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Urbanization and Human Population Favor Species Richness of Alien Birds

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Abstract: Human activities like urbanization and agriculture affect spatial biodiversity patterns. The presence and activities of humans richly benefit alien species, but native species usually decline in human-impacted areas. Considering that the richness of alien and native species are inter-related, we explored the effect of human population density, human-related land uses (agricultural and urban), and natural land area on avian (alien and native) species richness of Massachusetts for two time periods using Generalized Additive Models. Avian alien species richness increased with native species richness in both time periods. Despite the predominant role of native species richness as a major driver of alien species richness, human activities play an important additional role in shaping species richness patterns of established aliens. Human-related land uses (urban and agricultural) and human population favored alien species richness in both time periods. Counter to expectations, human activities were also positively associated to native avian species richness. Possible explanations of these patterns may include habitat heterogeneity, increased availability of resources, and reduced predation risk.

Keywords: alien species richness; native species richness; breeding birds; human land uses; agricultural area; urban area; Massachusetts

1. Introduction

The human-mediated dispersal of species outside their native range, either deliberately or accidentally, has long been part of human history [1]. Global trade and extensive transport networks have increased and are expected to continue to increase the rate of alien species introductions [2–6]. For instance, 900 introductions of bird species have been reported since 2000 [7]. Alien species may pose a major threat to native species richness [8] and ecosystem functioning [9], with collectively significant global socioeconomic impact [10]. Therefore, understanding patterns and drivers of species distribution, as well as of alien diversity emerges as a critical issue for biodiversity conservation [11].

The facilitative role of human population density, human-induced disturbance, and land-use changes on driving establishment and species richness patterns of alien species has been highlighted for different taxonomic groups [12–16]. Humans are not only responsible for the transport of the alien species to new areas (first stage of invasion process), but human activity is also a major driver of the establishment and spread of alien species. Urban landscapes promote alien species richness [15,17–20]. The latter responds along an urbanization gradient (i.e., from downtown to rural residential areas) and exhibits a pattern of increasing species richness from most to least urbanized areas [21], from the edges to the interiors of urban parks [22], and/or from exurban developments to cattle ranges

and nature reserves [20]. Human-altered landscapes provide "niche opportunities", increased resources, decreased competition, and ideal environmental conditions to alien species [23–25]. Some native species may not be able to exploit ecological opportunities [26] due to a lack of suitable traits to cope with the new environmental conditions of these converted landscapes [27]. For example, human-impacted habitats often harbor alien species because their unique functional traits enable them to adapt to disturbed habitats [28]. On the other hand, land-use changes may provoke the decline of native species richness [29].

Alien species establishment and inter-relation with native species change the community structure, and result in an increase [30] or decrease of total species richness over time [31,32]. The relationship between alien and native species richness is scale-dependent [33,34]. The niche competition between native and alien species may result in a negative relationship, especially on small spatial scales [34–36], while both alien and native species may benefit from higher resource availability, especially on larger scales, often resulting in a positive relationship [37,38]. Therefore, to better understand the effect of human impact on alien species richness, we must consider the relationship between alien and native species richness.

In the present study, we explored the effect of human population density, human-related land use (agricultural and urban), and natural land uses on avian species richness patterns with an emphasis on the established aliens, using data on breeding birds from Massachusetts for two time periods. Specifically, we address the following questions: (a) Is the relationship between alien and native species richness positive or negative? (b) Do established alien birds benefit from human-dominated land uses, given that human population density and human-altered landscapes are considered to promote alien species richness? (c) Does the effect of human population density and different land uses change over time?

2. Materials and Methods

2.1. Avian Data

Distribution maps of the breeding birds were obtained by the first and second atlas of Massachusetts [39,40], with surveys taking place in 1968–1972 (MS-1968) and 2007–2011 (MS-2007), respectively. In the atlases, the Massachusetts state was divided into blocks (1/6th of a 7.5 min of the United States Geological Service quadrangle map) of approximately 25 km² size. For our analyses, we used only blocks (hereafter called grid cells) that were surveyed in both time periods. Each cell was surveyed for at least 20 hours by volunteers of the Massachusetts Audubon Society. The datasets comprised of the presence–absence data of bird species that showed confirmed breeding. For some species, the mating season was year-round, but most of the surveys took place from April to September. The nomenclature of bird species follows the American Ornithological Society (AOS) Birds of North and Middle America Checklist [41]. Alien bird species were identified following the Global Avian Invasions Atlas (GAVIA), a database of global alien bird distributions [42].

2.2. Land-Use and Human-Population Data

Land-use data were obtained by the US Geological Land-Use Survey [43] for 1970s–1980s, and by the 2006 version of the National Land Cover Database (NLCD) [44] for the second time period. Both land-use databases were for the United States and measured 30 m resolution. The land-use data layers were combined with Atlas grid cells, and we estimated the area of different land uses per grid cell. Then, we calculated the total area per grid cell of three land-use categories: urban, agricultural, and natural land uses. The grouping of different land uses into the three formulated categories is presented in Table S1. Furthermore, human population density per grid cell was estimated using 1980 and 2005 data from HYDE Gridded Population version 3.1 [45,46].

2.3. Statistical Analysis

We estimated the species richness of native and alien birds per grid cell for the two time periods. To explore if species richness was significantly different between the two periods, we implemented

permutational ANOVA separately for alien and native species with the *aovp* function of the *lmPerm* package [47]. Then, we formulated Generalized Additive Models (GAMs) [48] with the *gam* function of the *mgcv* R package [49], predicting the alien species richness of the different time periods as a function of the area of different land uses (natural, agricultural, and urban) and human population density. Given that native species richness is considered a strong driver of alien species richness, native species richness was included in the GAMs as predictor. Furthermore, we explored the relationship between native species richness, and the area of land uses and human population density using GAMs. In all formulated GAMs, the predictors entered the model as smooth predictor variables with thin-plate regression splines (3 knots per spline in order to capture unimodal relationships; Poisson error distribution and log-link function), and the grid cells' co-ordinates were also used as smooth predictors to account for spatial autocorrelation. Finally, we repeated the analysis removing the spatial autocorrelation effect to detect the contribution of predictors to the observed patterns.

3. Results

A total of 175 native and 25 alien species were found in the first time period, and 181 native and 24 alien species in the second time period in the state of Massachusetts (Figure 1a,b). Mean native species richness per grid cell was 39.22 ± 16.74 species in the first time period, and increased significantly over time to 47.92 ± 13.25 species in the second time period (Figure 2a, p < 0.001). Similarly, mean alien species richness increased significantly, from 8.27 ± 4.16 to 11.31 ± 3.15 species (Figure 2b, p < 0.001). Regarding land uses, agricultural and natural areas shrank. We observed a decrease in approximately 60% of the grid cells, while urban areas increased in approximately 80% of the grid cells (Supplementary Material, Figure S1).
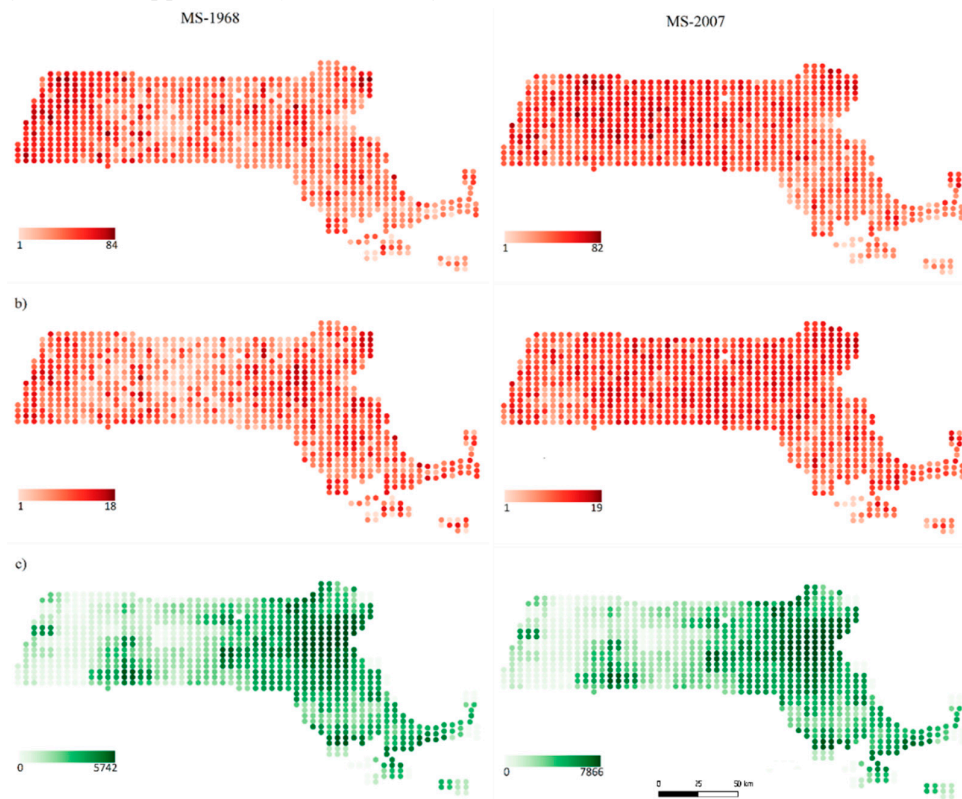

Figure 1. Distribution of (**a**) native species richness, (**b**) alien species richness, and (**c**) human population density in each grid cell (grid cell size approximately 25 km²) in the state of Massachusetts for the first time period MS-1968 (left column) and the second time period MS-2007 (right column).
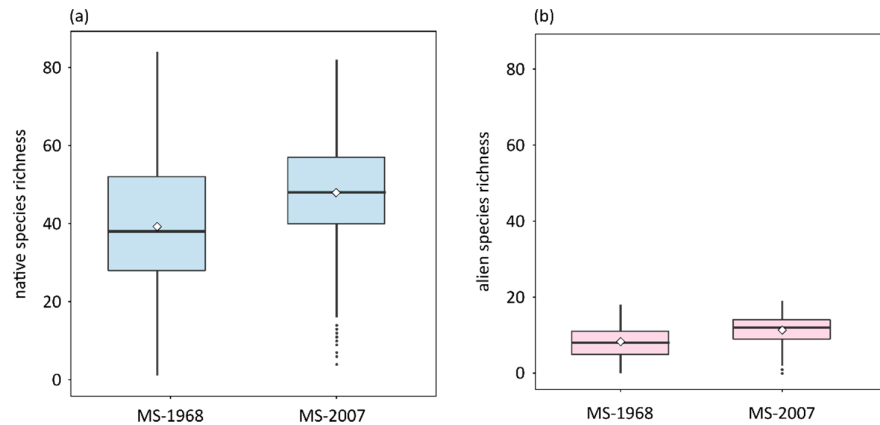
Figure 2. Boxplots of (**a**) native and (**b**) alien species richness in the first (MS-1968) and the second (MS-2007) time period of breeding birds of Massachusetts per grid cell (grid cell size approximately 25 km^2). Diamonds and lines depict mean and median values, respectively.

The richness of the MS-1968 alien species increased significantly with native species richness, agricultural area, and urban area, while natural area and human population did not exert a significant effect (Figure 3; Supplementary Material, Table S2). The GAM explained 66.20% of the deviance of alien species richness. By removing the spatial autocorrelation effect, i.e., longitude and latitude as predictors of alien species richness, the explained deviance was approximately 52% (Supplementary Material, Table S3). In the second time period, the significant positive relationship between alien and native species richness remained. Furthermore, MS-2007 alien species richness increased with human population and exhibited a unimodal relationship with area of natural land uses, while the remaining examined predictors did not show a significant effect (Figure 3; Supplementary Material, Table S2). The explained deviance of the GAM was equal to 58.10% after accounting for spatial autocorrelation. Removing the spatial autocorrelation effect, the explained deviance was approximately 56% (Supplementary Material, Table S3).
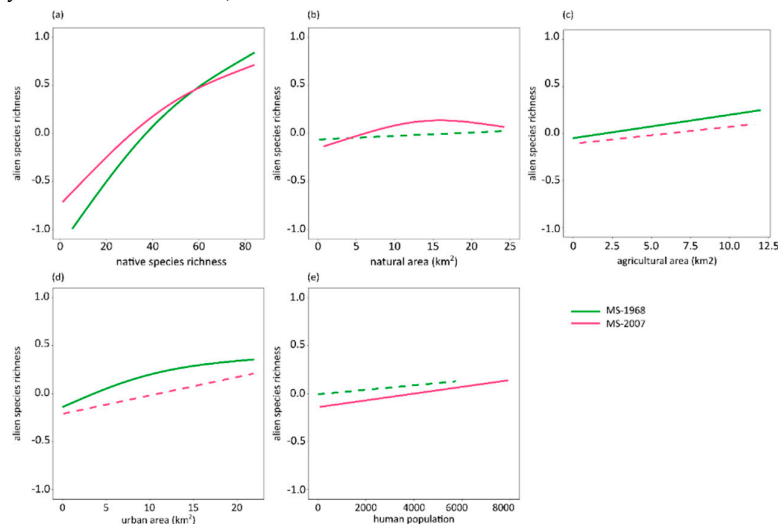

Figure 3. Effect plots showing results of Generalized Additive Models using as response variable the alien species richness of breeding birds of Massachusetts, and as predictors, native species richness (**a**), area of different land uses (natural, agricultural, urban; **b–d**), and human population (**e**) for the first (MS-1968, green lines) and the second time period (MS-2007, red lines), after accounting for spatial autocorrelation. All predictors entered model as smooth functions; thus, y-axis presents mean-centered alien species richness summing up to zero. Significant relationships depicted with solid lines; dashed lines denote non-significant relationships.

MS-1968 native species richness increased significantly with the area of the different land uses, while it decreased with human population density (Figure 4; Supplementary Material, Table S4). The GAM explained 35.50% of deviance after accounting for spatial autocorrelation (explained deviance was approximately 7% after removing spatial autocorrelation effects; Supplementary Material, Table S5). MS-2007 native species richness decreased with human population density, and followed a unimodal relationship with the area of natural land uses [46.50% explained deviance after accounting for spatial autocorrelation (Supplementary Material, Table S4), and 13.30% after removing the spatial effect (Supplementary Material, Table S5)].
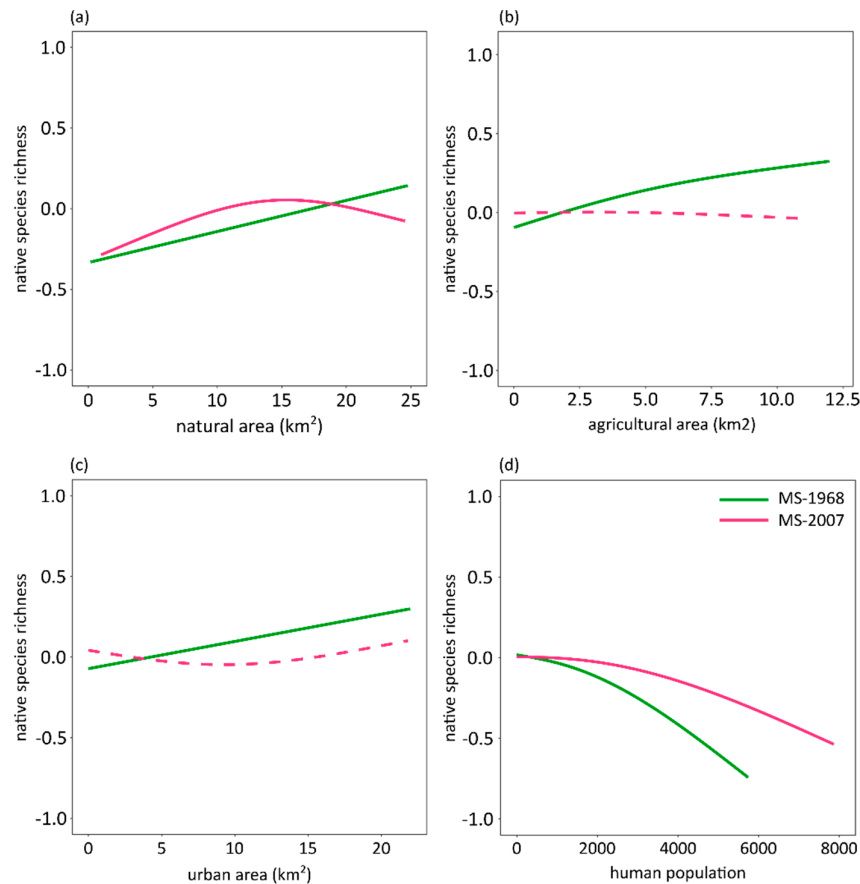
Figure 4. Effect plots showing results of Generalized Additive Models using as response variable the native species richness of breeding birds of Massachusetts, and as predictors area of different land uses (natural, agricultural, urban; **a–c**) and human population (**d**) for the first (MS-1968, green lines) and the second time period (MS-2007, red lines) after accounting for spatial autocorrelation. All predictors entered model as smooth functions; thus, y-axis presents mean-centered native species richness summing up to zero. Significant relationships depicted with solid lines; dashed lines denote non-significant relationships.

4. Discussion

What are the impacts of human-dominated land uses of urbanization and agriculture on avian richness? The short answer might be that they increase avian abundance, while decreasing avian species richness and simultaneously favoring the introduction and establishment of alien/exotic species [50,51]. Our results only partially support this answer. Human-related variables (agriculture, urbanization, and human-population density) were indeed positively associated with alien breeding bird species richness in the State of Massachusetts across both examined time periods (1968–1972 and 2007–2011), but explained only a small proportion of the variance of alien breeding species richness. Native species richness emerged as the strongest predictor of alien species richness in

accordance with predictions of the biotic acceptance hypothesis, as previously reported for a similar scale of analysis [33,52]. Although the same human-related variables were positively associated with native bird species richness, human-related variables perhaps favored more alien than native species, as their contribution in driving alien species richness spatial patterns was positive and additive to that of native species richness.

The positive relationship between alien and native species richness, as well as the effect of human-related variables on them, can be explained by different mechanisms. Food availability, especially lack of it during the adverse season of the year, is a major factor regulating avian abundance and diversity [23,53,54]. Cities might offer plentiful food resources to birds by importing vast amounts of energy and materials, such as natural vegetation patches, human-generated garbage, and bird feeders [23,55,56]. For example, millions of households sustain bird feeders in their gardens, providing huge quantities of supplementary food to birds in North America [57,58]. Therefore, by providing food to birds throughout the year, urban areas attract birds, given that birds possess traits to adapt to human-disturbed habitats; this is particularly manifested in alien species, but also true for many common native species [59,60]. Furthermore, birds are strongly associated with vegetation structure and composition, and increased habitat heterogeneity might allow both the regional and local coexistence of native and alien birds [29,61]. Human-dominated landscapes, apart from areas unsuitable for birds, also include a wide array of different vegetation types (e.g., hedgerows, gardens, parks, and fields) [62,63]. Moreover, the greater availability of exotic plants in urban and agricultural areas may offer an opportunity for alien bird species that native species may not exploit, thus explaining the additional benefit for established alien species in these areas [64]. On the other hand, natural habitats might be more suitable and preferable to birds, but an extensive contiguous area of a natural type of vegetation (e.g., forest) can support only one functional guild of birds [65,66]. Finally, in urban areas, predation rates on birds are significantly lower than those in rural areas [67] due to the lower abundance of bird predators (with the exception of cats, which are generalist predators [68]), and evidence supports birds with lower parasite infestation than those in natural areas [69–71], thus resulting in higher species richness. This may be more evident in alien species for which their successful establishment might be explained by the absence of enemies (e.g., predators, parasites, pathogens) in the new range, i.e., the enemy release hypothesis [72,73].

Human population density played a different role for the two species groups. Native bird species richness was negatively associated with human population density, while alien diversity was positively associated. The positive association of native diversity with urbanization, but negative with population density, may reflect the "luxury effect" [74,75]. Within a city, areas of low population density (often coinciding with areas occupied by higher-income residents) denote areas with more vegetation (either in private gardens or in public parks), with lower traffic congestion, and, consequently, lower levels of noise and air pollution. The higher availability of nesting resources (vegetation) and lower disturbance levels might foster native species richness. Contrarily, alien species are more adapted to human presence and less susceptible to human disturbance [76], perhaps face reduced competition with native species in densely populated areas, and thus appear positively associated with human population density [16,77].

Our initial expectation that human-related variables would be associated with lower native species richness was not confirmed. It is possible that the increased species richness may be due to the predominance of common widespread species, and masks the loss of phylogenetically or functionally unique species. Another possible explanation could be that native species surviving in relatively high latitudes in this temperate region of the continental USA is characterized by relatively wide environmental tolerances, thus persisting even in human-dominated areas. A third possible explanation might be that the scale of our analysis, i.e., the grid cell size of approximately 25 km^2 masks the relationship between native species richness and human-related variables. It is possible that native species richness may not change if the blocks remain relatively the same, even if assuming land-use changes within the block, e.g., agricultural to urban areas, meadows to forests, and forests to urban areas.

In conclusion, we found that human-related land uses promote alien species richness more than native species richness, as human activity perhaps modifies the landscape and habitats, and creates favorable conditions facilitating alien species. However, in terms of species richness, both alien and native species showed positive associations to human land uses, and contrasting results to human population, implying there are a few similarities in drivers that shape the species richness patterns of native and established alien species.

Supplementary Materials: The following are available online at www.mdpi.com/xxx/s1. Figure S1: Distribution of the coverage of different land uses (natural, agricultural, and urban areas) and the human population of Massachusetts for two time periods, Table S1: Grouping of different land uses of Massachusetts of two time periods into three broad categories: natural, agricultural, and urban, Tables S2 and S3: Results of Generalized Additive Models predicting alien species richness of breeding birds of Massachusetts as function of native species richness, area of different land uses, and human population with and without accounting for spatial autocorrelation, Tables S4 and S5: Results of Generalized Additive Models predicting native species richness of breeding birds of Massachusetts as function of different land uses and human population with and without accounting for spatial autocorrelation.

Conflicts of Interest: The authors declare no conflict of interest.

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