



Untangling the positive association of phylogenetic, functional, and taxonomic diversity with alien bird species richness

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Citation: Andrikou-Charitidou, A., G. Boutsis, E. Karadimou, and A. S. Kallimanis. 2020. Untangling the positive association of phylogenetic, functional, and taxonomic diversity with alien bird species richness. *Ecosphere* 11(2): e03007. 10.1002/ecs2.3007

Abstract. Understanding the ecological mechanisms behind biological invasions remains a major focus of conservation biology and ecosystem management. Several hypotheses highlight that different facets of native biodiversity affect the establishment and spread of alien species. Here, we approach this question by examining the spatiotemporal relationship between alien bird species richness and different facets of biodiversity (taxonomic, functional, and phylogenetic) using breeding bird atlases for three U.S. states and for two time periods in each state. We associated native species richness, and functional and phylogenetic diversity with alien species richness, using generalized least squares models. Our results show that, consistently, across the three states and two time periods examined, alien species richness is positively associated with native diversity, and particularly with phylogenetic diversity. The relative importance of biodiversity metrics reflecting the functional or phylogenetic range occupied by the assemblage seems to advocate in favor of the importance of resource diversity as a main driver of both native and alien diversity. The secondary importance of biodiversity facets reflecting species functional or phylogenetic similarity, along with the lack of importance of functional or phylogenetic clustering or overdispersion, implies that if this relationship is shaped by biotic interactions, then biotic interactions facilitating coexistence (including even processes like predator-mediated coexistence) are far more important than adversarial interactions like competition, at least at the scale of our analysis. Finally, the dominance of phylogenetic metrics over functional ones highlights the adaptive potential of a community accumulated over long lineage history may play an additional role as a source of information on evolutionary processes driving diversity patterns.

Key words: alien species; biological invasions; breeding birds; coarse spatial scale; functional diversity; native species; phylogenetic diversity; taxonomic diversity.

Received 20 June 2019; revised 22 October 2019; accepted 7 November 2019. Corresponding Editor: Paige S. Warren.

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INTRODUCTION

The invasion of alien species is one of the major causes of biodiversity loss, having severe economic and environmental consequences throughout the world (Millennium Ecosystem Assessment 2005). Therefore, understanding the factors shaping the susceptibility of natural communities to invasions remains a key focus of invasion ecology. In this framework, the role that local biodiversity plays in the establishment and

spread of alien species is one of the oldest and still ongoing debates in invasion ecology. Elton (1958) was the first to suggest that fairly rich natural communities would resist the invasion of alien species, since species-rich communities could utilize the available resources more effectively, leaving less resources for alien species (Levine et al. 2004), and/or since they will host a wider array of enemies, parasites, or pathogens that could increase the communities' resistance to invasions (Maron and Vilà 2001). While these

hypotheses remained ingrained in invasion ecology for decades, empirical studies led to the formulation of an opposing hypothesis, which proposes that species-rich communities are more inviting to alien species, since high species richness could indicate higher resource availability for both native and alien species (Stohlgren et al. 2003, 2006).

As a result, the native–alien diversity relationship has been extensively studied over the last two decades, but there is yet no consensus. The bulk of this literature quantifies diversity as species richness, and several studies support the resistance hypothesis, that is, that higher native species' richness is negatively associated with alien species introduction or establishment, using in most cases experimental treatments of plant communities at fine spatial scales (Fridley et al. 2007, Ackerman et al. 2017). However, observational studies examining several taxa (including birds) at coarser spatial scales found consistently positive associations among native and alien species richness (Dyer et al. 2017a, McKinney and Kark 2017, Peng et al. 2019).

The association between native diversity and alien species is not supposed to be an effect of diversity per se, but it is the product of diversity usage as a proxy for other harder to quantify processes (like resource utilization, or biological control through enemies and parasites). On that account, though taxonomic diversity quantified as species richness is the most widely studied facet of biodiversity, it may not be the most informative for the issue at hand. Recently, research has started examining other facets of biodiversity. Functional diversity could be a better indicator of resource partitioning and utilization in the communities than species richness (Dukes 2001), while phylogenetic diversity could add an evolutionary dimension (Gerhold et al. 2011).

So far, there are few studies examining the role of phylogenetic diversity as a driver for alien species. Most of these studies focus on the phylogenetic relatedness between alien and native species, probing if more related species have a greater chance of establishment, since they would share similar ecological needs and limitations, or lower chance of establishment, due to higher levels of interspecific competition (e.g., Carboni et al. 2016). But far less research has focused on the role that the phylogenetic

diversity of the resident community plays in shaping an area's invasibility. To date, these studies are overwhelmingly pointing to the same direction. Phylogenetically poor communities are more inviting to alien species (Gerhold et al. 2011). High phylogenetic diversity has been associated with a decrease in alien species abundance in an experimental plant community (Whitfield et al. 2014), as well as in natural plant communities (Iannone et al. 2016, Ng et al. 2019). Studying bacteria communities, Ketola et al. (2017) found negative or no association between phylogenetic diversity and invasion success. So far, there are no empirical results of a positive association between phylogenetic diversity and the establishment or spread of alien species.

Another biodiversity facet that is thought to influence a community's association with alien species is functional diversity. Extensive research has investigated the functional similarity among native and alien species and the traits promoting the establishment and spread of alien species (Catford et al. 2019). Communities with high native functional diversity are expected to use available resources more effectively and exhaustively (Hejda and de Bello 2013) and provide fewer opportunities for alien species to establish compared to communities with low functional diversity (Fridley and Sax 2014, Lososová et al. 2015). It stands to reason that we would expect studies of functional diversity to explain the phenomenon more efficiently than phylogenetic diversity, which is commonly (and perhaps inappropriately) used only as a proxy for functional diversity (Gerhold et al. 2015). Empirical studies have shown that functionally diverse communities contain less alien species (Hooper and Dukes 2010). Native species' functional richness has been reported to help native communities resist alien species establishment (Maron and Marler 2007) or reduce the available resources and indirectly resist the successful establishment of alien species (Dukes 2001). On the other hand, high functional diversity may also be an indicator of high resource diversity and a sign of more opportunities for establishment. Thus, it is also likely that communities with high native species functional diversity would be more prone to invasion. Despite the lack of studies documenting a positive association among functional diversity and aliens in the current literature,

Mason et al. (2017) have shown that functional richness did not affect the invasibility of experimental plant communities.

Functional and phylogenetic clustering or overdispersion (quantified as deviations from random expectations given the species richness) is often used to infer community assembly mechanisms like limiting similarity or environmental filtering (de Bello et al. 2012, Karadimou et al. 2015). But community assembly mechanisms, like competition (which is thought to lead to overdispersion), might signify a local community that is more resistant to biotic invasions. The link between phylogenetic or functional clustering or overdispersion of the native communities and its vulnerability to alien species has produced ambiguous results. Lososová et al. (2015) showed that alien species favored more clustered communities and a negative association between phylogenetic diversity and alien species richness. Iannone et al. (2016) showed that increased phylogenetic clustering limits alien species dominance and establishment.

So far, the debate over how biodiversity affects a region's invasibility remains far from settled, with evidence for both positive and negative associations. The use of different facets of biodiversity in this debate highlighted the existence of multiple mechanisms, most of which are not mutually exclusive. The use of all these facets of diversity simultaneously may provide insight into the relative importance of these multiple hypotheses on the relationship between native and alien biodiversity: (1) If resource partitioning was the main driver of this relationship, variables like similarity among species in the community or community assembly metrics indicating limiting similarity would dominate producing negative associations. (2) If resource diversity was the main driver, then metrics of the range of functional trait diversity should prove to be important, producing positive associations. (3) If adaptive potential to novel species is the main driver, then phylogenetic diversity may play a pivotal role. (4) If facilitative interactions among species (promoting coexistence) are more important than negative interactions (like competition), we would expect positive associations among native and alien diversity across the spectrum of diversity facets.

To our knowledge, there has yet to be a study that simultaneously investigates the relative

importance of the various facets of biodiversity in regard to communities' invasibility. Here, we try to untangle the relative importance of the different aspects of native biodiversity in determining the area's invasibility, that is, the diversity of alien species present. Most previous studies examined only one study area or time period, striving to extract the large-scale patterns, while we examined three different U.S. states (New York, Pennsylvania, Massachusetts) at two different time periods (twenty years apart) in each case. We used a wide array of biodiversity metrics: (1) from the most often used species richness (reflecting taxonomic diversity) to (2) functional diversity metrics encapsulating either the range of traits observed in an area (functional richness) or (3) the functional similarity among the species of the area (functional dispersion, Rao's quadratic entropy) and (4) phylogenetic diversity metrics reflecting the length of the phylogenetic tree occupied by the species in the community (Faith's PD) or (5) the phylogenetic relatedness among the species (mean nearest taxon distance [MNTD], mean pairwise distance [MPD]). Furthermore, to quantify functional or phylogenetic clustering or overdispersion, we used null model analysis to estimate the deviance of the observed values of all these metrics from random expectations given the species richness.

MATERIALS AND METHODS

Breeding bird species data sets

We analyzed data on avian species diversity and distribution for three U.S. states of the East Coast: New York, Pennsylvania, and Massachusetts, from the Breeding Bird Atlases of these states for two distinct time periods (1980s and 2000s). For the New York state, we used The Atlas of Breeding Birds in New York State from a long-term volunteer-based program that was conducted from 1980 to 1985 (Andrle and Carroll 1988), as well as The Second Atlas of Breeding Birds in New York State that was conducted from 2000 to 2005 (McGowan and Corwin 2008). For the Pennsylvania state, we used the first Atlas of Breeding Birds in Pennsylvania (Brauning 1992), covering the 1980s period, as well as the second Atlas of Breeding Birds in Pennsylvania (Wilson et al. 2012), covering the period from 2004 to 2009. For the Massachusetts

state, we used the Massachusetts Breeding Bird Atlas 1 project, which mapped the distribution of the breeding birds in the state and cover the period from 1974 to 1979 (Petersen and Meservey 2003). The Massachusetts Breeding Bird Atlas 2 covers the period 2007 and 2011 (Kamm et al. 2013).

Breeding bird distribution data for New York were collected by dividing the state in 25-km² cells. In Pennsylvania and Massachusetts, the basic survey unit was defined as one-sixth of a standard U.S. Geological Survey 7.5-min topographic map (approximately 24.8 km²). Only the common cells between the two atlases of each state were included in the analysis, for comparison reasons. In New York, 5216 cells were used in the analyses, in Pennsylvania 4763, and in Massachusetts 931. The three data sets analyzed comprised of the presence data of bird species. Nomenclature of bird species follows the American Ornithological Society Birds of North and Middle America Checklist (Chesser et al. 2018). We identified alien species status in each state following the Global Avian Invasions Atlas, a database of worldwide alien bird distributions (Dyer et al. 2017b). For each atlas, we calculated the total number of native and alien species and the mean number of native and alien species per cell (i.e., native and alien species richness). For each native and alien species, we calculated the percentage of cells occupied in each atlas.

Functional traits

We compiled 16 ecological and life-history traits for the bird species recorded at each of the three states on the basis of the traits data set published by Barnagaud et al. (2017) and followed the same methodology to compile data for the additional species present in our data sets (Appendix S1: Table S1). The (categorical and quantitative) functional traits used in this analysis are grouped into three categories: (1) ecological traits (primary habitat, nest location, nest type, foraging strategy, main diet) reflecting the extent to which species overlap in their use of habitat and dietary resources; (2) life-history traits (territoriality, migration, developmental mode, log-transformed body mass, wingspan, body length) that separate sedentary species with large body sizes and large home ranges

from smaller species with smaller territories; and (3) reproductive traits (number of broods per year, clutch size, mating, chick-rearing mode, maximum life span) that are related to breeding performances and duration of life cycle (Barnagaud et al. 2017).

Taxonomic, phylogenetic, and functional diversity

Taxonomic diversity is represented in this study by species richness (i.e., the number of different species recorded in each atlas cell). For quantifying native species' functional diversity, we applied the approach of the multidimensional space, where each trait represents an axis and each species a point in the multidimensional space defined by the traits describing each species. We used three multidimensional functional diversity metrics, which explore different facets of functional diversity: (1) functional richness (FRic), (2) functional dispersion (FDis), and (3) Rao's quadratic entropy (RaoQ) for each atlas cell. All metrics were calculated using the FD package in R (Laliberté et al. 2014).

We calculated three metrics of phylogenetic diversity for the native species, using the avian supertree constructed by Jetz et al. (2012): (1) Faith's phylogenetic diversity (PD), the sum of the total phylogenetic branch length connecting the native species in each cell, (2) MPD, the average value of the pairwise phylogenetic distances among the native species, and (3) MNTD, the average value of the distances between each native species and its nearest phylogenetic neighbor in each cell, using the picante package in R (Kembel et al. 2010).

All metrics were calculated for each pair of atlases for the three U.S. states.

Null models

The diversity metrics used in this analysis (both functional and phylogenetic) are (strongly or weakly) positively (FRic, RaoQ, PD, MPD) or negatively (MNTD) correlated with species richness. Therefore, we used a null model approach based on the standardization of the metrics to the observed species richness in each cell. The simulated assemblages were constructed using the natives' species pool. For each metric, the standardized effect size (SES) was estimated comparing the observed value with the mean value from the simulations standardized by the

variance of the simulations. The SESs of the phylogenetic metrics were calculated with the picante package in R (Kembel et al. 2010). Positive SES values indicate an observed diversity value higher than average null value (i.e., overdispersion), and negative values indicate an observed diversity value that is lower than average (i.e., clustering; Swenson 2014). Since we have standardized the effect size, SES values are more comparable across communities.

Data analysis

We analyzed the relationship between the metrics of biodiversity (species richness, and functional and phylogenetic metrics) and alien species richness. We correlated each metric with alien species richness using the modified t-test from the R package SpatialPack (Osorio and Vallejos 2014).

Next, we examined which combination of metrics best explained alien species richness patterns in each atlas. To account for spatial autocorrelation, we used generalized least squares models, using the nlme package in R (Pinheiro et al. 2014), starting with a full model that contained all of the biodiversity indices as predictors and alien species richness as the response variable, and used a backward model selection based on the Akaike information criterion (AIC) with the stepAIC function of the MASS R package (Venables and Ripley 2002), to reach the minimum adequate models (MAMs) with the smallest AIC values, containing the smallest possible number of predictors. For each MAM, we calculated a pseudo- R^2 to estimate the explanatory capability of the models, using the rcompanion package in R (Mangiafico 2019). Furthermore, we followed the same process generating multiple predictor models using (1) only the functional indices and (2) only the phylogenetic indices as predictors. All analyses were performed in R (R Development Core Team 2018).

RESULTS

Alien species richness

Alien species accounted for about the 10% of total avifauna recorded in the three states (Table 1). In New York, 245 species were recorded in the first atlas, 25 of which were alien. In the second atlas, 251 species were recorded, 25

of which were alien. In Pennsylvania, 210 species were recorded in the first atlas, of which 21 were alien, while in the second atlas, 226 species were recorded, 22 of which were alien. In Massachusetts, 200 species were recorded in the first atlas, 25 of which were alien, while in the second atlas, 205 species were recorded, 24 of which were alien. In all atlases, the proportion of the atlas cells occupied by native species was greater than the proportion of cells occupied by alien species (Table 1). The mean occupancy of native species ranged between 15% in Pennsylvania and 25% in New York, while the mean occupancy of alien species ranged between 3% and 5%. Overall in New York and Massachusetts, there was a slight increase in occupancy values between 1980s and 2000s, while in Pennsylvania, there was a slight decrease (Table 1).

In all atlases, the number of native species per cell was greater than the number of alien species per cell (Table 1). The mean richness of native species per cell ranged between 33.9 in Pennsylvania and 63.3 in New York, while the mean richness of alien species per cell ranged between 6.6 in Pennsylvania and 11.2 in Massachusetts. In New York and Massachusetts, there was a slight increase in richness values between 1980s and 2000s, while in Pennsylvania, there was a slight decrease over time (Table 1). Overall, in 62% of the cells in New York the number of alien species increased between 1980s and 2000s, while in 32% it decreased and in 6% it remained the same. Massachusetts displayed a comparable pattern of change between 1980s and 2000s, with increase in 69% of cells, decrease in 28% of the cells, and no change in 3% of the cells. Pennsylvania, on the other hand, had fewer alien species per atlas cell in the second atlas (2000s) compared to the first atlas (1980s), alien species richness decreased in 53% of the cells, while it increased in 43% of the cells, and 4% showed no change.

Native species diversity indices and alien species richness

The results of the correlations between native species diversity indices and alien species richness analyses show a clear positive relationship. Each state displayed a slightly different pattern on the ranking of the relative importance of different aspects of biodiversity (species richness,

Table 1. Mean number of native and alien species per cell and mean percentage of cells occupied by each native and alien species in the three sets of atlases analyzed.

Atlas	No. of native species	No. of alien species	Mean per cell		Mean percentage of cells occupied	
			Native species	Alien species	Each native species	Each alien species
New York 1980s	220	25	60.7	7.9	24	3
New York 2000s	226	25	63.3	9.2	25	4
Pennsylvania 1980s	189	21	35.6	6.9	17	3
Pennsylvania 2000s	204	22	33.9	6.6	15	3
Massachusetts 1980s	175	25	39.2	8.3	19	4
Massachusetts 2000s	181	24	47.6	11.2	23	5

functional diversity, or phylogenetic diversity) on the native–alien relationship.

Single predictor models

All of the native species diversity indices correlated positively with each other, except for MNTD, which had a negative correlation with the rest of the indices. The results of the single predictor models show each indices' separate relationship with alien species richness.

For New York, phylogenetic diversity showed the strongest correlation with alien species richness, while functional richness showed the weakest correlation with alien species richness and MNTD was not correlated with alien species richness (Table 2). For Pennsylvania, phylogenetic diversity showed the strongest correlation with alien species richness, while MNTD had the weakest correlation, which was negative (but MNTD correlated negatively with native species richness, PD and MPD; Table 2). Similar results for Massachusetts, as phylogenetic diversity, showed the highest correlation with alien species richness and MNTD the lowest (Table 2).

Across all states and time periods, SESs of all indices (indicators of clustering or overdispersion) showed weak to nonsignificant correlations with alien species richness (Table 2).

Multiple predictor models

Backward selection and hierarchical partitioning of the multiple predictor models showed that the variables that contributed the most were native phylogenetic diversity (which was important in five of the six models and the most important in four of the six) followed by functional richness (which was important in four of the six

models; Table 3). Analyzing the diversity indices with the highest contribution (>18%) to the MAMs, native species richness had this level of importance in only two of the six models. The SES values of the functional and phylogenetic indices were almost always not important (except the SES values of FDis in two models). Pseudo- R^2 showed that the MAMs have an adequate explanatory capability for alien species richness (Table 3).

The multiple predictor models using only phylogenetic diversity indices as predictors had higher explanatory capability compared to the models using only functional diversity indices as predictors (Table 4). PD was the sole contributor in two of the six models, and the combination of PD and MNTD was the most common (four out of six models). Even when PD was the only predictor in the MAM, it explained more variance than all functional diversity indices together.

DISCUSSION

We found that alien species richness is strongly positively associated with native biodiversity for the breeding birds of three U.S. states over two time periods. Contrary to published studies, the functional and phylogenetic diversity facets, examined in this study, repeatedly displayed positive correlations with alien species richness across space and time. Among the different aspects of biodiversity, phylogenetic diversity displayed systematically the strongest positive correlations with alien species richness, followed by functional richness and species richness. The phylogenetic and functional diversity metrics quantifying the range of the species assemblage

Table 2. Single predictor model results of the correlations between native species diversity indices and alien species richness in the three pairs of atlases analyzed.

Predictors	New York 1980s	New York 2000s	Pennsylvania 1980s	Pennsylvania 2000s	Massachusetts 1980s	Massachusetts 2000s
Species Richness	0.42 (343)***	0.53 (125)***	0.65 (2749)***	0.69 (476)***	0.66 (159)***	0.69 (57)***
FRic	0.32 (733)***	0.36 (238)***	0.66 (645)***	0.67 (719)***	0.76 (160)***	0.56 (232)***
FDis	0.51 (55)***	0.53 (127)***	0.45 (428)***	0.40 (704)***	0.29 (261)***	-0.05 (90) <i>ns</i>
RaoQ	0.46 (74)***	0.48 (197)***	0.45 (478)***	0.40 (790)***	0.30 (261)***	-0.03 (109) <i>ns</i>
PD	0.55 (150)***	0.59 (110)***	0.72 (476)***	0.75 (582)***	0.77 (149)***	0.74 (108)***
MPD	0.46 (102)***	0.41 (214)***	0.48 (422)***	0.34 (792)***	0.41 (248)***	0.15 (268)***
MNTD	0.14 (108) <i>ns</i>	-0.03 (207) <i>ns</i>	-0.17 (1200)***	-0.28 (1412)***	-0.15 (593)***	-0.36 (98)***
SES.FRic	0.15 (214)*	0.15 (279)*	0.10 (918)**	0.03 (1839) <i>ns</i>	0.08 (249) <i>ns</i>	-0.08 (271) <i>ns</i>
SES.FDis	0.28 (49)*	0.29 (130)***	0.07 (423) <i>ns</i>	0.01 (715) <i>ns</i>	-0.08 (198) <i>ns</i>	-0.25 (51) <i>ns</i>
SES.RaoQ	0.20 (57) <i>ns</i>	0.23 (168)**	0.01 (463) <i>ns</i>	-0.06 (798) <i>ns</i>	-0.11 (209) <i>ns</i>	-0.26 (55) <i>ns</i>
SES.PD	0.52 (71)***	0.39 (174)***	0.19 (611)***	0.02 (752) <i>ns</i>	0.09 (273) <i>ns</i>	-0.11 (66) <i>ns</i>
SES.MPD	0.28 (68)*	0.15 (171) <i>ns</i>	0.06 (425) <i>ns</i>	-0.15 (690)***	-0.14 (308)*	-0.22 (63) <i>ns</i>
SES.MNTD	0.44 (93)***	0.32 (217)***	0.36 (775)***	0.19 (1006)***	0.17 (28)***	-0.03 (113) <i>ns</i>

Notes: Standardized effect size (SES) of the functional and phylogenetic indices was estimated by comparing the observed value of the indices to the mean value estimated from 999 simulations, standardized by the variance of the simulations. Table shows the R value of the correlations. The degrees of freedom of the models after accounting for spatial autocorrelation are given in the parentheses. Nonsignificant correlations are presented in italics.

ns $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 3. Native species diversity indices with the highest contribution (>18%) to the minimum adequate models (MAMs) and pseudo- R^2 of the MAMs.

Predictors with the highest contribution to the MAMs	Atlas	pseudo- R^2
PD + FDis + RaoQ + SES.FDis	New York 1980s	0.41
SR + PD + FRich + SES.FDis	New York 2000s	0.44
PD + FRich	Pennsylvania 1980s	0.53
SR + FRich + FDis + RaoQ	Pennsylvania 2000s	0.55
PD + MPD + FRich	Massachusetts 1980s	0.63
PD + MNTD	Massachusetts 2000s	0.49

Notes: Standardized effect size (SES) of the functional and phylogenetic indices was estimated by comparing the observed value of the indices to the mean value estimated from 999 simulations, standardized by the variance of the simulations. All indices with contribution to the MAMs are included in Appendix S1: Table S2.

seem to play a more important role than the metrics of pairwise similarities among species. Additionally, the metrics used to assess clustering or overdispersion seem to be weakly to nonsignificantly associated with alien species richness. These patterns have not changed over the 20 yr between the first and the second atlases of the breeding birds and across the three U.S. states analyzed.

For species richness, positive native–alien associations have been previously reported for large spatial scales, similar to the scale of analysis in our study (McKinney and Kark 2017). These patterns are in accordance with the rich-get-richer biotic acceptance hypothesis (Stohlgren et al. 2003). So far, the vast majority of the literature examining the relationship between native and alien biodiversity focuses exclusively on species richness (e.g., Hejda and de Bello 2013, Loiola et al. 2018). Our analysis indicates that this common practice may need rethinking. Although species richness is the easiest to calculate aspect of biodiversity, it is not the most informative, since it did not display the strongest correlations with alien species richness, but, in most cases, it offered little to no additional information to other, more informative, diversity aspects.

Elton (1958) kicked off the debate on biodiversity impacts on biological invasions, positing that, in biodiversity-rich areas, it would be more likely that all the available niches are occupied, and alien species would fail to establish. Since functional diversity metrics quantify precisely this facet of biodiversity (the range of traits present in the species assemblage), the intuitive expectation (as also depicted in most of the published results) indicated that functional diversity

Table 4. Diversity indices with contribution to the minimum adequate models (MAMs) using only (1) the functional indices as predictors and (2) the phylogenetic indices as predictors and pseudo- R^2 of the MAMs.

Predictors with contribution to the MAMs	Atlas	pseudo- R^2
<i>Functional indices</i>		
FRich + FDis + RaoQ	NY 1980s	0.25
FRich + FDis + RaoQ	NY 2000s	0.30
FRich + FDis + RaoQ	PA 1980s	0.41
FRich + FDis + RaoQ	PA 2000s	0.42
FRich + FDis + RaoQ	MA 1980s	0.54
FRich + FDis + RaoQ	MA 2000s	0.31
<i>Phylogenetic indices</i>		
PD + MPD + MNTD	NY 1980s	0.38
PD + MNTD	NY 2000s	0.30
PD	PA 1980s	0.48
PD + MNTD	PA 2000s	0.48
PD	MA 1980s	0.60
PD + MNTD	MA 2000s	0.46

should display the strongest associations with alien species richness. The relationship between a community's functional diversity and its invasibility has been studied mainly through small-scale experimental treatments of plant communities, where more functionally diverse communities inhibit the establishment and growth of alien species (Dukes 2001, Maron and Marler 2007, Zheng et al. 2018). Our large-scale observational study results contradict these findings, since high native functional diversity was positively associated with alien species richness. A possible explanation for this contradiction is that, in small-scale studies, biotic interactions (such as competitive exclusion) are more likely to be detected, but other processes (like predation and parasitism) are hard to become established and monitor. Also, in experimental manipulations, functional diversity does not reflect resource diversity and availability or habitat heterogeneity, since the latter are held constant across functional diversity levels. According to our results, among functional diversity metrics, functional richness displayed the strongest correlation with alien species richness in New York, but, in Massachusetts and Pennsylvania, functional dispersion displayed stronger correlation with alien species richness. Also, functional richness was the functional diversity metric that contributed the most to the multiple

predictor models. These findings seem to imply that the diversity of resources may play a more important role than competitive species interactions in shaping alien biodiversity patterns. Alternatively, if biotic interactions are the main driver, the consistently positive relationship between native biodiversity and alien species richness may indicate that positive cooperative interactions with native species (like facilitation) could play a far more important role in shaping alien biodiversity patterns than adversarial ones (like competition).

Although native functional diversity appears to be important, native phylogenetic diversity was proven a systematically stronger factor in driving alien diversity. That was not what we expected. A possible explanation might be the trait selection conundrum, that is, the probable dependence of the functional diversity patterns on the traits selected for the quantification of functional diversity (Tsiangou and Kallimanis 2016, 2019). Thus, while we did use the traits most commonly studied in birds (like body size, reproductive strategy, feeding habits, and habitat preference), it is possible that these traits were not the most relevant for the native–alien interaction. Therefore, we could not exclude the possibility that some other traits might be more effective for quantifying the biotic interactions between natives and aliens, and their functional diversity patterns might perform better. A likely explanation for the superior performance of phylogenetic diversity is that it is a source of information on evolutionary processes driving diversity patterns. Phylogenetic diversity reflects the accumulation of adaptations through species' evolutionary history, so it stands to reason that preadaptation may play an important role in explaining the observed patterns. Phylogenetic diversity also includes the evolutionary relationships between species. The aggregation of a wide array of evolutionary lineages persisting in the same area might imply the accumulation of several adaptations, some of which could reflect the potential of a different purpose from the one they currently serve (a phenomenon known as preadaptation, e.g., see Donoghue 2008). In our case, this alternative purpose could promote the coexistence between natives and aliens.

Another alternative explanation, that we could not explicitly test, could involve enemies and

parasites theory (Maron and Vilà 2001). Areas with high phylogenetic diversity are expected to additionally host a wider array of enemies, parasites, and pathogens of these native species. The existence of diverse enemies in a community increases the probability that some of these enemies could also affect the alien species that invade the community. The existence of enemies may lead to the extirpation of aliens, but it may also lead to control of their population abundance so as not to become unusually numerous. Thus, the control of population growth may lead to coexistence, even in cases where the native community could competitively exclude species, through phenomena like predator-mediated coexistence. This could not be confirmed in our study, since we analyzed only the presence of alien species and not their population abundances.

Functional and phylogenetic clustering or overdispersion is often used to infer community assembly and, in some cases, community resistance to invasions (e.g., Iannone et al. 2016). In our analysis, functional and phylogenetic diversity per se played a more important role in shaping alien diversity patterns, while clustering or overdispersion had little to no added value in our analysis. Even further, if we rely only on such estimates, we will underestimate the role of biodiversity as a driver of alien species patterns, since their explanatory power is considerably lower than indices quantifying the range of traits or lineages observed.

Our multifaceted analysis of breeding bird biodiversity revealed that, across three regions and two time periods, there is a strong positive association between native and alien biodiversity. Among the different facets of biodiversity, the easiest to measure and most often used in the literature (species richness) was not the best predictor and, more often than not, had little additional value to other aspects of biodiversity. The strongest main effect was that of phylogenetic diversity followed by functional richness (i.e., indices quantifying the range of traits or phylogenetic tree the assemblage occupies), while metrics quantifying pairwise species similarity (either functionally or phylogenetically) were less important. Furthermore, indices of functional or phylogenetic clustering or overdispersion were very weakly (to not at all) associated with alien

species richness. All these results taken together seem to imply that the environmental factors that drive native diversity (like resource diversity) are also driving alien diversity. Alternatively, if biotic interactions are the main driver, then the biotic interactions facilitating coexistence (including even processes like predator-mediated coexistence) are far more important than adversarial interactions (like competition). The supremacy of facilitative interactions (including ecosystem-level processes) may also explain the contradiction between our results on the role of competitive exclusion of aliens and published experimental results, since experimental studies kept resource diversity and availability constant among treatments and did not explicitly examine complex ecosystem processes promoting coexistence. Finally, the predominance of phylogenetic facets of biodiversity compared to functional or taxonomic ones may advocate for the role of the adaptive potential that is included in the long lineage history and is hard to measure, that phylogenetic diversity can reveal the evolutionary processes that drive species diversity patterns.

ACKNOWLEDGMENT

This research is co-financed by Greece and the European Union (European Social Fund—ESF) through the Operational Program “Human Resources Development, Education and Lifelong Learning 2014-2020” in the context of the project “Examination of multiple hypotheses on the ecological mechanisms behind alien species invasions” (MIS 5004812).

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