

Alien bird species decrease the diversity of bird communities across human-disturbed landscapes

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Abstract

Introduced alien species have direct and indirect effects on native communities, leading to lower taxonomic diversity and negative impacts on ecosystem functioning. Moreover, other aspects of diversity could be negatively affected, through alteration of functional and phylogenetic diversity of a community. This is particularly evident in habitats where human disturbance may favour alien species, posing an additional stressor on native communities. Following the community resistance hypothesis (higher diversity, higher resistance to invasion), we hypothesized: i) higher taxonomic, functional and phylogenetic diversity (TD, FD and PD respectively) in non-invaded bird communities (i.e. no alien bird species); and, ii) lower alien species impact on all diversity metrics in less human-disturbed areas. We surveyed bird communities in a modified Mediterranean landscape subject to varying levels of human disturbance. We tested whether TD, FD and PD indices were significantly different between non-invaded and invaded bird communities, and assessed the effect of landscape composition and configuration on these indices. We found that non-invaded communities retained higher TD and FD than invaded communities. Alien birds occupied novel parts of the functional space in invaded communities, but that they did not fully compensate for the taxonomic and functional diversity loss caused by the absence of native species. These results were consistent across different habitats, suggesting weak environmental filtering of communities. Generally, both communities were negatively affected by more human-disturbed areas (e.g. agriculture and urban areas) and enhanced by forest areas and by landscape heterogeneity. Our results suggest that the occurrence of alien birds negatively affects TD and FD (but not PD) of bird community assemblages, but that this impact is stronger in human-modified landscapes. Therefore, since the conservation of biodiversity in anthropogenic habitats is a worldwide challenge, researchers should prioritize efforts to assess the effects of alien species on communities inhabiting those habitats.

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Keywords: biological invasion; bird assemblage; diversity metrics; human-altered landscape; non-native species; community resistance;

Introduction

Biological invasions are well-established as one of the greatest threats to ecosystems worldwide due to their negative impacts on native species, communities and ecosystem functioning (Pyšek et al., 2020; Vilà & Hulme, 2017). The introduction of alien species has direct and indirect effects on native biodiversity, potentially disrupting the recipient community structure (White et al., 2006) through alterations of functional and phylogenetic diversity (FD and PD, respectively; Ricciardi et al., 2013). This can occur through expansion or contraction of native functional and phylogenetic space, affecting ecosystem functioning and biodiversity maintenance (Finerty et al., 2016; Gerhold et al., 2011). Studying FD and PD in synergy could lead to a more comprehensive approach to understanding impacts of alien species on communities (Cadotte, 2013; Galland et al., 2019), since FD is associated with ecosystem functioning (Matuoka et al., 2020; Saavedra et al., 2014), and PD can express differences between species that are not captured by FD (Whitfeld et al., 2014).

Community resistance (i.e. the capacity of a community to withstand disturbance; Lake, 2013) to invasion has been hypothesised to be affected in two distinct and opposite ways. Taxonomically, functionally and phylogenetically diverse communities may be more resistant to alien establishment due to higher competition and greater effectiveness in using the resources available (Hejda & de Bello, 2013; Lososová et al., 2015). On the other hand, more diverse communities may have high resource availability that could be also exploited by alien species, inferring a lower resistance to invasion (Andrikou-Charitidou & Kallimanis, 2021; Klingbeil & Willig, 2016). Another important ecological property of a community lies in the concept of ecological resilience, which measures the ability of a given system to absorb changes in order to maintain the same identity (Folke et al. 2010). Since resistance is inversely correlated with the degree of change following a disturbance event (Justus, 2007), a resilient ecological system should better resist disturbance events such as invasions, climate or land use changes (Haegeman et al., 2016). Functional evenness (a component of FD) has been used as a proxy for the resilience of communities (Lee & Martin, 2017; Morelli et al., 2020; but see Kosman et al., 2019) and can be a useful measure to assess species resource use in a given space (Mouchet et al., 2010). High functional evenness represents efficient use of resources by species in the community (Lee & Martin, 2017), and low functional evenness implies under-exploitation of available resources, leading to higher susceptibility of communities to disturbance (e.g. biological invasions; Shea & Chesson, 2002).

Disturbed areas (e.g. human-modified landscapes such as urban and agricultural areas) are well known to favour alien species establishment in several taxa (Cardador & Blackburn, 2020; Hulme, 2009; Pyšek et al., 2010). Alien birds, for example, are better than native bird species at exploiting the ecological opportunities that arise in human-modified landscapes (the ‘opportunism hypothesis’; Sol et al., 2012). Anthropized areas are thus highly diversified repositories of alien bird species (e.g. Bonter et al., 2010; Chiron et al., 2009) and land-use changes caused by the expansion of urban areas and human-managed landscapes worldwide will likely increase the spread of generalist, opportunistic non-native species at the expense of native species (McKinney, 2006). Moreover, bird communities in disturbed areas are at risk of biotic homogenization

processes acting on the three diversity dimensions (taxonomical, functional and phylogenetic; Liang et al., 2019), leading to a generalized decrease in diversity. Since, at a local scale, several studies have reported how high levels of FD and PD lead to higher resistance to invasion (Gerhold et al., 2011; Lososová et al., 2015), the decrease in these diversity dimensions in communities inhabiting disturbed areas could hamper their resistance, making them more susceptible to invasion.

Recent studies on above three diversity dimensions in bird communities have focused on the association between native and alien bird diversity at a regional scale, finding a positive association between the two (Andrikou-Charitidou & Kallimanis, 2021; McKinney & Kark, 2017). Nonetheless, it is at the local community scale that impacts on biodiversity and ecosystem functioning take place (Loiola et al., 2018). At this scale, the impact could be predicted by two contrasting scenarios (Loiola et al., 2018): alien species establish in a portion of functional and phylogenetic space formerly occupied by native species (increasing the similarity between species in invaded communities); or alien species fill the niche-gap in a community (limiting similarity), expanding the functional and phylogenetic space of invaded communities, leading to higher FD and PD compared to non-invaded communities.

To assess which of these two mechanisms could impact native communities, a set of tests comparing the three diversity dimensions between non-invaded and invaded communities is needed (Loiola et al., 2018; Thuiller et al., 2010): i) non-invaded vs invaded communities (i.e. assessing the overall effect of invasion); ii) non-invaded vs invaded communities excluding alien species (assessing if invaded communities are more prone to invasion than non-invaded communities or if alien species replace native species' functional and phylogenetic space in invaded communities); iii) invaded vs invaded communities excluding alien species (i.e. assessing the difference in the functional and phylogenetic space between alien and native species of the same community).

In this study, we applied this approach to assess the impact of alien birds on bird community diversity by characterising TD, FD, and PD in a highly human-modified landscape in southern Portugal with several alien birds that are currently establishing new populations or expanding existing ones. To do this we ran the three tests on the three diversity dimensions, accounting for the effect of landscape. It is hypothesised that higher resilience and lower alien species impact (higher FD and PD) is more prevalent in non-invaded bird communities inhabiting less human-disturbed areas. The novelty of our study lies in the understanding of the degree of impact of alien bird species on the diversity of bird communities, and how this interacts with human modification of the landscape, in order to better assess the vulnerability of native communities to alien bird species invasion.

2. Materials and methods

2.1. Study area

We conducted the study in the Tagus estuary area, Portugal (Fig. 1). The landscape is characterised by agriculture (e.g. annual crops, rice fields, olive groves, pastures; 34.1%), forest (e.g. pine forest, agro-forest systems [montado]; 31.1%), urban and anthropized areas (e.g. city of Lisbon, road and railways; 20.1%), and wetland areas (e.g. salines, marshes; 14.7%). The entire area can be defined as Mediterranean from a climatic point of view, with four-five months of aridity during summer (Espírito-Santo et al., 2021).

2.2. Study design

We selected 189 points using a random sampling method (minimum distance between points was 473 m; Fig. 1), stratified according to the main three land-uses: agricultural, $n = 86$; forest, $n = 50$; and urban = 53. To characterise the landscape around each point, we considered composition and configuration variables within a buffer of 500 m radius. Composition was expressed as the percentage cover of seven categories of land-use (Carta de Ocupação do Solo maps available for Portugal; IGP, 2020) that were *a priori* considered as potentially relevant to bird distributions within different (decreasing) levels of human disturbance: i) urban and industrial, ii) intensive agriculture, iii) rice-fields, iv) extensive agriculture, v) shrubland, vi) plantation forest, and vii) native forest (e.g. montado). Landscape configuration was calculated using the Shannon-Weiner

diversity index of the seven land use categories (SHDI). Landscape composition and configuration variables were calculated using QGIS 3.26.3-Buenos Aires and *landscapemetrics* R package (Hesselbarth et al., 2019). We scaled all landscape variables to better evaluate collinearity (Cade, 2015), testing for multicollinearity through the Spearman correlation coefficient. We retained all variables since Spearman’s Rho was lower than 0.63 in all cases (Dormann et al., 2013). For a more detailed description, see Supporting Information 1.

2.3. Bird survey and bird traits

Bird surveys were conducted by a single observer (anon.) using 10-min point counts (Bibby et al., 2000). Points were visited twice per year (late March-early April and late April-late May) in two consecutive years (20021-22) during the early morning under calm and dry weather conditions. To avoid possible bias due to variation in diurnal activity of birds, points were visited in a different order during the second survey period, leaving at least three weeks between consecutive visits to the same point. All birds contacted, visually and acoustically, were recorded within five distance bands of increasing radius from the centre of the point (0–25 m, 25–50 m, 50–75 m, 75–100 m and >100 m). We later excluded birds flying over (e.g. swallows, swifts *Apus* sp.), aquatic birds (i.e. Ardeidae species), raptors and migrating species from the analysis that were inadequately sampled by our approach (see Supporting Information 1) (Marcolin et al., 2021).

Species were classified as native or alien, the latter being species whose native range is outside Europe and for whom their provenance in Europe is known or very strongly suspected to be through deliberate or accidental introduction by humans (5 species, see Supporting Information 1). The exception was Feral Pigeon *Columbia livia* var. *domestica* whose status is unclear. Although this species derives from the wild Rock Dove, a declining species which still has native populations in Europe, the long history of domestication of this species has led some to classify it as alien (Boano et al. 2019, Lowther & Johnston, 2020). Given this and the often very significant numbers of Feral Pigeon, we carried out the main analyses considering it both as a native and as an alien species.

We classified the surveyed bird species using a set of 10 functional traits that reflected resource-use of individuals (Flynn et al., 2009) and resource overlap between species (Andrikou-Charitidou et al., 2020), and that influence species response ability to habitat changes (Anderle et al., 2022): i) clutch size; ii) number of broods per year; iii) body mass; iv) migratory status; v) territoriality; vi) breeding season habitat use; vii) breeding season diet; viii) foraging stratum; ix) foraging technique; and, x) nesting habit (see Supporting Information 1 for a detailed description and data sources). Apart from clutch size, number of broods per year and body mass, the categories from the other traits were translated into binary variables (i.e. each trait was either present or absent for a given species; Supporting Information 1). To account for the different scales of continuous traits, clutch size, broods per year and body mass (previously log transformed) were scaled to values between 0 and 1. There was no marked intercorrelation between trait variables (all Pearson’s $r < 0.7$).

To test the effect of alien bird species presence on the diversity metrics of bird communities, we followed Loiola et al. (2018): community type was defined for each point as *invaded* when at least one alien species was found in at least one visit (*non-invaded* vs *invaded* communities). Moreover, to study the contribution of alien species to the diversity metrics of the native component of a community, we considered a third community type, that of the native species in *invaded* communities, i.e. excluding alien species from the *invaded* communities (*invaded no alien* ; Supporting Information 1).

2.4. Taxonomic, functional and phylogenetic diversity metrics

For abundance estimates of each bird species, we pooled the data using the maximum abundance recorded between the two survey periods, per point, per year. We calculated several diversity metrics to characterize each community and community type, based on taxonomic diversity (TD), functional diversity (FD) and phylogenetic diversity (PD). As a measure of TD, we used the species richness observed. To have a comprehensive understanding of the functionality of bird communities, we computed two metrics of FD based on the 10 functional traits: functional divergence (FDiv), and functional evenness (FEve). FEve was used as proxy for the resilience of communities (Lee & Martin, 2017; Morelli et al., 2020). We assessed the amount

of phylogenetic variation of each community through one PD metric: Mean Pairwise Distance (MPD). To calculate phylogenetic diversity, 1,000 phylogenetic trees based on the Hackett backbone (Hackett et al., 2008) were downloaded from <http://birdtree.org/> (Jetz et al., 2012). Since PD metrics are dependent on species richness, we calculated standardised effect size (ses) for the MPD metric (sesMPD). To do so, we compared the observed MPD of a community with the expected MPD of 999 null communities generated with null models dependent on the “independent swap” algorithm (Swenson, 2014). This procedure removed the effect of species richness (Swenson, 2014). Both MPD and sesMPD metrics were calculated as a mean value from the 1,000 values for each community (based on the 1,000 trees; Cosset and Edwards, 2017). Then, we used a two-tailed Wilcoxon signed rank test to test the difference between observed and expected MPD (Erdős et al., 2022). We calculated all the metrics using the packages ‘FD’ (Laliberte & Legendre, 2010), ‘adiv’ (Pavoine, 2020) and ‘picante’ (Kembel et al., 2010) in R version 4.1.1 (R Development Core Team, 2021).

2.5. Data analysis

Comparison of diversity metrics between community types

We compared TD, FD and PD metrics between community types, following the three tests used in Loiola et al., 2018: 1) comparing non-invaded and invaded communities (*non-invaded* vs *invaded*; Test 1); 2) comparing native species of non-invaded communities and native species of invaded communities (*non-invaded* vs *invaded no alien*; Test 2); and 3) within invaded plots including and excluding alien species (*invaded* vs *invaded no alien*; Test 3). We performed the above tests *across* and *within* the main three land-uses, trying to assess the effect of environmental filtering on the specific species pool within a given land-use (Loiola et al., 2018). To evaluate whether differences of the various metrics between community types were significant, we performed univariate analysis of variance (ANOVA) followed by Tukey’s test.

Effect of landscape configuration and composition on diversity metrics

To assess the effect of landscape variables on diversity metrics, we built linear mixed-effect models (GLMM) with normal errors using the maximum log-likelihood method, considering all landscape composition and configuration variables as fixed effects. Moreover, to account for the dependence of observations from the same location in different years, we used point ID as a random effect. Models were run separately for each community type. We calculated Akaike’s Information Criterion (AIC) to rank each candidate model. Then, we carried out model averaging (Richards, 2008) on all models with < 2 [?]AICc using the R package MuMIn (Bartoń, 2022). To account for spatial autocorrelation, we used spline correlograms (Bjørnstad & Falck, 2001) with 1,000 bootstrap resamples, both on raw data and on model residuals (Santana et al., 2017). We inspected spline correlogram plots of full model residuals (Zuur et al., 2009), and assumed absence of spatial autocorrelation when 95% Confidence Intervals included (see Supporting Information 2).

3. Results

We observed a total of 9476 birds belonging to 69 species (Supporting Information 1). The most abundant species were House Sparrow (*Passer domesticus*), Spotless Starling (*Sturnus unicolor*) and Feral Pigeon (36% of all observed birds; Supporting Information 1). Out of the 189 points, 100 points were found to be inhabited by *non-invaded* communities, while 89 were inhabited by *invaded* communities (Supporting Information 1).

3.1. Comparison of diversity metrics between community types

The comparison between *non-invaded* and *invaded* communities (Test 1) revealed significantly higher TD (species richness), FD (FDiv and FEve), but not MPD, in the *non-invaded* communities (all p-values < 0.041 , $df = 2$; Fig. 2; Supporting Information 3). We found similar results between *non-invaded* and *invaded no alien* communities (Test 2). In addition, MPD was significantly higher in *non-invaded* communities (all p-values < 0.017 , $df = 2$; Fig. 2; Supporting Information 3). When we compared *invaded* vs *invaded no alien* communities (Test 3), there were no significant differences except for TD and FDiv. In these cases,

the metrics were always lower for *invaded no alien* than *invaded* communities (all p-values < 0.048, df =2; Fig. 2; Supporting Information 3). There was a significant difference between observed and null communities for MPD only for *invaded no alien* communities when we considered the Feral Pigeon as an alien species (negative sesMPD values; $V = 12380$, p-value < 0.01). Finally, the three tests performed *within* land-uses showed similar patterns as the tests *across* land-uses, except for MPD that was higher in *invaded* than *non-invaded* communities in urban areas (Supporting Information 2-3).

Trends for TD (species richness) and FD (FDiv and FEve) were similar but clearer in communities considering Feral Pigeon as alien compared to communities considering Feral Pigeon as native (for all three Tests). Regarding MPD, the trend for Test 1 & 2 remained unaltered considering feral pigeon as alien while, for Test 3, *invaded* communities showed a significantly higher MPD metric than *invaded no alien* communities (Supporting Information 2-3).

Effect of landscape configuration and composition on diversity metrics

TD was positively associated with agricultural and forest areas, along with SHDI, in *non-invaded* communities (Fig. 3; Supporting Information 3). Native forest and SHDI were positively correlated with TD both in *invaded* and *invaded no alien* communities, whereas rice field areas were negatively correlated in both communities (Fig. 3; Supporting Information 3). In *non-invaded* communities, FDiv was positively correlated with SHDI, while intensive agricultural areas negatively affected this metric (Fig. 3; Supporting Information 3). In *invaded no alien* communities, FDiv was negatively correlated with agricultural (intensive and extensive) and rice field areas along with SHDI (Fig. 3; Supporting Information 3). The FEve (i.e. resilience) was negatively affected by urban (*non-invaded* and *invaded no alien* communities) and intensive agricultural areas (*non-invaded* communities), and was positively associated with plantation forest in both *invaded* and *invaded no alien* communities (Fig. 3; Supporting Information 3)

Rice field areas were negatively associated with MPD in the three communities (Fig. 3; Supporting Information 3). MPD was also negatively correlated with intensive agricultural areas and SHDI in *invaded* communities, while was negatively correlated with urban areas in *invaded no alien* communities (Fig. 3; Supporting Information 3).

Averaged GLMM models showed similar results, in both approaches, for TD on *non-invaded* communities, and the MPD of *invaded* communities (Supporting Information 2-3). The major differences between the two approaches were found for FDiv and FEve of *invaded no alien* communities, and MPD of *non-invaded* communities (Supporting Information 2-3).

4. Discussion

Our study showed how *non-invaded* bird communities retained higher taxonomical and functional diversity (TD and FD respectively) than *invaded* communities in a highly human-modified landscape, supporting the idea that higher species diversity shapes community resistance to invasions (Gerhold et al., 2011; Lososová et al., 2015). Moreover, we found that it is more likely that alien birds occupy novel parts of the functional space in bird communities characterised by low TD and FD (*invaded vs invaded no alien*), but that they do not fully compensate for the taxonomic and functional biodiversity loss caused by the absence of native species in invaded sites. Our findings also highlighted how these trends were stronger in less human-modified and more heterogeneous areas, whereas the diversity metrics were negatively affected in more human-modified areas. Finally, these results were similar (but stronger) when we considered those communities where the Feral Pigeon was present as *invaded* (i.e. it was treated as an alien species), suggesting that this ubiquitous bird has more characteristics of an alien than native species.

4.1. Diversity metrics and community types

In our study, the higher TD and FD found in *non-invaded* than *invaded* bird communities (Test 1) across land-uses likely suggests a general negative impact of alien species on native bird communities inhabiting the area. TD and FD were also higher in *non-invaded* than *invaded no alien* communities (i.e., *invaded* communities considering only native species; Test 2). This impact could reflect in a loss of ecosystem functioning in

the invaded bird communities (e.g. through loss of functional groups; Flynn et al., 2009; Cadotte et al. 2011). For example, high functional divergence (FDiv) infers a high niche differentiation in the community (Cosset & Edwards, 2017), suggesting that the *non-invaded* communities provide a more diverse pool of functional processes than *invaded* communities (Edwards et al., 2013). Similar reasoning could be applied when accounting for functional evenness (FEve), since high values of FEve infer efficient use of resources by species in the community (Lee & Martin, 2017). Therefore, *non-invaded* showed higher resilience (i.e. FEve) than *invaded* communities (Test 1), but lower susceptibility to disturbance than *invaded no alien* communities (Test 2). This is consistent with the biotic resistance hypothesis stating that higher diversity should promote resistance to invasion (Ordonez, 2010).

Following Test 3 (*invaded* vs *invaded no alien*), our results showed how alien species were functionally different from native species of the resident invaded community assemblages. In fact, FDiv was higher in *invaded* than *invaded no alien* communities. This suggests that alien species provide a set of functional traits that are different from those of the native species. For example, in Portugal, the common waxbill (*Estrilda astrid*) has successfully established in unsaturated communities, occupying a marginal niche (Batalha et al., 2013). Therefore, most alien species may show different adaptations to native species, leading to higher niche differentiation of the *invaded* communities, suggesting that alien species usually occupy a different ecological niche in those communities (Hejda & de Bello 2013). Nonetheless, the FEve showed no significant difference between *invaded* vs *invaded no alien* communities. Thus, despite that alien species have a higher niche differentiation in *invaded* communities, they do not provide a more efficient use of resources than the native species in the community.

From a PD point of view, we found that *invaded* communities had similar Mean Pairwise Distance (MPD) to both *non-invaded* and *invaded no alien* communities (Test 1 and 3), while species in *invaded no alien* communities were more clustered (lower MPD) than species in *non-invaded* communities (Test 2). The latter, along with the TD and FD results, supports the resistance hypothesis. In fact, higher PD could infer a community characterized by several adaptations, leading to increased competition and hampering alien species spread (Ketola et al., 2017). Finally, since the addition of alien species closes this phylogenetic gap with *non-invaded* communities (Test 1), it is more likely that alien species are favoured in more clustered communities (Lososová et al., 2015), occupying novel phylogenetic space in the invaded community (e.g. *Psittacula krameri*).

These patterns were also partially true when we compared the diversity metrics *within* land-uses to exclude the effect of environmental filtering on bird community assemblage (Loiola et al., 2018). Nonetheless, MPD was higher for *invaded* than *non-invaded* bird communities of urban areas, suggesting a higher vulnerability to alien species invasion (i.e. a phylogenetic gap). Moreover, no differences were found between community types within forest, either due to the low proportion of *invaded* communities, or because alien bird species seem to be weakly influenced by environmental filtering compared to its effect on the structure of native bird communities (Lazarina et al., 2022).

4.2. Landscape effect on diversity metrics

Diversity metrics were affected differently by landscape composition and configuration in the study area. Opposite trends between diversity metrics were found for various taxa (Sayer et al., 2017; Wong et al., 2020), showing that TD, FD and PD might not respond in the same way along landscape or invasion gradients. Plantation and native forest (montado) cover had a positive effect on TD across each community type, as did the diversity of landscape patches (i.e. SHDI). Nonetheless, agricultural areas (both intensive and extensive) also positively contributed to TD in *non-invaded* communities, while rice field areas negatively affected TD both in *invaded* and *invaded no alien* communities. Indeed, more disturbed areas (extensive and intensive agricultural, urban and rice field areas) had negative effects both on FD and PD. This decrease in FD and PD is usually followed by biotic homogenization of bird communities inhabiting disturbed areas (Liang et al., 2019; Morelli et al., 2016). Therefore, bird communities inhabiting those areas could be more susceptible to future alien species establishment (both for *non-invaded* and *invaded* communities) as they are likely better at exploiting novel opportunities in disturbed areas compared to native species (the ‘opportunism

hypothesis'; Sol et al., 2012). Apart from plantation forest (*invaded* communities) and landscape diversity (SHDI for *non-invaded* communities), FD and PD were not enhanced in less disturbed areas. In the first case, a similar pattern was found in New Zealand where alien forest bird species were associated more with “exotic forest” (Barnagaud et al., 2022). In the latter, higher diversity of the landscape could support the higher niche differentiation of *non-invaded* communities, since it could be characterized by a more diverse set of resources available.

4.3. Conservation and management implications

Our study shows the negative impacts that alien species have on native bird communities, and also show that the functional and taxonomic diversity that alien species contribute does not compensate for that caused by the loss of native species. Urban and agricultural landscapes were more vulnerable to alien bird species invasion and, since we should also rely on these disturbed areas for biodiversity conservation (Batáry et al., 2020), future management strategies must prioritize habitat restoration in these areas (e.g. increasing urban green spaces, improving heterogeneity features in agricultural landscapes) to minimise the chances of establishment of alien species, and to increase the resistance of invaded communities. In our study region at least, this should include the classification of the near-ubiquitous Feral Pigeon as an alien species. Restoration strategies are well supported by the EU “Nature Restoration Law” (i.e. European Green Deal) and should be implemented along the impact assessment of alien birds on native bird communities, through functional and phylogenetic perspective, instead of focusing on a single alien species or diversity metric. Nonetheless, future study following this direction, would need to include also the three metrics of beta-diversity to have a better understanding of the role of alien species on biodiversity and ecosystem functioning of *invaded* communities (Soares et al., 2022).

References

- Anderle, M., Paniccia, C., Brambilla, M., Hilpold, A., Volani, S., Tasser, E., Seeber, J., & Tappeiner, U. (2022). The contribution of landscape features , climate and topography in shaping taxonomical and functional diversity of avian communities in a heterogeneous Alpine region. *Oecologia* , 0123456789 . <https://doi.org/10.1007/s00442-022-05134-7>
- Andrikou-Charitidou, A., Boutsis, G., Karadimou, E., & Kallimanis, A. S. (2020). Untangling the positive association of phylogenetic, functional, and taxonomic diversity with alien bird species richness. *Ecosphere* , 11(2). <https://doi.org/10.1002/ecs2.3007>
- Andrikou-Charitidou, A., & Kallimanis, A. (2021). The different facets of native bird diversity (taxonomic, functional and phylogenetic) as predictors of alien birds increasing richness and expanding range in Great Britain. *Acta Oecologica* , 112. <https://doi.org/10.1016/j.actao.2021.103750>
- Barnagaud, J. Y., Brockerhoff, E. G., Mossion, R., Dufour, P., Pavoine, S., Deconchat, M., & Barbaro, L. (2022). Trait-habitat associations explain novel bird assemblages mixing native and alien species across New Zealand landscapes. *Diversity and Distributions* , 28 (1), 38–52. <https://doi.org/10.1111/ddi.13432>
- Bartoń, K. (2022). MuMIn: Multi-Model Inference. R package version 1.46. 0, <https://cran.r-project.org/package=MuMIn>.
- Batalha, H. R., Ramos, J. A., & Cardoso, G. C. (2013). A successful avian invasion occupies a marginal ecological niche. *Acta Oecologica* , 49 , 92–98. <https://doi.org/10.1016/j.actao.2013.03.003>
- Bibby, C. J., Burgess, N. D., Hillis, D. M., Hill, D. A., & Mustoe, S. (2000). Bird census techniques. Elsevier.
- Bjørnstad, O. N., & Falck, W. (2001). Nonparametric spatial covariance functions: Estimation and testing. *Environmental and Ecological Statistics* , 8 (1), 53–70. <https://doi.org/10.1023/A:1009601932481>
- Boano, G., Perco, F., Pavia, M., & Baldaccini, N. E. (2019). [*Columba livia* domestic breed, invasive entity also alien for Italy]. *Rivista Italiana Di Ornitologia* , 88(2), 3–10. <https://doi.org/10.4081/rio.2018.356>. In Italian.

- Bonter, D. N., Zuckerberg, B., & Dickinson, J. L. (2010). Invasive birds in a novel landscape: Habitat associations and effects on established species. *Ecography* , 33(3), 494–502. <https://doi.org/10.1111/j.1600-0587.2009.06017.x>
- Cade, B. S. (2015). Model averaging and muddled multimodel inferences. *Ecology* , 96(9), 2370–2382. <https://doi.org/10.1890/14-1639.1>
- Cadotte, M. W. (2013). Experimental evidence that evolutionarily diverse assemblages result in higher productivity. *Proceedings of the National Academy of Sciences of the United States of America* , 110(22), 8996–9000. <https://doi.org/10.1073/pnas.1301685110>
- Cadotte, M. W., Carscadden, K., & Mirotchnick, N. (2011). Beyond species: Functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, 48(5), 1079–1087. <https://doi.org/10.1111/j.1365-2664.2011.02048.x>
- Cardador, L., & Blackburn, T. M. (2020). A global assessment of human influence on niche shifts and risk predictions of bird invasions. *Global Ecology and Biogeography* , 29(11), 1956–1966. <https://doi.org/10.1111/geb.13166>
- Chiron, F., Shirley, S., & Kark, S. (2009). Human-related processes drive the richness of exotic birds in Europe. *Proceedings of the Royal Society B: Biological Sciences* , 276(1654), 47–53. <https://doi.org/10.1098/rspb.2008.0994>
- Cosset, C. C. P., & Edwards, D. P. (2017). The effects of restoring logged tropical forests on avian phylogenetic and functional diversity. *Ecological Applications* , 27 (6), 1932–1945. <https://doi.org/10.1002/eap.1578>
- Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D., & Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography* , 36 (1), 27–46. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>
- Edwards, F. A., Edwards, D. P., Hamer, K. C., & Davies, R. G. (2013). Impacts of logging and conversion of rainforest to oil palm on the functional diversity of birds in Sundaland. *Ibis* , 155 (2), 313–326. <https://doi.org/10.1111/ibi.12027>
- Erdős, L., Ho, K. V., Bátori, Z., Kröel-Dulay, G., Onodi, G., Tolgyesi, C., Torok, P., & Lengyel, A. (2022). Taxonomic, functional and phylogenetic diversity peaks do not coincide along a compositional gradient in forest-grassland mosaics. *Journal of Ecology*. <https://doi.org/10.1111/1365-2745.14025>
- Espirito-Santo, D., Costa, J. C., Arsenio, P., Mesquita, S., Ribeiro, S., Capelo, J., & Aguiar, C. (2021). A vegetacao de Portugal. Imprensa Nacional Lisbon. In Portuguese.
- Finerty, G. E., de Bello, F., Bila, K., Berg, M. P., Dias, A. T. C., Pezzatti, G. B., & Moretti, M. (2016). Exotic or not, leaf trait dissimilarity modulates the effect of dominant species on mixed litter decomposition. *Journal of Ecology*, 104(5), 1400–1409. <https://doi.org/10.1111/1365-2745.12602>
- Flynn, D. F. B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B. T., Lin, B. B., Simpson, N., Mayfield, M. M., & DeClerck, F. (2009). Loss of functional diversity under land use intensification across multiple taxa. *Ecology Letters* , 12 (1), 22–33. <https://doi.org/10.1111/j.1461-0248.2008.01255.x>
- Folke, C., Carpenter, S. R., Walker, B., Scheffer, M., Chapin, T., & Rockstrom, J. (2010). Resilience Thinking: Integrating Resilience, Adaptability and Transformability. *Ecology and society* , 15(4).
- Galland, T., Perez Carmona, C., Gotzenberger, L., Valencia, E., & de Bello, F. (2020). Are redundancy indices redundant? An evaluation based on parameterized simulations. *Ecological Indicators*, 116. <https://doi.org/10.1016/j.ecolind.2020.106488>

- Gerhold, P., Partel, M., Tackenberg, O., Hennekens, S. M., Bartish, I., Schaminee, J. H. J., Fergus, A. J. F., Ozinga, W. A., & Prinzing, A. (2011). Phylogenetically poor plant communities receive more alien species, which more easily coexist with natives. *American Naturalist* , 177(5), 668–680. <https://doi.org/10.1086/659059>
- IGP. (2020). IGP Carta de ocupacao do solo [Land cover maps] Instituto Geografico Portugues (2018). Retrieved 01.03.21, from <https://www.dgterritorio.gov.pt/Carta-de-Usa-e-Ocupacao-do-Solo-para-2018>. In Portuguese
- Hackett, S. J., Kimball, R. T., Reddy, S., Bowie, R. C. K., Braun, E. L., Braun, M. J., Chojnowski, J. L., Cox, W. A., Han, K. L., Harshman, J., Huddleston, C. J., Marks, B. D., Miglia, K. J., Moore, W. S., Sheldon, F. H., Steadman, D. W., Witt, C. C., & Yuri, T. (2008). A phylogenomic study of birds reveals their evolutionary history. *Science* , 320 (5884), 1763–1768. <https://doi.org/10.1126/science.1157704>
- Haegeman, B., Arnoldi, J.-F., Wang, S., De Mazancourt, C., Montoya, J. M., & Loreau, M. (2016). Resilience, Invariability, and Ecological Stability across Levels of Organization. <https://doi.org/10.1101/085852>
- Hejda, M., & de Bello, F. (2013). Impact of plant invasions on functional diversity in the vegetation of Central Europe. *Journal of Vegetation Science*, 24(5), 890–897. <https://doi.org/10.1111/jvs.12026>
- Hesselbarth, M. H. K., Sciaini, M., With, K. A., Wiegand, K., & Nowosad, J. (2019). landscapemetrics: an open-source R tool to calculate landscape metrics. *Ecography* , 42 (10), 1648–1657. <https://doi.org/10.1111/ecog.04617>
- Hulme, P. E. (2009). Trade, transport and trouble: Managing invasive species pathways in an era of globalization. In *Journal of Applied Ecology* (Vol. 46, Issue 1, pp. 10–18). <https://doi.org/10.1111/j.1365-2664.2008.01600.x>
- Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., & Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature* , 491 (7424), 444–448. <https://doi.org/10.1038/nature11631>
- Justus, J. (2007). Complexity, diversity, and stability. *A Companion to the Philosophy of Biology*, 321–350.
- Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., Blomberg, S. P., & Webb, C. O. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* , 26 (11), 1463–1464. <https://doi.org/10.1093/bioinformatics/btq166>
- Ketola, T., Saarinen, K., & Lindstrom, L. (2017). Propagule pressure increase and phylogenetic diversity decrease community’s susceptibility to invasion. *BMC Ecology* , 17(1). <https://doi.org/10.1186/s12898-017-0126-z>
- Klingbeil, B. T., & Willig, M. R. (2016). Matrix composition and landscape heterogeneity structure multiple dimensions of biodiversity in temperate forest birds. *Biodiversity and Conservation*, 25(13), 2687–2708. <https://doi.org/10.1007/s10531-016-1195-6>
- Kosman, E., Burgio, K. R., Presley, S. J., Willig, M. R., & Scheiner, S. M. (2019). Conservation prioritization based on trait-based metrics illustrated with global parrot distributions. *Diversity and Distributions* , 25(7), 1156–1165.
- Lake, P. S. (2013). Resistance, Resilience and Restoration. *Ecological Management and Restoration*, 14(1), 20–24. <https://doi.org/10.1111/emr.12016>
- Laliberte, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology* , 91 (1), 299–305. <https://doi.org/10.1890/08-2244.1>
- Lazarina, M., Sgardelis, S. P., Michailidou, D. E., Tsianou, M., Andrikou-Charitidou, A., Touloumis, K., & Kallimanis, A. S. (2022). Replacement drives native β -diversity of British avifauna, while richness differences shape alien β -diversity. *Diversity and Distributions* . <https://doi.org/10.1111/ddi.13641>

- Lee, M. B., & Martin, J. A. (2017). Avian species and functional diversity in agricultural landscapes: Does landscape heterogeneity matter? *PLoS ONE* , 12 (1), 1–21. <https://doi.org/10.1371/journal.pone.0170540>
- Liang, C., Yang, G., Wang, N., Feng, G., Yang, F., Svenning, J. C., & Yang, J. (2019). Taxonomic, phylogenetic and functional homogenization of bird communities due to land use change. *Biological Conservation*, 236, 37–43. <https://doi.org/10.1016/j.biocon.2019.05.036>
- Loiola, P. P., de Bello, F., Chytrý, M., Götzenberger, L., Carmona, C. P., Pyšek, P., & Lososová, Z. (2018). Invaders among locals: Alien species decrease phylogenetic and functional diversity while increasing dissimilarity among native community members. *Journal of Ecology* , 106 (6), 2230–2241. <https://doi.org/10.1111/1365-2745.12986>
- Lososová, Z., de Bello, F., Chytrý, M., Kühn, I., Pyšek, P., Sádlo, J., Winter, M., & Zelený, D. (2015). Alien plants invade more phylogenetically clustered community types and cause even stronger clustering. *Global Ecology and Biogeography* , 24(7), 786–794. <https://doi.org/10.1111/geb.12317>
- Lowther, P. E., & Johnston, R. F. (2020). Rock Pigeon (*Columba livia*), version 1.0. In *Birds of the World* (S. M. Billerman, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. <https://doi.org/10.2173/bow.rocpig.01>
- Marcolin, F., Lakatos, T., Gallé, R., & Batáry, P. (2021). Fragment connectivity shapes bird communities through functional trait filtering in two types of grasslands. *Global Ecology and Conservation* , 28. <https://doi.org/10.1016/j.gecco.2021.e01687>
- Matuoka, M. A., Benchimol, M., Almeida-Rocha, J. M. de, & Morante-Filho, J. C. (2020). Effects of anthropogenic disturbances on bird functional diversity: A global meta-analysis. *Ecological Indicators*, 116. <https://doi.org/10.1016/j.ecolind.2020.106471>
- McKinney, M. L. (2006). Urbanization as a major cause of biotic homogenization. *Biological Conservation*, 127(3), 247–260.
- McKinney, M., & Kark, S. (2017). Factors shaping avian alien species richness in Australia vs Europe. *Diversity and Distributions* , 23(11), 1334–1342. <https://doi.org/10.1111/ddi.12625>
- Morelli, F., Benedetti, Y., Ibáñez-Álamo, J. D., Jokimäki, J., Mänd, R., Tryjanowski, P., & Møller, A. P. (2016). Evidence of evolutionary homogenization of bird communities in urban environments across Europe. *Global Ecology and Biogeography* , 25 (11), 1284–1293. <https://doi.org/10.1111/geb.12486>
- Morelli, F., Benedetti, Y., Ibáñez-Álamo, J. D., Tryjanowski, P., Jokimäki, J., Kaisanlahti-Jokimäki, M. L., Pérez-Contreras, T., Sprau, P., Suhonen, J., Yosef, R., Díaz, M., & Møller, A. P. (2020). Insurance for the future? Potential avian community resilience in cities across Europe. *Climatic Change* , 159 (2), 195–214. <https://doi.org/10.1007/S11584-019-02583-7>
- Mouchet, M. A., Villéger, S., Mason, N. W., & Mouillot, D. (2010). Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology* , 24(4), 867–876.
- Ordóñez, A., Wright, I. J., & Olff, H. (2010). Functional differences between native and alien species: A global-scale comparison. *Functional Ecology* , 24 (6), 1353–1361. <https://doi.org/10.1111/j.1365-2435.2010.01739.x>
- Pavoine, S. (2020). adiv: An r package to analyse biodiversity in ecology. *Methods in Ecology and Evolution* , 11 (9), 1106–1112. <https://doi.org/10.1111/2041-210X.13430>
- Pyšek, P., Bacher, S., Chytrý, M., Jarošík, V., Wild, J., Celesti-Grapow, L., Gassó, N., Kenis, M., Lambdon, P. W., Nentwig, W., Pergl, J., Roques, A., Sádlo, J., Solarz, W., Vilà, M., & Hulme, P. E. (2010). Contrasting patterns in the invasions of European terrestrial and freshwater habitats by alien plants, insects and vertebrates. *Global Ecology and Biogeography*, 19(3), 317–331. <https://doi.org/10.1111/j.1466-8238.2009.00514.x>
- Pyšek, P., Hulme, P. E., Simberloff, D., Bacher, S., Blackburn, T. M., Carlton, J. T., Dawson, W., Essl, F., Foxcroft, L. C., Genovesi, P., Jeschke, J. M., Kühn, I., Liebhold, A. M., Mandrak, N. E., Meyerson, L.

- A., Pauchard, A., Pergl, J., Roy, H. E., Seebens, H., ... Richardson, D. M. (2020). Scientists' warning on invasive alien species. *Biological Reviews*, 95(6), 1511–1534. <https://doi.org/10.1111/brv.12627>
- R Core Team. (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing. Retrieved from <https://www.r-project>
- Ricciardi, A., Hoopes, M. F., Marchetti, M. P., & Lockwood, J. L. (2013). Progress toward understanding the ecological impacts of nonnative species. In *Ecological Monographs* (Vol. 83, Issue 3, pp. 263–282). <https://doi.org/10.1890/13-0183.1>
- Richards, S. A. (2008). Dealing with overdispersed count data in applied ecology. *Journal of Applied Ecology*, 45 (1), 218–227. <https://doi.org/10.1111/j.1365-2664.2007.01377.x>
- Saavedra, F., Hensen, I., Beck, S. G., Böhning-Gaese, K., Lippok, D., Töpfer, T., & Schleuning, M. (2014). Functional importance of avian seed dispersers changes in response to human-induced forest edges in tropical seed-dispersal networks. *Oecologia*, 176(3), 837–848. <https://doi.org/10.1007/s00442-014-3056-x>
- Santana, J., Reino, L., Stoate, C., Moreira, F., Ribeiro, P. F., Santos, J. L., Rotenberry, J. T., & Beja, P. (2017). Combined effects of landscape composition and heterogeneity on farmland avian diversity. *Ecology and Evolution*, 7 (4), 1212–1223. <https://doi.org/10.1002/ece3.2693>
- Sayer, C. A., Bullock, J. M., & Martin, P. A. (2017). Dynamics of avian species and functional diversity in secondary tropical forests. *Biological Conservation*, 211, 1–9.
- Shea, K., & Chesson, P. (2002). Community ecology theory as a framework for biological invasions. *Trends in Ecology & Evolution*, 17(4), 170–176.
- Soares, F. C., Palmeirim, J. M., Rodrigues, A. S. L., Cardoso, P., & de Lima, R. F. (2022). Bird extinctions and introductions are causing taxonomic and functional homogenization in oceanic islands. *Functional Ecology*. <https://doi.org/10.1111/1365-2435.14196>
- Sol, D., Bartomeus, I., & Griffin, A. S. (2012). The paradox of invasion in birds: Competitive superiority or ecological opportunism? *Oecologia*, 169(2), 553–564.
- Swenson, N. G. (2014). Functional and Phylogenetic Ecology in R. In *Use R!* Springer New York. <https://doi.org/10.1007/978-1-4614-9542-0>
- Thuiller, W., Gallien, L., Boulangeat, I., de Bello, F., Münkemüller, T., Roquet, C., & Lavergne, S. (2010). Resolving Darwin's naturalization conundrum: A quest for evidence. In *Diversity and Distributions* (Vol. 16, Issue 3, pp. 461–475). <https://doi.org/10.1111/j.1472-4642.2010.00645.x>
- Vilà, M., & Hulme, P. E. (Eds.). (2017). *Impact of biological invasions on ecosystem services* (Vol. 12). Cham: Springer International Publishing.
- Villéger, S., Mason, N. W. H., & Moullot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, 89(8), 2290–2301. <https://doi.org/10.1890/07-1206.1>
- Webb, C. O. (2000). Exploring the Phylogenetic Structure of Ecological Communities: An Example for Rain Forest Trees. *The American Naturalist*, 156(2), 145–155. <https://doi.org/10.1086/303378>
- White, E. M., Wilson, J. C., & Clarke, A. R. (2006). Biotic indirect effects: A neglected concept in invasion biology. In *Diversity and Distributions* (Vol. 12, Issue 4, pp. 443–455). <https://doi.org/10.1111/j.1366-9516.2006.00265.x>
- Whitfeld, T. J. S., Lodge, A. G., Roth, A. M., & Reich, P. B. (2014). Community phylogenetic diversity and abiotic site characteristics influence abundance of the invasive plant *Rhamnus cathartica* L. *Journal of Plant Ecology*, 7(2), 202–209. <https://doi.org/10.1093/jpe/rtt020>
- Wong, M. K., Guénard, B., & Lewis, O. T. (2020). The cryptic impacts of invasion: functional homogenization of tropical ant communities by invasive fire ants. *Oikos*, 129 (4), 585–597.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). Mixed Effects Models and Extensions in Ecology with R. In *PhD Proposal* (Vol. 1). <https://doi.org/10.1017/CBO9781107415324.004>

Table 1 . Diversity metrics used for the analysis: Taxonomic Diversity, Functional Diversity, and Phylogenetic Diversity.

Diversity type	Diversity index	Description
TD	Species Richness	Number of species per community
FD	FDiv (Functional Divergence)	Degree of functional dissimilarity within the community
	FEve (Functional Evenness)	Regularity of distribution of species abundances
PD	MPD (Mean Pairwise Distance)	Average nodal distance on a phylogenetic tree between two randomly selected species
	sesMPD (standard effect size Mean Pairwise Distance)	MPD adjusted for species richness. Positive sesMPD indicates higher phylogenetic diversity than expected by chance

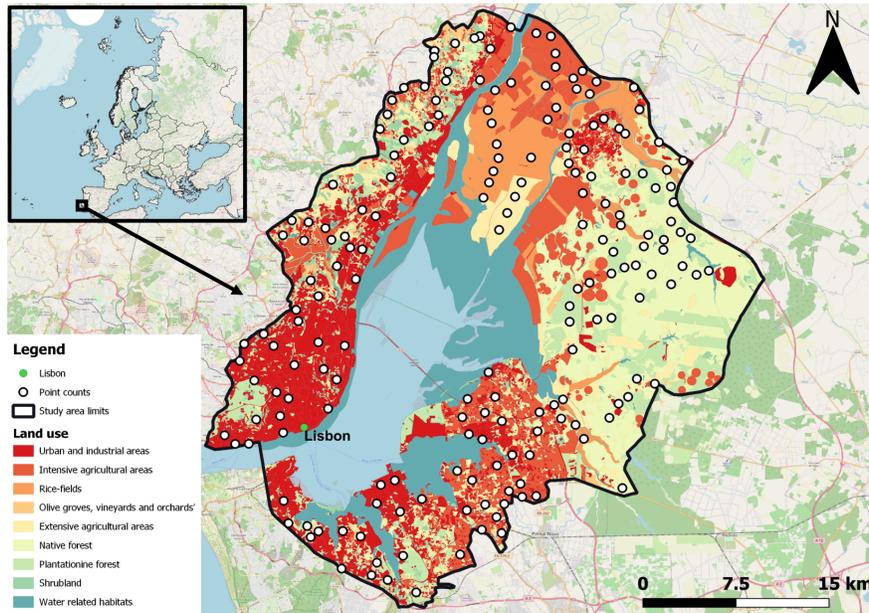


Fig. 1. Study area around the Tagus Estuary, Portugal. White dots represent the random points where bird point counts were performed. Dark green: forest; Light yellow: farmland; Light green: meadow; Grey: urban area; Light blue: water surface. Map source: ©Open Street Map 2022.

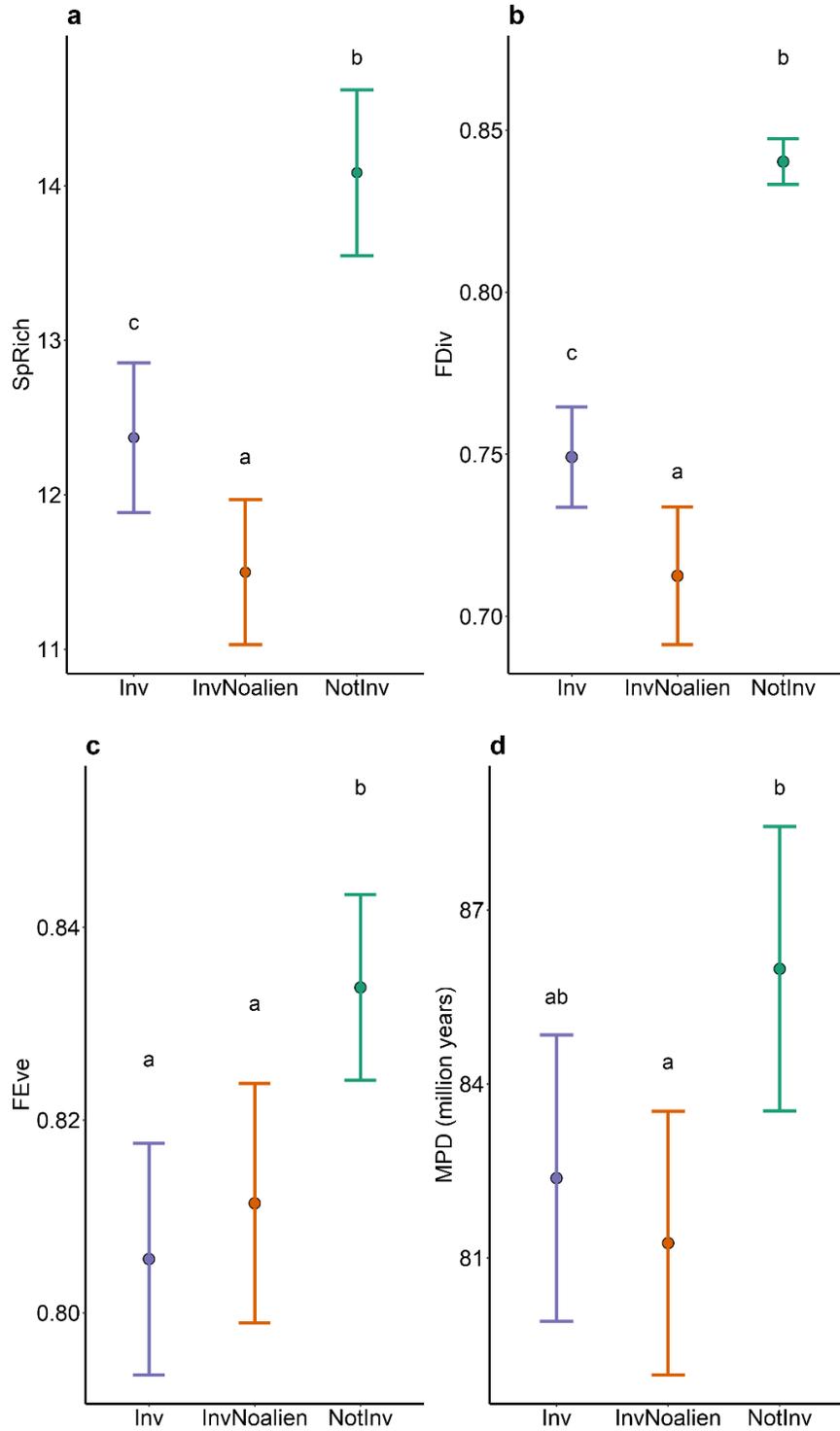


Fig. 2. Taxonomic Diversity (Species Richness; a), Functional Diversity (Functional Divergence, Functional Evenness; b-c) and Phylogenetic Diversity (MPD; d) of communities. Inv = bird communities invaded by alien species (purple). InvNoalien = bird communities invaded by alien species accounting only for native

species (orange). Notinv = non-invaded bird communities (green). Shared letters indicate no significant difference; different letters indicate significant difference. Points represents the average estimate values, lines are the range of the 95% CI. For metric description, see Table 1.

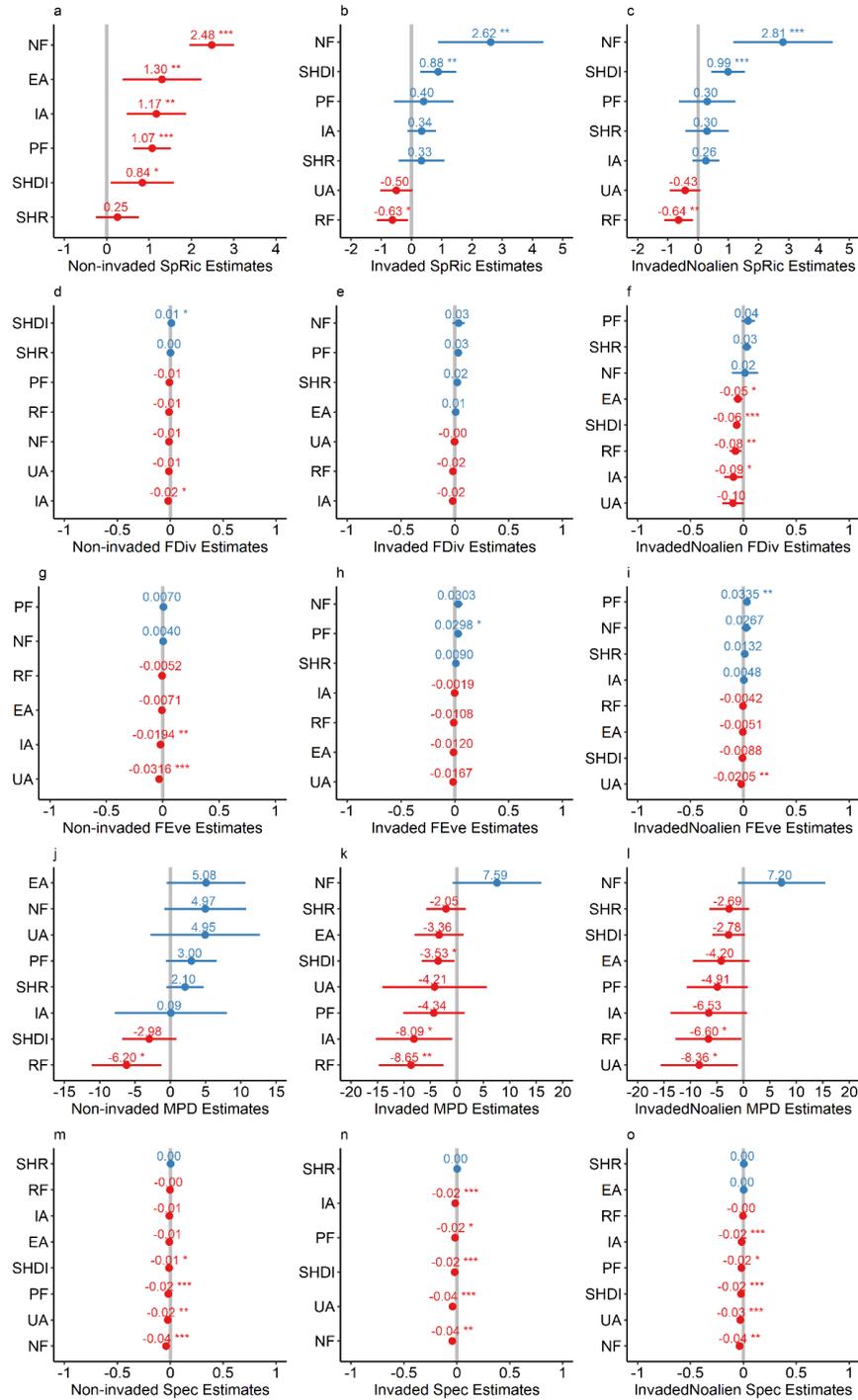


Fig. 3. Estimates from the model averaging of landscape variables on diversity metrics of communities. Taxonomic Diversity: SpRic - Species Richness, a-c; Functional Diversity: FDiv - Functional Divergence d-f; FEve - Functional Evenness, g-i. Phylogenetic Diversity: MPD – Mean Pairwise Distance, j-l. Non-invaded = non-invaded bird communities. Invaded = bird communities invaded by alien species. Invadedalien = bird communities invaded by alien species accounting only for native species. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. Red lines: negative estimates (except in 'a'); Blue lines: positive estimates. Points represents the average estimate values, lines are the range of the 95% CI. Grey lines are for reference purpose (95% CI intersecting with 0 are not significant). For landscape variables abbreviation, see Supporting Information 1.