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Abiotic and Biotic Factors from the Past as Predictors of Alien Bird Richness and Temporal Beta-Diversity

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Abstract: The challenge of predicting the distribution of alien species has long been a focus of invasion ecology. Herein, we assessed biotic and abiotic factors from the 1980s as potential predictors of alien bird species patterns 20 years later in the state of New York. To assess the ability of each factor to predict future alien species patterns, we analysed the influence of biotic (native taxonomic, functional and phylogenetic diversity, and human population density) and abiotic (climate and land use) factors from the 1980s on the observed alien species richness patterns in the 2000s and the temporal change in the composition of the alien communities between the 1980s and the 2000s using both single-predictor and multivariate models. Alien species richness from the 1980s was a reliable predictor of the alien species richness and temporal beta-diversity patterns in the 2000s. Among abiotic factors, maximum temperature and agricultural land-uses constituted sufficient predictors of future alien species richness and better predictors than the native biotic factors. The performance of single-predictor models was generally weaker in predicting temporal alien beta-diversity; however, past alien species richness and maximum temperature again outperformed the other factors. Predictions and management decisions should focus on warm and agricultural areas, as well as areas with an already high number of established alien species.

Keywords: alien species richness; alien species temporal beta-diversity; climate; land use; functional diversity; phylogenetic diversity



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1. Introduction

The growing accumulation of species outside of their native ranges (alien species) is an important concern in ecological research [1–3]. Alien species can be an immediate cause of biodiversity loss [4] and have considerable impacts on multiple ecosystem properties, as well as ecosystem services, economic activities and human health [5]. The type, intensity and modulation of the impacts, and the invasion process itself, are affected by the characteristics of the recipient communities [6], the functional traits of alien species, as well as spatial and temporal processes [7,8]. Abiotic (e.g., environmental conditions and land-use) and biotic factors (e.g., native community composition and diversity) affect all stages of the invasion process and can shape distributional and diversity patterns of alien species across space and time [9]. Disentangling the importance of the various factors that influence the establishment and spread of alien species in large spatial scales and over long timeframes is crucial for management decisions and the timely mitigation of potential impacts [10,11].

Taxonomic native diversity, usually quantified as species richness, has been extensively used to infer the complex processes (e.g., resource utilization, competition or facilitation) that affect alien species' successful establishment and spread [12]. However, taxonomic diversity cannot reflect the roles that species fill in their communities and taking into consideration functional or phylogenetic diversity can offer new perspectives on invasion mechanisms. Yet, native species functional traits or phylogenetic relationships are rarely considered concurrently with taxonomic diversity in the examination of the patterns of alien

species [13–15]. Functional diversity might be a better indicator of resource partitioning and utilization in the communities than species richness [16], while phylogenetic diversity adds an evolutionary perspective in explaining the receptiveness or resistance of natural communities to the establishment of alien species [17].

Phylogenetically diverse native communities were proven to be more resistant to alien species compared to phylogenetically poorer ones [17–20]. Simultaneously, there is documentation of positive associations between native phylogenetic diversity and alien species [21,22]. Phylogenetic relations between species might reflect functional similarity [23] and phylogenetic diversity was proposed as a proxy for immeasurable functional diversity [24]. However, phylogenetic diversity is not merely a proxy of functional diversity, but there is complementarity between the effect of these two aspects of diversity on the invasibility of natural communities [19,25]. Native phylogenetic diversity is a more reliable predictor of the resistance to alien species establishment, compared to taxonomic diversity [26]. Native functional diversity is considered to enhance native communities' resistance to invasions [16]. Functionally dissimilar native species might exploit the available resources more effectively, leaving fewer empty niches for aliens to occupy [17,27]. On the other hand, a functionally and phylogenetically diverse community may be the result of abundant and/or diverse available resources, which could lead to unoccupied phylogenetic and functional niches within the range of native communities [23], thus rendering these communities more receptive to alien species [28].

Alien species must be adapted to the abiotic conditions prevailing in the invaded regions to establish viable populations and expand their range into new regions, i.e., climatic conditions of the regions are expected to match the ones prevailing in the native ranges of alien species. Abiotic factors might be of primary importance in large spatial scales, where the effects of competition and predation tend to be weaker [29]. Temperature and precipitation were consistently found to drive alien species distribution, richness, or occurrence [30–32]. Factors reflecting resource availability, such as land cover diversity, were positively associated with alien species richness [33]. Human-altered landscapes provide favourable conditions (e.g., access to resources or decreased competition) for the establishment and spread of alien species [12,34–36], regardless of taxonomic group and habitat [37]. Additionally, alien species tend to proliferate in areas with high human population density, as alien species can often efficiently exploit nesting and feeding resources in human-altered and/or disturbed habitats [38–41].

The variation in species composition in space or time, i.e., beta-diversity patterns, can offer invaluable insights into the underlying mechanisms shaping alien communities [42–44]. Research focused on the differences in spatial turnover patterns between native and alien species [44,45], highlighting the role of human-related factors and climate [42], that modify local conditions leading to higher spatial turnover in ecological communities [46]. Furthermore, native biodiversity can influence an alien community's spatial patterns, with native species richness affecting variation in alien species composition [47]. Temporal beta-diversity quantifies the species composition changes of a single assemblage through time. Mapping temporal beta-diversity patterns, and identifying the underlying processes that influence these patterns, are critical steps to decipher natural communities' responses to disturbances such as the ongoing climate change, thus contributing to more effective biodiversity management and conservation. However, only recently has temporal beta diversity gained interest in the field of invasion ecology, while our knowledge about temporal changes of alien communities' composition and the drivers of these changes remains limited.

Here, using breeding bird atlas data from the USA state of New York collected at two time periods, 20 years apart (in the 1980s and the 2000s), we assess the potential of abiotic (climate and land-use) and biotic (native species taxonomic, functional and phylogenetic diversity, and human presence) factors from the 1980s as predictors of alien species richness in the 2000s and alien communities' temporal beta-diversity from the 1980s to the 2000s. We implemented an integrated approach, which is considered a powerful tool in invasion

ecology [48]. We aimed to identify the factors with the highest individual predictive ability of future alien species richness and temporal beta-diversity patterns. Such an approach was scarcely used, with studies focusing on the determinants of alien species diversity or distribution patterns using contemporaneous data [13,15], or simulated projections of alien species distributions in the future [49]. Past factors as predictors of future alien patterns, to our knowledge, were used only on predicting the distribution of a specific species [50], without considering biotic and abiotic predictors concurrently. These factors may vary across space and time and affect different aspects of alien species diversity [15], and multiple factors might be important for different reasons. Alien species had already passed through the initial abiotic filters and had established viable populations in the 1980s. Thus, we hypothesize that alien species richness in the 2000s was mainly influenced by the abiotic factors from the 1980s (especially human-related factors), and that the biotic factors affected mainly the temporal beta-diversity patterns of alien species. We explored the effect of each factor separately with single-predictor models and then, we built a multivariate model for each response variable including all the abiotic and biotic factors. Single-predictor models can help us identify key drivers of alien species diversity, i.e., factors facilitating or hindering alien species diversity. Multivariate models allow us to comprehend the complex interactions of abiotic and biotic factors and their combined effects on alien species diversity. Thus, using single-predictor and multivariate models provide complementary insights into diversity patterns of alien species, allowing us to gain a more nuanced understanding of the underlying processes driving alien species diversity patterns.

2. Materials and Methods

2.1. Data

We analysed presence–absence data of bird species in the USA state of New York for two distinct time periods (1980s and 2000s), using “The Atlas of Breeding Birds in New York State” [51] and “The Second Atlas of Breeding Birds in New York State” [52]. Nomenclature followed the American Ornithological Society (AOS) Birds of North and Middle America Checklist [53]. We identified alien species status following the Global Avian Invasions Atlas (GAVIA), a database of worldwide alien bird distributions [54]. For our analyses, after excluding cells that did not contain species and abiotic data were not available in both time periods, we used 5105 cells with a resolution of 25 km².

2.1.1. Alien Species Diversity

We calculated alien species richness in each atlas cell for the two time periods (1980s and 2000s). Temporal beta-diversity can be quantified with different metrics. Among them, pairwise similarity or dissimilarity indices were often used in spatial analyses [55]. Instead of comparing between two regions, a pairwise comparison is drawn between two time periods. We quantified the temporal beta-diversity of alien species’ communities in each atlas cell with the presence/absence-based pairwise Jaccard dissimilarity index:

$$\beta = \frac{A + B - 2 \times A \cap B}{A + B - A \cap B}$$

where A is the total number of species in the 1980s, B is the total number of species in the 2000s and $A \cap B$ is the intersection of the number of species present in both time periods, using the “betapart” package [56] in R [57]. Jaccard’s dissimilarity index was proven to be a suitable index to compute temporal beta diversity for occurrence and presence-absence data formats [58].

2.1.2. Biotic and Abiotic Predictors

Biotic Factors: Native Taxonomic, Functional and Phylogenetic Diversity, and Human Population Density

We estimated native diversity in the first time period used in our analyses (the 1980s). Native taxonomic diversity was quantified by native species richness per cell. Native

functional diversity was quantified through the approach of the multidimensional space, where each trait represents an axis and each species a point in the multidimensional trait space defined by the species traits. We compiled 16 ecological and life-history traits of the native bird species recorded in the 1980s atlases, retrieved from the trait data set published by Barnagaud et al. [59]. We followed the approach of Barnagaud et al. [59] to compile data for the species not included in the aforementioned data set (Supplementary Table S1). The selected traits captured the aspects of the species' biology and ecology that may affect their distributions. Specifically, the traits were grouped into three categories: (i) the ecological traits that reflect the species' use of habitat and dietary resources; (ii) life-history traits that separate sedentary species with large body sizes and large ranges from smaller species with smaller territories, and (iii) reproductive traits that were related to breeding performances and duration of life cycle [59]. We applied a Gower species distance matrix [60] and performed principal coordinates analysis (PCoA) [61] to ordinate species along the major axes and plot them in a multidimensional functional trait space. For each atlas cell, we quantified functional dispersion (FDis), which describes the spread of functional types and their relationship to the centre of the functional space [62], using the R package "FD" [63]. Native phylogenetic diversity was quantified using the avian supertree derived from <http://birdtree.org> (accessed on 3 March 2020) [64]. For each atlas cell, we calculated the phylogenetic Mean Pairwise Distance (MPD), which was the average value of the pairwise phylogenetic distances among the native species, using the R package "picante" [65]. Finally, we obtained gridded data on human population density (PopDen) in the 1980s from the Global Population Density Grid Time Series Estimates v1 (1970–2000) 1 km² resolution data [66] and extracted the maximum human population density value in each atlas cell, to be used as a predictor in our analyses.

Abiotic Factors: Climate and Land-Use

The climatic variables maximum temperature (Tmax) and precipitation (PPT) were obtained from the TerraClimate dataset [67] for a 20-year period (from 1968 to 1988) ending approximately at the time of the publication of the first atlas. The monthly values of the climate data were averaged over the 20-year period and their mean values were upscaled from their original resolution (4 km²) to match the atlas' resolution by estimating the mean value for each atlas cell.

Land use vector data were obtained from the Land-Use and Land-Cover Data Sets of the U.S. Geological Survey for the period 1970–1980 [68]. The land use data were clipped with the atlas grid and the total area covered by human-related land use types (developed and agricultural) in the 1980s for each cell was estimated. Furthermore, we calculated Shannon's diversity index of land uses (LandDiv) in each atlas cell, weighed by the total area occupied by each land use type in each cell.

The selection of the aforementioned predictors was based on two principles: (i) the relevance of the factors to the examined hypotheses and (ii) the relationship between the factors. The selected biotic and abiotic factors were found to adequately explain the spatial patterns of alien species richness in the same region (Eastern U.S.A.) in a contemporary setting [21,40]. Additional biotic and abiotic factors were considered, such as evapotranspiration, mean temperature, other land use types, and different functional and phylogenetic metrics. Prior to the analyses, we tested for multicollinearity amongst the considered factors using a stepwise variance inflation factors (VIF) function from the R package "Ranalytica" [69]. This function iterates the VIF analysis and at each step excluded the variable with the highest VIF score. The process was repeated until all remaining variables had VIF scores below a specific threshold and were free from multicollinearity. The factors used as predictors in our analysis scored VIF values <10 [70].

2.2. Statistical Analysis

We fitted generalized least squares (GLS) Models with maximized log-likelihood to model alien species richness and temporal beta-diversity in the 2000s as functions of the

different biotic and abiotic factors from the 1980s. We explored the effect of each individual predictor on each response variable separately, to detect the potential of each individual factor to predict future alien species richness and temporal beta-diversity. To account for spatial autocorrelation, we included an exponential spatial correlation structure in each model. The Spatial GLS models were built with the `gls` function of the R package “nlme” [71], which provides the benefit of accounting for spatial autocorrelation.

We evaluated the strength of the different models by comparing the AIC values of the GLS models. A further comparison was conducted with the coefficient of determination R^2 of a generalized linear model (GLM) regressing the alien species richness and temporal beta-diversity values predicted from the GLS models against their observed values in the 2000s (Poisson error distribution for species richness and Gaussian error distribution for temporal beta-diversity). We also built a multivariate GLS model for each response variable, to assess the cumulative predictive ability of the factors. Finally, to assess the relative importance of each factor and compare these effects, we implemented hierarchical partitioning using all the factors included in the multivariate models as predictors and alien species richness and temporal beta-diversity in the 2000s as the response variables. We used the R package “relaimpo” [72] that partitions the model’s predictors R^2 s by averaging over orders and sums their relative importance to 100%.

3. Results

In the 2000s, 25 alien bird species (out of a total of 251) were recorded in the state of New York (~10% of total avifauna). Mean alien species richness per atlas cell increased between the 1980s and the 2000s from 7.9 ± 3.2 to 9.2 ± 3.2 . Alien species richness and alien communities’ temporal beta-diversity showed contrasting spatial patterns, with areas of higher alien species richness exhibiting lower temporal beta-diversity and vice versa (Figure 1).

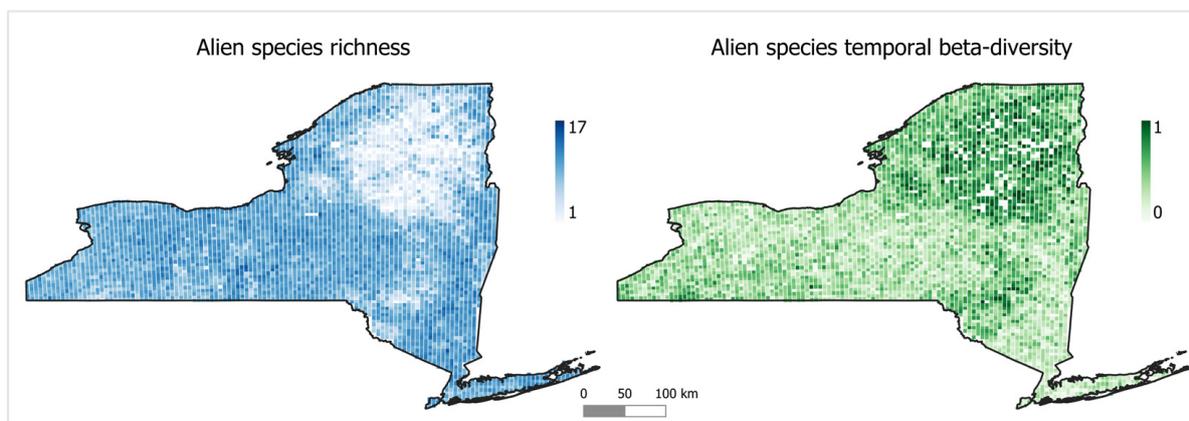


Figure 1. Alien bird species richness in the 2000s (blue coloured map), and alien species communities’ temporal beta-diversity from the 1980s to the 2000s (green coloured map) in the State of New York.

In the 1980s, 220 native species were recorded in the state of New York, with a mean native species richness of 61 species (± 13.6) per cell. Mean native functional dispersion was 0.23 ± 0.01 and the phylogenetic mean pairwise distance was 117 ± 9.2 per cell. Regarding the abiotic conditions in the 1980s, the recorded mean maximum temperature was 12.7 ± 1.4 °C and mean precipitation was 85.9 ± 9.8 mm per cell. Agricultural land uses accounted on average for 33% of the cells’ cover and developed land uses accounted for 8%. The abiotic factors showed less temporal variability from the 1980s to the 2000s compared to the biotic factors (Supplementary Table S2).

Among single-predictor models, alien species richness in the 1980s had the strongest relationship with alien species richness in the 2000s (Table 1). Beyond 1980s alien species richness, abiotic factors were better predictors of future alien species richness compared to the biotic factors (Table 1). However, only maximum temperature and agricultural land

uses emerged as relatively strong predictors (Table 1). Of the remaining abiotic and biotic factors from the 1980s, native functional dispersion demonstrated the most important relationship with alien species richness in the 2000s (Table 1). However, the multivariate model exhibited higher predictive ability than single-predictor models for both 2000s alien species richness and alien temporal beta diversity.

Table 1. AIC values of the single-predictor generalized least squares (GLS) models predicting alien species richness and alien species temporal beta-diversity as functions of different abiotic and biotic factors, and of the multivariate GLS models that include all of the predictors. Fit (adjusted R^2 values) of a generalized linear model (GLM) between the predicted values of each GLS model and the observed values of alien species richness and temporal beta-diversity in the 2000s. The number of asterisks next to each R^2 value indicates the p -value of the GLM. Abbreviations: Tmax = 20 year (1968–1988) average of maximum temperature, PPT = 20 year (1968–1988) average of precipitation, Developed = % area covered by developed land-uses in the 1980s, Agricultural = % area covered by agricultural land-uses in 1980s, LandDiv = Shannon’s diversity index of land uses, PopDen = 1980s human population density, Alien SR and Native SR = 1980s alien and native species richness, Native FDis = native functional dispersion, Native MPD = native phylogenetic Mean Pairwise Distance.

Predictors (1980s)	Alien Species Richness (2000s)		Alien Temporal Beta-Diversity	
	AIC	R^2	AIC	R^2
Tmax	21,304.59	0.343 ***	−4199.23	0.258 ***
PPT	21,466.01	0.088 ***	−3840.59	0.0391 ***
LandDiv	21,410.64	0.065 ***	−3847.55	0.0192 ***
Developed	21,526.44	0.036 ***	−3861.10	0.0599 ***
Agricultural	21,448.51	0.232 ***	−3932.30	0.134 ***
PopDen	21,540.96	0.013 ***	−3814.484	0.0246 ***
Alien SR	21,120.53	0.451 ***	−5387.39	0.457 ***
Native SR	21,347.59	0.032 **	−4025.42	0.040 ***
Native FDis	21,411.59	0.1494 ***	−3936.52	0.114 ***
Native MPD	21,500.44	0.048 ***	−3968.500	0.086 ***
Multivariate model	20,554.29	0.569 ***	−5526.491	0.480 ***

** $p < 0.01$; *** $p < 0.001$.

Similar patterns were observed in the examination of the spatial patterns of alien species temporal beta-diversity (Table 1). Lower temporal beta-diversity in the 2000s was observed in cells with higher alien species richness in the 1980s. Furthermore, lower values of temporal beta-diversity in the 2000s were observed in cells with higher temperatures in the 1980s, but the relationship was of moderate strength. The remaining biotic and abiotic factors from the 1980s—perhaps with the exception of native species functional dispersion—exhibited weak relationships with alien species communities’ temporal beta-diversity in the 2000s.

The multivariate GLS model for both 1980s alien species richness and alien temporal beta-diversity outperformed single-predictor models according to the R^2 values of the regressions between the values predicted by each model and the observed values of alien species richness and temporal beta-diversity in the 2000s. Specifically, the multivariate model explained approximately 57% and 48% of 2000s alien species richness and alien temporal beta-diversity, respectively, opposed to the 45% (in both cases) explained by the best-fitting single predictor model. As in the case of the single-predictor model, almost all the factors exerted a significant positive effect on 2000s alien species richness (Table 2, Figure 2). The exceptions were the precipitation that exerted a negative effect and the human population density that did not affect significantly the 2000s alien species richness. Human population, diversity of land uses, native species richness, and MPD did not affect significantly alien temporal beta-diversity (Table 2). The remaining abiotic factors exerted a negative significant effect. Among the biotic factors, 1980s alien species richness and 1980s native FDis had a negative and positive relationship with alien temporal beta-

diversity, respectively (Figure 2). The results of the GLS models and the hierarchical partitioning showed that the relative importance of each factor was in accordance with the single-predictor models (Figure 3). Specifically, 1980s alien species richness had the highest relative importance accounting for 31% and 48% of the explained variance of 2000s alien species richness and alien temporal beta-diversity, respectively. Following alien species richness, 1980s maximum temperature and agricultural land uses were the most important predictors of alien species richness and temporal beta-diversity in the 2000s in the multivariate model.

Table 2. Results of the multivariate generalized least squares (GLS) models predicting alien species richness and alien species temporal beta-diversity in the 2000s as functions of different abiotic and biotic factors from the 1980s. Abbreviations: Tmax = 20 year (1968-1988) average of maximum temperature, PPT = 20 year (1968-1988) average of precipitation, Developed = % area covered by developed land-uses in the 1980s, Agricultural = % area covered by agricultural land-uses in 1980s, LandDiv = Shannon’s diversity index of land uses, PopDen = 1980s human population density, Alien SR and Native SR = 1980s alien and native species richness, Native FDis = native functional dispersion, Native MPD = native phylogenetic Mean Pairwise Distance.

	Alien Species Richness (2000s)			Alien Temporal Beta-Diversity		
	Coef.	SE	<i>p</i>	Coef.	SE	<i>p</i>
(Intercept)	−3.806	1.004	0.000	0.727	0.060	0.000
Tmax	0.717	0.046	0.000	−0.006	0.003	0.020
PPT	−0.017	0.006	0.005	−0.001	0.000	0.010
LandDiv	0.997	0.108	0.000	−0.011	0.007	0.122
Developed	0.027	0.012	0.027	−0.004	0.001	0.000
Agricultural	0.102	0.007	0.000	−0.005	0.000	0.000
PopDen	0.000	0.000	0.562	0.000	0.000	0.562
Alien SR	0.194	0.017	0.000	−0.036	0.001	0.000
Native SR	0.021	0.003	0.000	0.000	0.000	0.120
Native FDis	28.749	3.707	0.000	0.972	0.279	0.001
Native MPD	−0.049	0.005	0.000	−0.001	0.000	0.064

AIC: 20,554.29, R² = 0.5687, *p* < 0.005 AIC: −5526.491, R² = 0.4803, *p* < 0.005

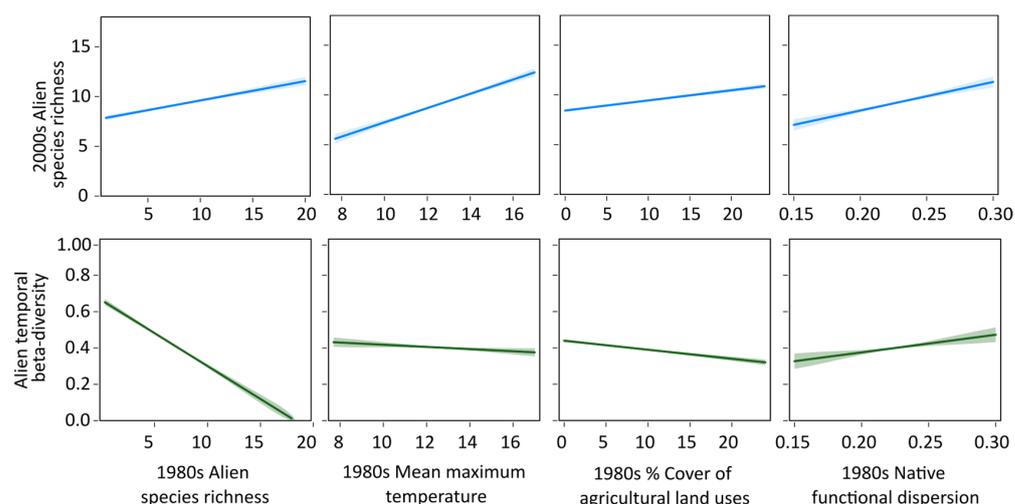


Figure 2. Effect plots showing the results of the multivariate Generalized Least Squares models predicting 2000s alien species richness and alien temporal beta-diversity as function of 1980s abiotic and biotic factors. In figure, factors with the highest relative importance according to hierarchical partitioning are presented (for details, see main text). The solid line represents the predicted values and the bands represent the 95% confidence interval for response variable richness, adjusted for spatial autocorrelation.

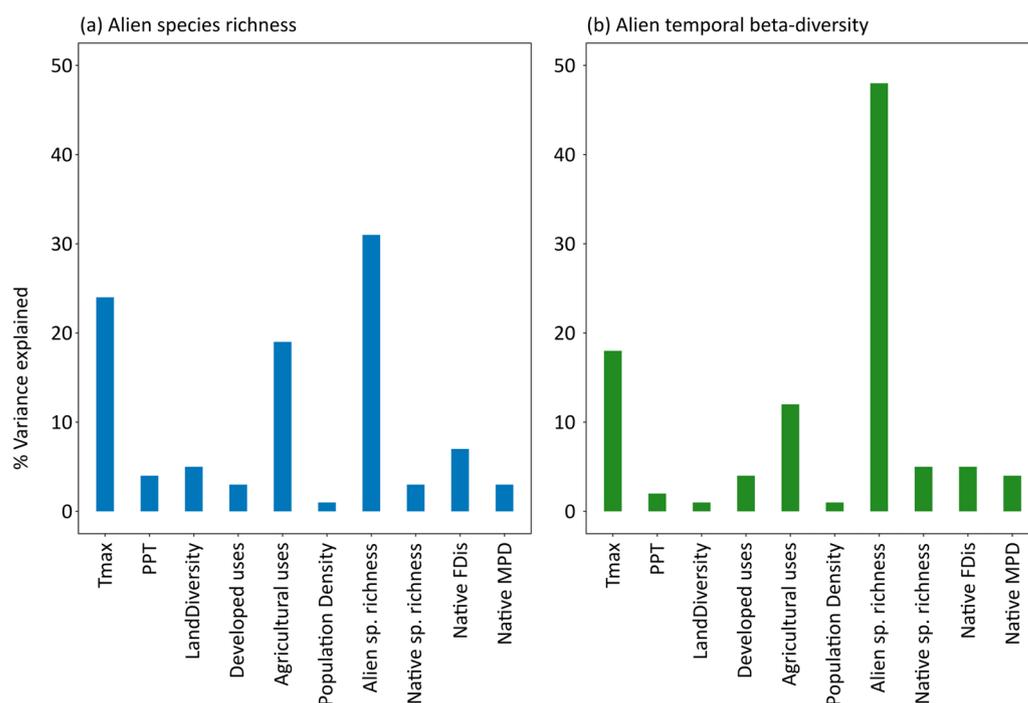


Figure 3. Relative importance (%) of variance explained by the multivariate model using the 1980s abiotic and biotic factors as predictors and the observed values of alien species richness and temporal beta-diversity in the 2000s as the response variables, calculated through a Hierarchical Partitioning approach. The values are normalized to sum to 100%. Abiotic factors: Tmax (20 year average of maximum temperature), PPT (20 year average of precipitation), Developed (% area covered by developed land-uses), Agricultural (% area covered by agricultural land-uses), LandDiv (Shannon's diversity index of land uses). Biotic factors: PopDen (1980s human population density), Alien SR and Native SR (1980s alien and native species richness), Native FDis (native functional dispersion), Native MPD (native phylogenetic Mean Pairwise Distance).

4. Discussion

Our results showed that multivariate models outperformed the single-predictor models, suggesting that multiple abiotic and biotic factors play a role in shaping future alien species richness and changes in alien species composition in time. Both single predictor and multivariate models were in accordance that among factors, past alien species richness was the strongest predictor of present alien species richness and temporal changes in alien species composition, with areas of higher alien species richness hosting species-richer communities in future and with fewer temporal changes in alien species composition. The regional alien species pool remained unchanged, as no new alien birds established populations in New York between the 1980s and the 2000s, and fewer alien species could have moved to areas of higher alien species richness in the 1980s compared to alien species-poorer areas. Furthermore, alien species richness, climate (and more specifically temperature), and agricultural land uses from one time period emerged as strong predictors of the next time period's alien species richness and temporal beta-diversity.

The mean maximum temperature of the 1980s was the best predictor of future alien species richness, confirming that environmental factors drive alien species diversity at regional spatial scales [30,73]. Higher temperatures may be indicative of ecosystems of higher productivity and higher resource availability and diversity [74]. Given that climate change is expected to affect the extreme values of environmental measures (i.e., minimum and maximum) [31], this positive relationship highlights climate changes' potential effect on biological invasions in the future. While precipitation levels are considered an important driver of the establishment of alien birds globally [15], it did not emerge as a predictor of future alien species richness and temporal beta-diversity in this study. This might

be because the examined alien species had already established populations by the 1980s (the first time period in this study). Additionally, alien species showed a preference for agricultural areas, which are regularly irrigated, therefore, freshwater availability might not have been a concern for many of these alien species.

We found a strong positive relationship between 1980s agricultural land use cover and 2000s alien species richness and alien temporal beta-diversity. Positive associations between human-related land uses such as agricultural and urban were previously reported [40]. Perhaps agricultural areas include more vegetation types or/and alien plant species that favour alien species or create opportunities that alien species exploit better than native ones. Developed areas and human population density were weak predictors of future alien species richness and temporal beta-diversity, even though disturbed habitats are considered to favour alien species [32,75]. A possible explanation is that urban habitats may be a point of introduction for alien species [32], but herein, we analysed patterns of established alien species rather than species introductions. As birds are highly mobile animals, it is possible that after their introduction, they moved to more suitable habitats [76], such as agricultural areas that might offer higher resource availability [77]. Alien birds tend to establish populations in areas where they can exploit the more opportunistic food sources provided by human activities [78], so it makes sense that they would prefer agricultural and peri-urban areas.

Our initial hypothesis was that alien species richness would be mainly affected by the abiotic factors of the past and temporal beta-diversity would be strongly associated with biotic factors, due to biotic interactions shaping the community composition after the initial abiotic filters. Indeed, the predictive ability of the biotic factors was overall significantly lower compared to the abiotic factors, and the various facets of native diversity showed a consistently poor ability to predict future alien species richness. However, contrary to our expectation, the same was the case for the prediction of alien species' temporal beta-diversity. The biotic factors' inferior predictive ability might be explained by the fact that native species distribution and composition patterns changed to a greater extent from the 1980s to the 2000s, compared to the abiotic factors (Supplementary Table S2). Thus, the explanatory power of the intertemporal models was possibly diminished, as the relationship between native diversity and alien species was found to be fairly strong in contemporaneous studies [21,33,41,79]. Abiotic conditions remained relatively stable over time, and their effect was possibly similar to that expected in a contemporaneous setting.

Native diversity is considered to be a strong predictor of alien diversity, with recent research highlighting that native species composition can be a strong predictor of areas that aliens can possibly establish [80]. Furthermore, Lazarina et al. [81] explored the range shifts and spatial patterns of Great Britain's alien and native breeding bird assemblages' beta-diversity in two distinct time periods and found that alien species expanded into new regions over time and that native species diversity was among the strongest drivers of the composition of alien species' communities. Given that alien species exhibit higher temporal dynamism than natives in their distributions, and that their diversity tends to increase over time, alien species can pose a major threat to native biodiversity [82]. Here, among the biotic factors, functional dispersion (following alien species richness) showed the strongest predictive ability of higher alien species richness and higher temporal beta-diversity (i.e., wider changes in alien communities' composition), perhaps because functionally dispersed communities occur in areas with more diverse resources [12] that can accommodate richer and more diverse communities. A recent study [21] found that phylogenetic diversity measures were better predictors of alien species richness compared to functional diversity metrics in a contemporaneous setting. However, we did not observe a strong effect of the phylogenetic mean pairwise distance on either alien species richness or alien temporal beta-diversity. These findings, combined with the abiotic factors effect, may indicate that resource availability is the major driver behind alien species richness patterns and perhaps more functionally dispersed native communities have more unoccupied niche space for alien species [83].

The relationship between the diversity of alien species and potential biotic and abiotic factors has long been a focus of invasion ecology [79,84], but to our knowledge, this is the first multifaceted analysis that combined information on past abiotic and biotic conditions to predict the observed patterns of alien bird species richness and temporal beta-diversity across a large region. Our findings showed that, overall, areas that were warmer and agricultural in the past tended to host more alien species in the future. Such findings can assist in designing management strategies and risk assessments to prioritize areas that may be susceptible to biological invasion. However, further research is required to explore the patterns of different taxonomic groups, biogeographic regions and scales, in order to identify the shared context under which generalizations are possible, robust, and interpretable.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d15030417/s1>, Table S1. The 16 functional traits data set used in this study, Table S2. *t*-test model results showing the correlations of the abiotic and biotic predictors' values.

Author Contributions: A.A.-C., E.K., G.B. and A.S.K. conceived and designed this study; A.A.-C., E.K. and G.B. performed data preparation; A.A.-C. performed the statistical analyses; A.A.-C., E.K., M.L., M.A.T., G.B. and A.S.K. contributed to the interpretation of the results and to the writing of the manuscript. All authors have read and agreed to the published version of the manuscript.

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