's proposed mechanism for this alternative pattern was a higher degree of competition between closely vs distantly related taxa (Darwin 1859), although it is clear that the same pattern could arise if closely related taxa shared more predators, parasites, or pathogens than distantly related taxa (Elton 1958, Hill and Kotanen 2009, Ness et al. 2011). The idea that successfully established exotics should be more distantly related to the pre-existing community than expected by chance became known as 'Darwin's naturalization hypothesis' (Daehler 2001).

Employing phylogenetic information to predict patterns of exotic species establishment makes the assumption that evolved ecological differences in species traits increase with evolutionary distance. As such, close relatives are expected to be more ecologically similar to each other than more distantly related species and, indeed, physiological traits, habitat affinities, and environmental tolerances are commonly shared within lineages (reviewed by Cavender-Bares et al. 2009). In the absence of competitive forces, closely related species are expected to be spatially clustered within like environments (Wiens and Graham 2005). Alternatively, exotics facing competition and/or shared enemies with close relatives may have reduced success relative to those with no close relatives in the extant community, particularly if priority effects and relative population sizes (Wilbur and Alford 1985) are important for determining the outcomes of competitive interactions. Whether the predominant pattern seen is dominated by environmental filtering or niche-based exclusion could depend on spatial scale, with the former dominating at large scales where environmental tolerances shape species' distributions, and the latter dominating at small scales, where biotic interactions may exert a stronger influence (Lovette and Hochachka 2006, Thuiller et al. 2010).

With increasing recognition of the economic and ecosystem-level impacts of species invasions (Pimentel et al. 2005, Hulme et al. 2009), there has been a recent surge of interest in Darwin's ideas for predicting invasion success (reviewed by Thuiller et al. 2010). Recent studies comparing the success rates of exotic species with vs without native congeners have supported the environmental filtering hypothesis (New Zealand plants, Duncan and Williams 2002) or have found no pattern (fish, Ricciardi and Mottiar 2006; Mediterranean plants, Lambdon and Hulme 2006). However, congeneric status has been characterized as a subjective and artificial measure of relatedness that may bias results (Thuiller et al. 2010). In contrast, phylogenetic branch length provides a more objective and quantitative measure of evolutionary relatedness. Strauss et al. (2006) used information on phylogenetic distance for grass species (Poaceae) in California and found that exotic species characterized as noxious invaders were more distantly related to the native taxa than were non-noxious, exotic species. These results implied that the presence of close relatives in the native flora reduced the deleterious impacts of exotic grasses on native communities. These results do not necessarily confirm Darwin's hypothesis, as invader impacts may not be strongly correlated with the success of invader establishment (the key response variable in Darwin's hypothesis) (Ricciardi and Cohen 2007). There have been few tests of Darwin's hypothesis using phylogenetic distance measures. These include an experimental test using laboratory bacterial communities (Jiang et al. 2010) and a study of reptile establishment in Florida and California (Van Wilgen and Richardson 2011), both supporting the naturalization hypothesis.

The opposing forces of competition/shared enemies versus environmental filtering are likely to lead to differing outcomes for invasion success, and the relative importance of these forces may depend, in part, on the taxonomic identities of the species being studied (Thuiller et al. 2010). Unfortunately, current analyses are taxonomically biased. Most studies that have tested Darwin's hypothesis using alternative methods (i.e. not the quantitative phylogenetic distance metrics discussed above) have focused on plants (7 of 9 studies reviewed by Thuiller et al. 2010), while patterns in terrestrial animal invasions have been generally neglected (but see Van Wilgen and Richardson 2011), despite the devastating impacts of animal invaders on native communities worldwide (O'dowd et al. 2003). Because mechanisms that drive community assembly patterns may differ according to taxon (as taxa vary in the relative importance of dispersal ability, trophic interactions, etc.), additional tests will increase the ability to predict the conditions under which Darwin's naturalization hypothesis applies.

Here we indirectly tested for the importance of competition/shared enemies versus environmental filtering in community assembly by examining patterns of invasion success in three avifaunas: Florida (~170 000 km²), New Zealand (~268 000 km²), and Hawaii (~16 600 km²). Because scale-dependent patterns were expected (see above), we examined the Hawaiian data at two spatial scales (across the archipelago as well as within each of the major islands, which range from 364 to 10 432 km²). For each region, we constructed a phylogenetic tree of the extant avifauna and estimated phylogenetic distances between focal introduced species (including both failures and successes) and the remaining members of the avifauna. At the scales tested, our results support a pattern of environmental filtering during bird invasions and do not uphold Darwin's naturalization hypothesis.

Methods

Avifaunas and species classification

We chose the avifaunas of three regions for inclusion in our analyses: Florida (Pranty 2004, Florida Ornithological Society Records Committee 2008), the Hawaiian archipelago (Pratt et al. 1987, Moulton 1993, Scott et al. 2001) and New Zealand (Long 1981, Ornithological Society of New Zealand 2003). In discussion of spatial scale (below), we define these three areas as 'regions' in contrast to individual islands which we define as the 'sub-regional' scale. These avifaunas were chosen because they had a large number of species, high ratios of introduced species relative to native species, and had data for both failed and successful introductions (Long 1981). Each region's published introductions totaled > 25% of the number of native species within that region. We chose such avifaunas because tests using alternatives (i.e. small avifaunas or those with few invaders) may lack sufficient statistical power to detect effects.

We use the term 'native' to refer to all species present within a region which were not introduced by humans after European arrival (either accidentally or deliberately). Exotic species were classified into those that successfully established (were able to maintain a self-sustaining population within the new geographic range) versus those that failed to do so. Introduced species in New Zealand, Hawaii and Florida were classified as a 'success' or 'failure' based on categorizations from Long (1981), Moulton et al. (2001a), Ornithological Society of New Zealand (2003), and Pranty (2004) respectively. Moulton et al. (2001a) based categorization of introduced species on presence or absence in 1990. Long (1981) did not provide a clear description of his categorization but it is presumably based on observed presence/absence. Only introduction attempts listed as certain failures or successes were included. Although Pranty (2004) did not designate species as a 'success' or 'failure', we considered species to be a 'success' if they had been reported breeding and had not been extirpated.

We follow Moulton et al. (2001a) in excluding introduced species from our analyses if our sources stated that fewer than five individuals were released (indicating a low probability of success). We excluded species if there was any documented uncertainty about whether the species had actually been introduced into the region of study. We also excluded reintroductions of native species and introductions of native species to new locations within a region. We excluded native species from New Zealand which had gone extinct prior to European settlement (Supplementary material Appendix 1) as these species would not have been encountered by the introduced species we analyzed. Hawaiian species classified as 'accidental stragglers' or known only from dead remains (Scott et al. 2001) were also excluded from our analyses. Aside from these exclusions, we included all species listed in

our sources. Our avifaunas thus consisted of both land-based and aquatic birds including seabirds, coastal breeders and migrants. The resulting species lists (Supplementary material Appendix 2) contained 150 native and 140 exotic species for Hawaii; 303 native and 85 exotic species for New Zealand; and 493 native and 214 exotic species for Florida.

Phylogeny construction

We created a phylogenetic tree for each regional avifauna using Mesquite ver. 2.72 (Maddison and Maddison 2009). The base topology of this tree was derived from Hackett et al. (2008, 2010), a phylogeny of 169 bird species based on 19 independent nuclear loci. These 169 species represent all major extant bird groups (Hackett et al. 2008). We then grafted taxa to the base phylogeny as follows: genera were represented as polytomies within each family, and species were represented as polytomies within each genus. Families that were not represented within the Hackett et al. (2008) phylogeny were added following the relationships supported by the Tree of Life Web Project (Maddison and Schulz 2007). The phylogenies which resulted from this process contained the initial species included in the Hackett et al. (2008) phylogeny as well as the species present in a given region, but lacked branch lengths. Branch lengths were added to our phylogenetic trees using the Comnode and Bladj algorithms in Phylocom (Webb et al. 2008) to apply node distances (in substitutions per site) derived from Hackett et al. (2008). This procedure sets branch lengths by spacing nodes of unknown distance evenly between nodes of known distance. The resulting branch lengths perform much better than node counts as measures of phylogenetic distance (Webb 2000). Each tree was then pruned to match a given regional species list, including both the native and exotic taxa from the region.

We explored alternative approaches to phylogeny construction and branch length estimation and found them impractical for our datasets. One alternative would be to stitch together phylogenies of various groups using a supertree approach. However, only 70% of the species in our study appear in a published phylogeny (based on our compilation and examination of 102 avian phylogenies), and furthermore these phylogenies do not use consistent measures of branch length, making standardization problematic. Another approach would be to use sequence data deposited in Genbank to build a new phylogeny for all species in the analysis. Again, missing data are a serious problem; only 49% of the species in our analyses have Genbank accessions, and not all of these species share sequence data for overlapping areas of the genome. Therefore, we believe our approach is the best practical solution.

Phylogenetic distance metrics

We used the Phydist algorithm in Phylocom (Webb et al. 2008) to calculate a matrix of phylogenetic distances between all species within each region. From these matrices we calculated the phylogenetic distance between each introduced species and the nearest native species (including those currently extinct but present during the introduction period) (NND_{native}), the phylogenetic distance between each introduced species and the nearest member of the entire avifauna (native plus naturalized: NND_{all}), and the distance between each introduced species and the subset of successfully established introductions ($NND_{naturalized}$). These metrics allowed us to compare the strength of the phylogenetic distance effect among these three types of assemblages (all species, native species only, and naturalized species only). In addition, we calculated the mean (MPD) and median (MedianPD) phylogenetic distances for each of the three assemblages. We explored MedianPD since it may perform better than MPD as a measure of central tendency when distributions of phylogenetic distances are non-normal, as in the present datasets. NND metrics are sensitive to how closely related a given focal species is to its nearest relative, which under phylogenetic conservation of traits likely represents the strongest competitor for resources and the species most similar in habitat preference. In contrast, MPD and MedianPD metrics reflect the relatedness of a focal species to the avifauna as a whole, including distantly related species. We thus predicted that introduction success would be more strongly correlated with NND than MPD or MedianPD metrics.

Statistical analysis

We used generalized linear models to examine whether phylogenetic distance metrics were associated with the probability of establishment success for bird introductions (Proc GENMOD, SAS ver. 9.1). The response variable was binary; each bird species introduction was classified as a success or failure. Our statistical model included a phylogenetic distance metric (continuous), region (categorical: Florida, Hawaii, or New Zealand), the assemblage (categorical: all, native, or naturalized) and all interactions. In particular, a statistically significant region $\times$ phylogenetic distance (or assemblage $\times$ phylogenetic distance) interaction would indicate that the direction and/or magnitude of the relationship between phylogenetic distance and success varied among the three regions (or assemblages). We conducted a separate analysis for each phylogenetic distance metric: NND, MPD and MedianPD. Within a region, each introduced bird species was considered the unit of replication; thus, observations were blocked by species (Proc GENMOD, repeated subject = species, SAS ver. 9.1). Because the bird species introduced to a pair of regions had low overlap (% of species in common out of the total combined number of species: Hawaii vs Florida = 13%; Hawaii vs New Zealand = 12%; Florida vs New Zealand = 6%; only twelve species were introduced to all three regions), we did not account for the non-independence of bird species introduced to more than one region; that is, we treated each bird species introduction within each region as an independent observation.

To characterize the relatedness of introduced species to native vs naturalized components of the avifauna, we used a mixed model (Proc MIXED, SAS ver. 9.1). We asked whether a given distance metric (NND, MPD, MedianPD) differed according to assemblage (native vs naturalized), region, and their interaction. Following significant assemblage $\times$ region interactions, within-region Tukey tests were

used to determine whether introduced species were phylogenetically closer to the native vs naturalized assemblages.

We additionally analysed a coarser estimate of phylogenetic relatedness, the number of congeneric native species, which has been commonly applied in the literature as a method to test Darwin's naturalization hypothesis (Duncan and Williams 2002, Ricciardi and Atkinson 2004, Ricciardi and Mottiar 2006, Thuiller et al. 2010). Here, we analyzed the success/failure of each bird species introduction (binary response) as a function of congeneric native species richness (continuous predictor), using the same generalized linear model described above.

Finally, the Hawaii dataset allowed for analyses at a finer geographic scale than across our three regions because species introductions and success/failure rates were recorded for individual islands in the archipelago. Patterns in phylogenetic composition may be scale-dependent (Lovette and Hochachka 2006, Thuiller et al. 2010), and so analyses at both the regional and sub-regional level allow us to test whether patterns which dominate at a regional scale differ from those at a smaller spatial scale. To test for differences among the six major islands within Hawaii, we analyzed the binomial response of success/failure as a function of island identity (Hawaii, Kauai, Lanai, Maui, Molokai, Oahu), phylogenetic distance, assemblage (all, native, naturalized), and all interactions. To test whether island size influenced the relationships between establishment success, phylogenetic distance, and assemblage, we repeated the above analysis but substituted island area (km^2) for island identity. We tested each of the three phylogenetic distance metrics, and again we treated each bird species introduction for each island as an independent observation. We were unable to use this approach for the North and South Islands of New Zealand as we were unable to locate introduction data recorded by island.

Results

Patterns of establishment success in Florida, Hawaii, and New Zealand

Patterns of establishment of exotic bird species in regional avifaunas did not support Darwin's naturalization hypothesis. Instead, the success of bird introductions increased with phylogenetic relatedness to the extant avifauna, a pattern that is consistent with the hypothesis of environmental filtering. For nearest neighbour distances, the strength of this effect depended on the assemblage to which distances were calculated, as indicated by a significant interaction between assemblage and phylogenetic distance (Table 1). The increase in invasion success at smaller phylogenetic distances was strongest for NND_{all} (Fig. 1a, $\chi^2 = 17.2$, p < 0.001), with a 43% higher NND for failures relative to successes (Fig. 1b). The relationship was weakest for NND_{native} ($\chi^2 = 8.4$, p = 0.004, Fig. 1c), with an 18% higher NND for failures relative to successes. For $NND_{naturalized}$, the relationship was not significantly different from NND_{all} or NND_{native} (Fig. 1e, f, $\chi^2 = 18.9$, p < 0.001). While there was some variation in the probability of establishment across regions, there was no significant interaction between region and phylogenetic distance in the NND analysis (Table 1), indicating that species with near neighbors had higher establishment success in all three regions.

Like NND, the MPD analysis showed that non-native bird species had a significantly higher probability of successful establishment if they were more closely related to the extant avifauna (Table 1). Unlike NND, the influence of MPD on establishment success did not vary with the assemblage to which the introduced species were compared (phylogenetic distance × assemblage n.s., Table 1). However, there was a significant interaction between phylogenetic distance and geographic region in the MPD analysis (Table 1). In Florida, there was no significant relationship between MPD and the probability of successful establishment (Fig. 2a, b; $\chi^2 = 0.1$, p = 0.929). In Hawaii, the probability of successful establishment was strongly associated with phylogenetic distance (Fig. 2c, $\chi^2 = 15.5$, p < 0.001,), with a 16% higher MPD for failures relative to successes (Fig. 2d). For New Zealand, there was a non-significant trend toward increasing success for bird species more closely related to the extant avifauna (Fig. 2e, $\chi^2 = 2.9$, p = 0.090), with a 5% higher MPD for failures relative to successes (Fig. 2f).

The MedianPD analysis also showed significantly higher establishment success with closer phylogenetic relationship to the extant avifauna (Table 1), with 7% higher MedianPD for failures relative to successes (mean ± SE: failure 0.49 ± 0.004, success 0.46 ± 0.005). The absence of significant

Table 1. Influence of phylogeny on establishment success of exotics in the avifaunas of Florida, the Hawaiian archipelago, and New Zealand. Assemblage refers to the assemblage of extant species (all, native, or naturalized) used when calculating the distance metrics.

	DF	NND		MPD		Median PD*	
		χ^2	p	χ^2	p	χ^2	p
Phylogenetic distance	1	18.4	**< 0.001**	7.9	**0.005**	4.9	**0.027**
Assemblage	2	0.2	0.920	0.5	0.785	2.1	0.149
Region	2	12.9	**0.002**	9.8	**0.007**	3.7	0.157
Phylogenetic distance × assemblage	2	8.9	**0.012**	0.6	0.745	1.3	0.250
Phylogenetic distance × region	2	1.8	0.412	6.3	**0.043**	2.4	0.298
Assemblage × region	4	8.2	0.083	4.3	0.369	1.9	0.385
Phylogenetic distance × assemblage × region	4	2.1	0.715	4.6	0. 337	1.3	0.523

Results from generalized linear models with the binary response of success/failure for each introduced bird species; likelihood ratio χ^2 values are given for three metrics measuring the phylogenetic distance of an introduced bird species to the extant avifauna. Significant p-values are shown in bold. Total number of observations (species introductions) = 436. Number of successfully introduced species = 132.
*Note: MedianPD values were exactly the same when calculated to the all and native assemblages; thus, for MedianPD, the assemblage factor included only all and naturalized, with 1 DF rather than 2.
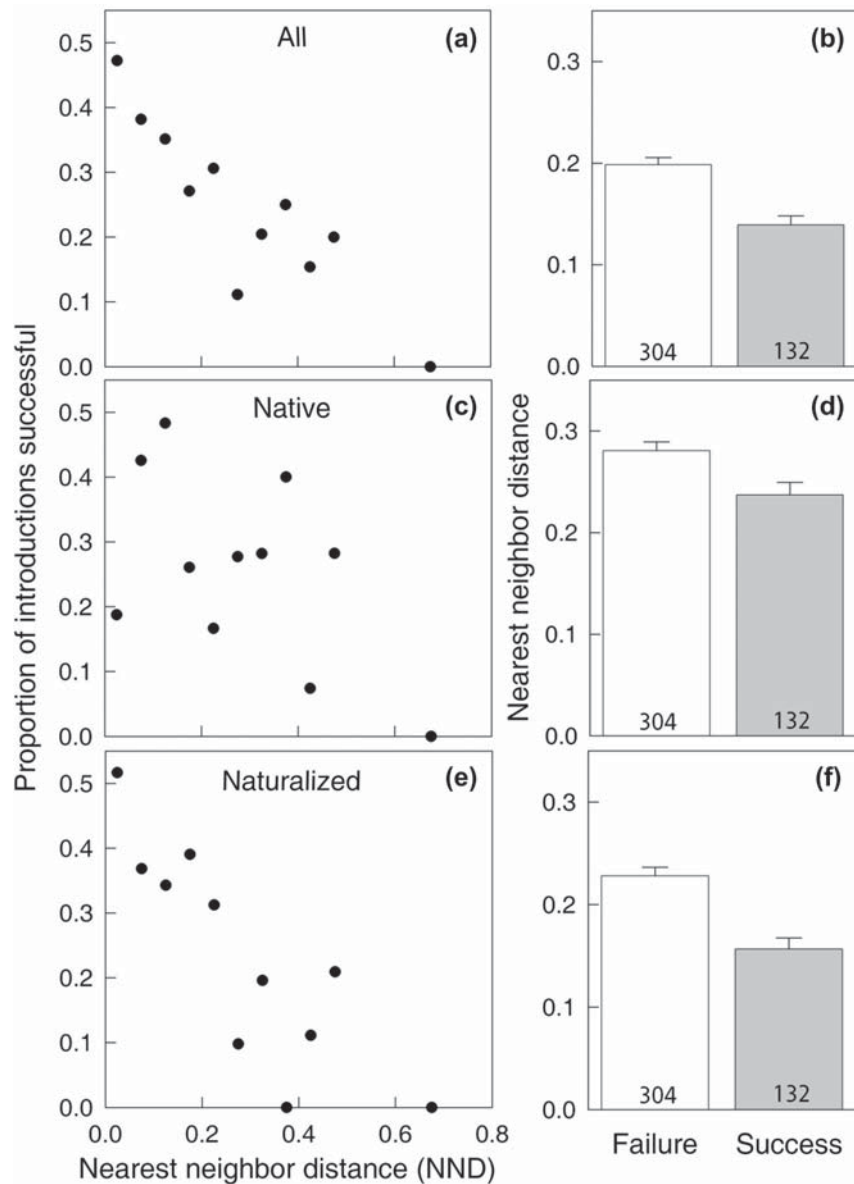
Figure 1. Establishment success of exotic birds increases with decreasing phylogenetic distance to nearest neighbors (NND); data are shown for a combined total of 436 introductions across the three regions (Hawaii, New Zealand, and Florida). Data are shown according to the assemblage to which NND was calculated: (a, b) all species (including both native and naturalized); (c, d) native species only, and (e, f) naturalized species only. The relationship was significantly stronger for NND_{all} vs NND_{native} ($\chi^2 = 7.7$, $p = 0.005$) but not significantly different for NND_{all} vs $NND_{naturalized}$ ($\chi^2 = 1.1$, $p = 0.293$) or NND_{native} vs $NND_{naturalized}$ ($\chi^2 = 2.9$, $p = 0.088$). The proportion of introductions that were successful (a, c, e) was calculated by binning the data at 0.05 intervals of the phylogenetic distance metric, allowing for a visualization of the linearity of the relationship. Mean distances ($\pm$ SE) for failed vs successful introductions are shown in (b, d, f) with sample sizes (number of introduced species) indicated at the base of the bar.

interactions of phylogenetic distance with assemblage or region (Table 1) indicates this response was consistent across our three regional datasets and across different subsets of the extant avifauna (all, native, naturalized) to which relatedness of focal introduced species was measured.

Dissimilarity of introduced species to the native assemblage

For most distance metrics, introduced species were on average significantly more closely related to the naturalized species in a

region than to native species (Fig. 3). Exceptions to this pattern were NND and MedianPD for Florida (p = 0.696 and 0.360, respectively) and MedianPD for New Zealand (p = 0.181), which showed no differences in phylogenetic distance from the introduced species to the native vs naturalized species.

Congeneric analyses: Florida, Hawaii, and New Zealand

We also examined a coarser metric of species relatedness that has commonly been adopted in invasion studies: the number
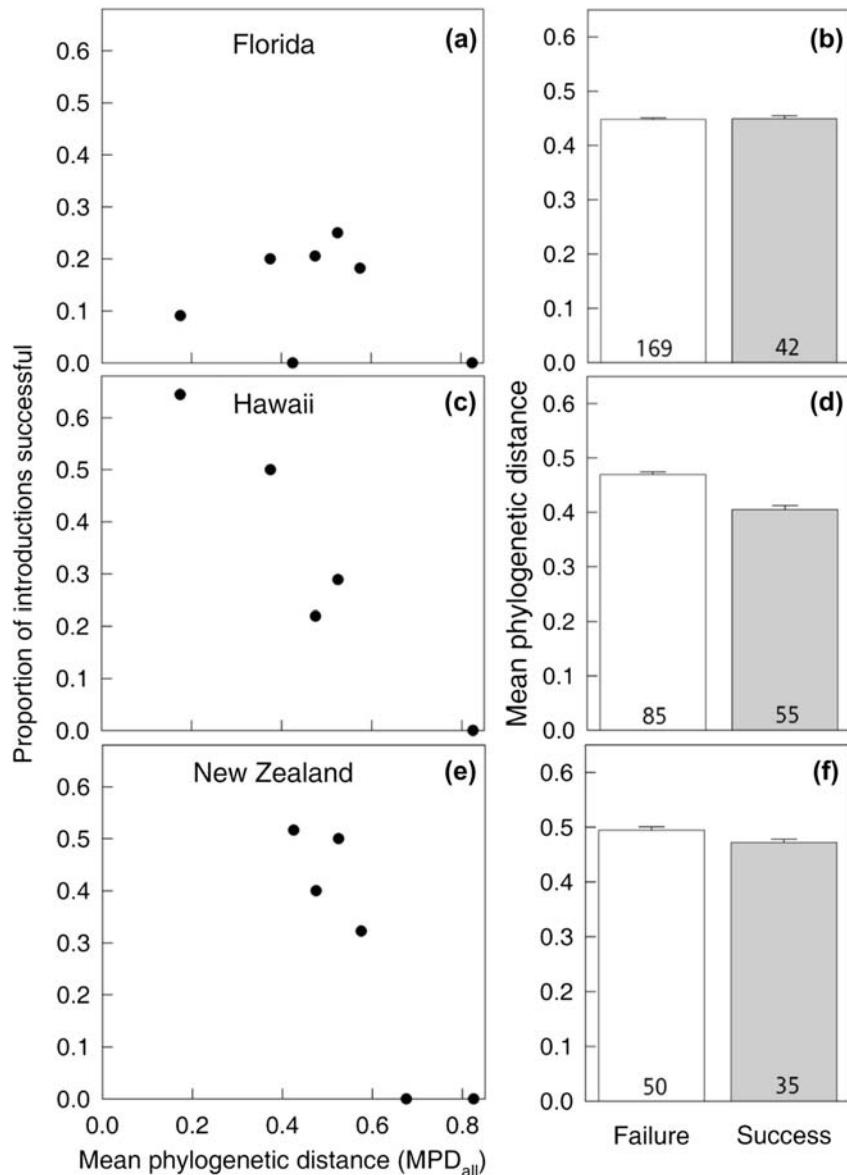
Figure 2. Establishment success of exotic birds increases with decreasing mean phylogenetic distance (MPD$_{all}$) to the extant avifauna in Hawaii (c, d) but not in Florida (a, b) or New Zealand (e, f). The proportion of introductions that were successful (a, c, e) was calculated by binning the data at 0.05 intervals of the phylogenetic distance metric, allowing for a visualization of the linearity of the relationship. Mean distances (± SE) for failed vs successful introductions are shown in (b, d, f) with sample sizes (number of introduced species) indicated at the base of the bar.

of native species in the genus of each introduced species. This commonly used metric failed to show any significant relationship with establishment success for the avifaunas we examined ($\chi^2 = 0.3$, p = 0.568, region $\chi^2 = 19.9$, p < 0.001, number × region $\chi^2 = 0.1$, p = 0.938).

Patterns of establishment success on individual Hawaiian islands

Because patterns of environmental filtering might predominate at larger spatial scales (results above) and patterns of niche-based exclusion might predominate at smaller spatial scales, we examined patterns of establishment success on individual Hawaiian islands. We tested whether individual

islands (n = 6) varied in the direction and strength of the relationship between phylogenetic distance and establishment success. Among the islands, Molokai had the highest percentage of successful introductions (72%, n = 36 introduced species) and Oahu had the lowest percentage (41%, n = 95 introduced species).

Islands differed in the strength (but not the direction) of the relationship between phylogenetic distance and establishment success depending on the assemblage considered (phylogenetic distance × assemblage × island, Table 2). Specifically, all island by assemblage combinations showed significant increases in the probability of establishment success with smaller NND (all p ≤ 0.047), excepting NND$_{naturalized}$ for the islands of Hawaii ($\chi^2 = 2.2$, p = 0.140), Kauai ($\chi^2 = 1.7$, p = 0.191), and Molokai ($\chi^2 = 3.5$, p = 0.063) and NND$_{all}$

Table 2. Influence of phylogeny on establishment success of exotics in the avifaunas of individual Hawaiian islands.

	DF	NND		MPD		MedianPD	
		χ^2	p	χ^2	p	χ^2	p
Phylogenetic distance	`1	13.6	**<0.001**	14.2	**<0.001**	7.2	**0.008**
Assemblage	2	5.8	0.056	11.2	**0.004**	7.4	**0.007**
Island	5	18.2	**0.003**	10.6	0.060	6.3	0.280
Phylogenetic distance × assemblage	2	3.0	0.224	13.6	**0.001**	6.7	**0.010**
Phylogenetic distance × island	5	7.9	0.163	8.0	0.156	5.0	0.417
Assemblage × island	10	17.9	0.056	24.6	**0.006**	17.6	**0.004**
Phylogenetic distance × assemblage × island	10	19.9	**0.030**	27.2	**0.002**	17.7	**0.003**

Results from generalized linear models with the binary response of success/failure for each introduced bird species; likelihood ratio χ^2 values are given for three metrics measuring the phylogenetic distance of an introduced bird species to the extant avifauna. Significant p-values are reported in bold. Total number of observations (species introductions) = 351. Number of successfully introduced species = 190.

for the islands of Hawaii ($\chi^2 = 3.3$, p = 0.070) and Kauai ($\chi^2 = 3.1$, p = 0.078).

For MPD, all combinations of island and assemblage showed significant reductions in the probability of successful establishment with increasing phylogenetic distance, but the strength of these relationships were strongest for MPD_{all} and MPD_{native}, and weakest for $MPD_{naturalized}$. Thus, islands within the Hawaiian archipelago typically showed the strongest relationship between establishment success and phylogenetic distance when invaders were compared to the native bird assemblage.

For MedianPD, all combinations of island and assemblage showed significant reductions in the probability of non-native establishment with increasing phylogenetic distance (p < 0.034), with three exceptions. For Hawaii, the relationship was significant for $MedianPD_{all}$ or $MedianPD_{native}$ ($\chi^2 = 11.8$, p < 0.001) but only marginal for $MedianPD_{naturalized}$ ($\chi^2 = 3.7$, p = 0.056). For Lanai, there was no significant relationship for any assemblage ($MedianPD_{all}$ or $MedianPD_{native}$, $\chi^2 = 2.3$, p = 0.134; $MedianPD_{naturalized}$, $\chi^2 = 1.8$, p = 0.176). For Maui, the pattern was significant only for $MedianPD_{naturalized}$ ($MedianPD_{all}$ or $MedianPD_{native}$, $\chi^2 = 1.9$, p = 0.170, $MedianPD_{naturalized}$, $\chi^2 = 8.9$, p = 0.003). Thus, with the exception of Maui, the trends for MedianPD followed those for MPD, with stronger negative relationships when phylogenetic distances were evaluated against the all or native assemblages than against the naturalized assemblage.

Finally, we evaluated whether island size influenced the relationships between establishment success, phylogenetic distance and assemblage across the Hawaiian islands. Island size was not predictive: main effects of island size on establishment success were insignificant (p = 0.152, 0.191, and 0.251 for NND, MPD, and MedianPD, respectively) and no significant 2- or 3-way interactions of island size with phylogenetic distance and/or assemblage were detected (p > 0.14 in all cases).

Discussion

Recent efforts have revealed the importance of evolutionary history for understanding patterns of biodiversity and community assembly (Webb et al. 2002, Kraft et al. 2007, Cavender-Bares et al. 2009). Utilizing phylogenetic data to predict the susceptibility of communities and regional species pools to invasions may thus provide critical information for managing ecosystems in this time of rapid global change. Our study used a phylogenetic distance approach to determine whether the degree of relatedness to extant taxa is associated with the success of exotic avian species establishment in the wild. In contrast to previous work that has supported Darwin's naturalization hypothesis and the 'shared-enemy hypothesis' for other taxa (Hill and Kotanen 2009, Jiang et al. 2010, Van Wilgen and Richardson 2011), our results suggest that exotic establishment success does not increase with phylogenetic distance to extant taxa at the regional scale, and instead suggest that environmental filtering mechanisms, rather than niche-based exclusion, may govern patterns of invasion for birds.

Phylogenetic patterns of exotic species establishment

Close relatedness to the extant avifauna was generally associated with increased establishment success of exotic birds. This relationship was consistent across the three regions for NND and MedianPD, but for MPD the strength of the relationship varied by region, with Hawaii showing the clearest pattern. Thus, for birds, it may be that the advantage of pre-adaptation to an environment (including abiotic and biotic factors) outweighs the opposing forces of competition and shared natural enemies in affecting establishment success.

We found that calculating phylogenetic distances to subsets of the extant avifauna (just natives or just naturalized species) did not increase the strength of the relatedness-establishment relationships, indicating that all species present were potentially important in predicting establishment success. This makes sense, given that the presence of both natives and exotics should provide complementary information on potential environmental filters. For example, many introduced species are associated with human-modified habitats (e.g. urban and agricultural habitats) (Duncan et al. 2003). Thus, for a given focal introduced species, close relationship to a naturalized species could indicate that it has the traits necessary to persist in such human-dominated areas. In turn, close relationship to natives could indicate that a species has the traits necessary to persist in the face of a region's particular abiotic and biotic conditions, such as temperature, rainfall, seasonality, predators, and parasites. Future work examining spatial clustering of naturalized species into particular habitats and the traits allowing their persistence would be valuable for validating this scenario.
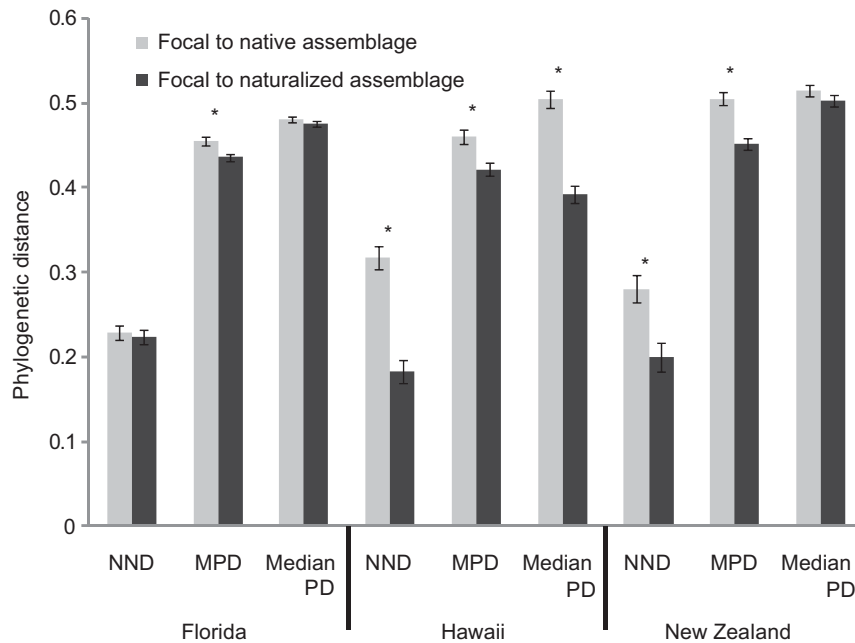
Figure 3. Introduced bird species are generally phylogenetically dissimilar to the native species assemblage: on average, focal introduced species are more closely related to naturalized species than to native species for at least some phylogenetic distance metrics. Asterisks indicate significant ($p < 0.004$) differences. For NND: assemblage $F_{1,361} = 49.1$, $p < 0.0001$; site $F_{2,72} = 2.3$, $p = 0.106$, assemblage $\times$ site $F_{2,72} = 17.5$, $p < 0.0001$. For MPD: assemblage $F_{1,361} = 3.1$, $p < 0.0001$; site $F_{2,72} = 14.0$, $p < 0.0001$, assemblage $\times$ site $F_{2,72} = 3.2$, $p = 0.045$. For MedianPD: assemblage $F_{1,361} = 49.2$, $p < 0.0001$; site $F_{2,72} = 27.4$, $p < 0.0001$, assemblage $\times$ site $F_{2,72} = 37.0$, $p < 0.0001$.

Our results contrast with recent work showing that the degree of establishment success of newly introduced species in both laboratory bacterial communities (Jiang et al. 2010) and natural reptile communities (Van Wilgen and Richardson 2011) declined with relatedness to the extant community. These opposing outcomes suggest that patterns may depend on the identities of the taxa, the environments, and/or the relative spatial scales examined. For example, Jiang et al. (2010) examined bacterial species introduced into communities within a 10 ml medium solution offering little environmental heterogeneity. Environmental heterogeneity also increases with spatial scale, potentially reducing competitive interactions and allowing higher levels of phylogenetic clustering (Cavender-Bares et al. 2009). Although heterogeneity is not a mechanism that would drive clustering, it could release taxa from the opposing action of biotic interactions. Thus, closely related species may be allopatric on a fine spatial scale, but show patterns consistent with environmental filtering on a regional scale (Lovette and Hochachka 2006, Thuiller et al. 2010). However, Van Wilgen and Richardson (2011) found evidence for Darwin's naturalization hypothesis in introduced reptile communities at a regional (California and Florida) scale, suggesting that factors other than spatial scale may also play a role in determining the relationship between community phylogenetic structure and establishment success.

Phylogenetic dissimilarity of introduced species to the native assemblage

Introduced bird species were on average significantly more closely related to the naturalized species than to the native species for at least one distance metric in each region (Florida: MPD; Hawaii: MPD, NND, MedianPD; New Zealand: MPD, NND). This is consistent with introductions being a non-random sample of the global species pool. This was expected because a large fraction of bird introductions are deliberate (Long 1981) and thus chosen based on specific traits valued by humans; because of niche and trait conservatism (Webb et al. 2002, Wiens and Graham 2005), these species are likely to be closely related. For example, in Hawaii, Galliformes were specifically selected for introduction by the Foreign Game Introduction Program of the U.S. Fish and Wildlife Service (Lewin 1971), presumably because these species possess traits which make them suitable as game (large body mass and large populations; Blackburn and Duncan 2001). In fact, most species of birds introduced to oceanic islands belong to just one of two orders, Passeriformes or Galliformes (Moulton et al. 2001b).

The pattern that an introduced bird species is likely to be phylogenetically closer to naturalized (vs native) species may also reflect phylogenetically conserved traits that make some species more successful at establishment (Lockwood 2005). These traits could be directly beneficial to establishment (e.g. wide environmental tolerances), or the traits could indirectly benefit establishment by increasing introduction pressure, which has been linked to greater establishment in birds (Cassey et al. 2004). For example, abundance is a trait that could increase introduction pressure (and may show phylogenetic signal; Hardy 2008); in previous work with birds, species that were more common in their native environment were more likely to be introduced to new habitats than were less common species (Blackburn and Duncan 2001). Importantly, however, we saw evidence that phylogenetic dissimilarity of those introductions to natives is not

a necessary condition for finding that phylogenetic distance predicts establishment success. For example, introduced species in Florida were equally related to the native vs naturalized assemblages via the NND metric (Fig. 3) but NND nevertheless predicted establishment success in Florida (Table 1, Fig. 1).

Phylogenetic distance versus taxonomy-based estimates of relatedness

Many studies correlating relatedness to native species with the establishment success of non-native species have relied on comparisons involving the number of congeneric species in the extant community (Daehler 2001, Duncan and Williams 2002, Lambdon and Hulme 2006, Ricciardi and Mottiar 2006). Here, we showed that the number of congeneric natives was not predictive of establishment success, despite significant results when using phylogenetic distance measures. These results suggest that the lack of relationship between the number of congenerics and establishment success in some previous studies (Lambdon and Hulme 2006, Ricciardi and Mottiar 2006) may indicate use of an inappropriate metric rather than the absence of a phylogenetic pattern. Given that generic circumscriptions are human constructs, the number of congeners is a more subjective and artificial measure for determining relatedness than quantitative distance measures. The non-equivalence of genera could potentially bias results because average relatedness among congeners is unlikely to be the same for any given pair of genera.

Implications and conclusions

Our results do not support Darwin's naturalization hypothesis as an explanation of regional species assembly patterns in birds. Instead, they suggest that environmental filtering may be more important than shared enemies or competition in the establishment of exotic bird species. It is important to note, however, that our failure to find evidence supporting a role of competition/shared enemies in determining avian establishment success does not necessarily imply that these processes are not important in avian community assembly, but may rather reflect our inability to detect evidence of these biotic interactions at a regional or sub-regional scale. Relatedness patterns likely reflect competition/shared enemies at small scales and environmental filtering at larger scales (Lovette and Hochachka 2006, Thuiller et al. 2010). In previous studies of the phylogenetic structure of native bird communities, evidence for competition has been found under certain conditions: at small spatial scales for North American wood-warblers (Lovette and Hochachka 2006), and at in wet, low elevation environments for tropical hummingbirds (Graham et al. 2009). Our results may differ from these studies because of our focus on highly invaded (as opposed to native) communities and on larger spatial and taxonomic scales. Our results also contrast with studies of mammals, which commonly demonstrate over-dispersed phylogenetic community structure relative to random models (Cardillo et al. 2008, Cooper et al. 2008). However, patterns of avian and mammalian community assembly may differ because of differing dispersal abilities (see Sax et al. 2002 for

a discussion of the outcomes of increased introduction pressure for groups differing in vagility) or other taxon-specific factors. Similarly, contrasts between results of this study and those of previous work examining establishment success of microbes (Jiang et al. 2010) and reptiles (Van Wilgen and Richardson 2011) suggest caution in making broad generalizations about the direction and strength of the relationship between phylogenetic distance and establishment success, as patterns may be unique to specific taxa, regions, and/or spatial scales. Our results also support the general utility of phylogenetic distance metrics for understanding community assembly and invasion.

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Supplementary material (Appendix E7176 at <www.oikosoffice.lu.se/appendix>). Appendix 1–2.