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How Five Decades of Land-Cover Change Reshaped Suitable Habitat for Puerto Rican Tree Species

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ABSTRACT

Aim: Human land-use has dramatically altered the amount, quality and connectivity of habitat for species worldwide. Understanding how these changes affect individual species is essential for predicting the overall consequences of land-use change for biodiversity.

Location: The Caribbean island of Puerto Rico. Forest cover on the island increased from about 18% to 45% from the late 1940's to the early 2000's.

Methods: Using data on modelled geographic distributions and functional traits for 546 tree species, we evaluated how the gain of modelled potential suitable habitat (i.e., climatically-suitable and forested) was related to species-specific climatic associations and life-history strategies. We estimated species-specific potential suitable habitat (climatically suitable and forested) with species distribution models and data on land cover. We characterized each species' niche breadth (the range of environmental conditions it occupies) and niche position (the environmental conditions it prefers) to compare with the niche characteristics of reforested lands (i.e., those that changed from nonforest to forest land cover).

Results: Species with relatively more potential suitable habitat in 1951 also had relatively larger gains in potential suitable habitat from 1951 to 2000. Species that tend to occur in conditions different from those common in reforested areas (i.e., associated with more 'marginal' habitats) gained relatively less potential suitable habitat and species with broad environmental niches gained more potential suitable habitat. Niche breadth was weakly associated with changes in connectivity among patches.

Main Conclusions: Our results show that Puerto Rico's reforestation preferentially increased potential suitable habitat for species that (1) already had suitable habitat in the landscape and (2) tolerate a wide range of climatic conditions. Our findings illustrate how land-use change in heterogeneous tropical landscapes can generate non-uniform habitat gains across species, which may favour generalist over specialist species and potentially alter community composition.

1 | Introduction

Human land-use can dramatically impact biodiversity by affecting the quality, amount and connectivity of habitat (Fahrig 2017; Hansen et al. 2012). While habitat loss and degradation due to land-use and land-cover change (LULCC) are recognized as primary drivers of biodiversity loss (IPBES 2024; Magioli et al. 2021), land-use changes that lead

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to habitat gains are also widespread (Ellis et al. 2013; Kauppi et al. 2006; Mather 1992; Rudel et al. 2009). For example, while the expansion of agricultural land remains a major driver of global forest cover loss (Diniz et al. 2022; Gibbs et al. 2010; Song et al. 2018), secondary forests now occupy large expanses of formerly agricultural land (Bousfield and Edwards 2025; Chazdon et al. 2009, 2016). Understanding the consequences of LULCC in terms of both habitat loss and gain is thus crucial for assessment of biodiversity risk exposure and conservation planning.

A large body of research on the forest transition theory (Mather 1992; Mather and Needle 1998) has focused on the socio-economic and biophysical drivers of land-use change leading to forest regrowth. One key lesson from this work is that LULCC does not occur randomly across landscapes. Rather, areas that are more accessible and of higher value for human use (e.g., highly fertile) tend to be exploited first and abandoned last (Helmer et al. 2008; Huston 2005; Scott et al. 2001). Moreover, protected areas (e.g., nature reserves) tend to be located in relatively less productive areas (Scott et al. 2001). The consequences of non-random patterns of land-use for biodiversity thus depend, in part, on how spatial patterns of land exploitation correspond to the particular environmental associations of individual species. Because species differ in their associations with different biophysical conditions, we may expect species-specific effects in terms of shifts in the amount and configuration of available habitat following LULCC (Hansen et al. 2012). Prior work on the consequences of LULCC for forest ecosystems has, however, focused largely on structural metrics (e.g., biomass), aggregate diversity patterns (e.g., species richness), species composition or species functional groups (e.g., Fang et al. 2022; Gei et al. 2018; Helmer et al. 2018; Martinuzzi et al. 2022; Poorter et al. 2016). In comparison, we have a limited understanding of species-specific impacts of LULCC in different environments.

Characterizing species in terms of their niche position and niche breadth may help generalize the impact of LULCC across species (Antão et al. 2022; Sexton et al. 2017) (Figure 1). Niche position refers to the favoured conditions of a species relative to the conditions available in the landscape. Metrics of niche position can thus reflect the magnitude of difference between a species' preferred conditions and the most commonly available conditions in a landscape (Morueta-Holme et al. 2013; Ohlemüller et al. 2008; Sheth et al. 2020). For example, species that prefer abiotic conditions similar to areas that change from agricultural to forest land cover would be expected to have larger gains in actual habitat compared to species that tend to occur in areas with other abiotic conditions (assuming no dispersal limitation). Species niche breadth Synge H., editor– or the range of conditions a species occupies - could also explain differences in the amount of available habitat following LULCC (Di Cecco and Hurlbert 2022). Generalist species (i.e., those with wider niche breadths) are typically expected to experience greater increases in suitable habitat under LULCC than specialist species. Consequently, LULCC can create ecological 'winners' and 'losers' within the same landscape by reshaping habitat availability and spatial configuration. These changes can drive divergent population dynamics and promote biotic homogenization among regenerating forests (Newbold et al. 2018; Sweeney and Jarzyna 2022). Importantly, the niche position and niche breadth hypotheses are not mutually exclusive. Jointly evaluating these mechanisms may therefore help explain species-specific habitat changes following LULCC as well as broader patterns of community reorganization across environmental gradients.

Traits that mediate life-history trade-offs (i.e., 'functional traits') may also help generalize species-specific responses in terms of habitat gains and losses following LULCC (Díaz 2025). As the amount of potential habitat available across regional abiotic gradients changes, species traits influence differential species growth, survival and recruitment across abiotic gradients

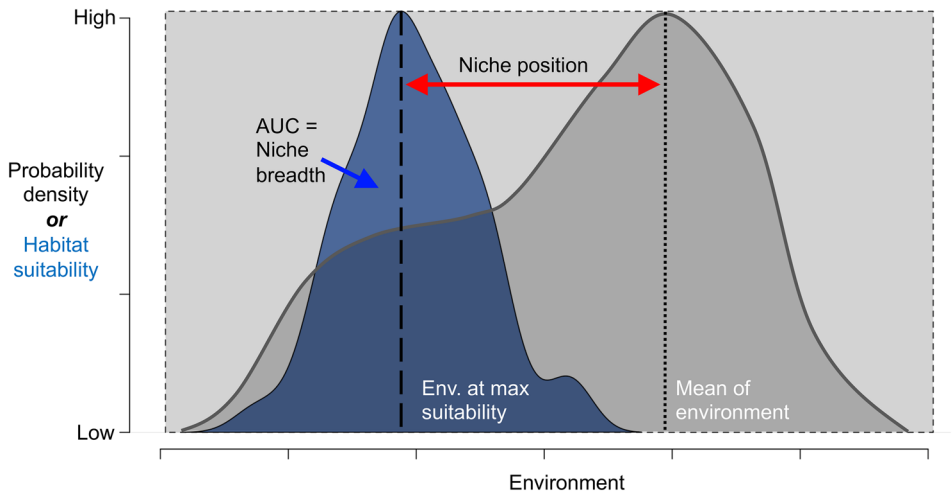

FIGURE 1 | Schematic diagram illustrating niche position and niche breadth metrics for a hypothetical species. The grey curve represents the distribution of environmental values available in the landscape. The blue curve represents the distribution of habitat suitability values (SDM predictions) along the same environmental gradient. Note that the two curves have different *y*-axes; probability density of environmental conditions for the grey curve and habitat suitability scores for the blue curve but both are scaled from 0 to 1. Niche position is computed as the absolute difference between the mean value of environmental conditions in the landscape (dotted vertical line) and the environmental conditions of maximum habitat suitability for the species (dashed vertical line). Niche breadth is computed as the area under the habitat suitability curve (blue curve), expressed as a proportion of the total area across the range of environment in the landscape (grey rectangle).

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could be related to patterns of habitat loss/gain. For example, trees in moist forests tend to have relatively low values of wood density (Muscarella and Uriarte 2016). If LULCC predominantly occurs in moist forests, trees with traits more commonly associated with those regions should experience larger gains in habitat. However, forests also typically contain species with a large range of functional variation (Muscarella and Uriarte 2016), which may indicate that traits are weak predictors of habitat gains/losses even if LULCC is biased with respect to abiotic conditions.

An ideal study system for assessing how niche position, niche breadth and functional traits may relate to species-specific changes in potential habitat availability following LULCC would include substantial LULCC dynamics, high species diversity and comprehensive data on geographic distributions and habitat preferences. The Caribbean island of Puerto Rico provides such a case study (Grau et al. 2003; Muscarella and Uriarte 2016; Yackulic et al. 2011). While exact estimates vary, forest cover in Puerto Rico generally increased from about 18% of the total land area in 1950 to ca. 55% in 2022, following the widespread abandonment of agricultural land (Martinuzzi et al. 2022; Rudel et al. 2000). Prior work has related this large gain in forest cover to a variety of socio-economic and biophysical drivers (e.g., Grau et al. 2004; Kennaway and Helmer 2007; Yackulic et al. 2011). Several studies have also investigated the implications of these changes for overall forest and land cover (e.g., Gould 2009; Helmer et al. 2002; Lugo and Helmer 2004), metrics of forest structure (e.g., biomass) (e.g., Martinuzzi et al. 2022), as well as the species and functional composition of forests (e.g., Brandeis et al. 2009; Muscarella et al. 2016). Although some species-specific habitat mapping has been done for Puerto Rican species (Gould et al. 2008), we lack a species-specific assessment of how potential habitat availability changed during this period.

Here we examined how LULCC in Puerto Rico during the second half of the 20th century (1950–2000) affected the amount of suitable habitat available for the vast majority ($N = 546$) of the island's tree species. We used a species-specific analysis of habitat suitability based on climatic and edaphic associations, and integrated data on species traits for a subset of 459 species to further assess these changes. We also quantified the degree to which changes in suitable habitat affected fragmentation of habitat patches. We asked three main questions: (1) How did the amount and fragmentation (i.e., distance between patches and spatial aggregation) of potentially suitable habitat change for different Puerto Rican tree species from 1951 to 2000? (2) What is the range of variation of potential species richness in these reforested areas of Puerto Rico? (3) To what extent are species-specific shifts in suitable habitat availability related to species niche position, niche breadth and functional traits?

We expected large differences among species in terms of habitat gain and loss. Since the largest bioclimatic zone in Puerto Rico is moist forest (Daly et al. 2003) and this is also where the largest gains of forest cover occurred (Helmer et al. 2002; Kennaway and Helmer 2007), we expected the largest gains in suitable habitat would be for species associated primarily with this forest type (i.e., low values of niche position). We also expected relatively large gains of potentially suitable habitat for species with relatively wide niche breadths due to their ability to occupy a broad range of conditions, as well as for species with relatively acquisitive functional traits. Importantly, by quantifying species-specific potential habitat changes for most tree species in Puerto Rico, this study moves beyond aggregate assessments of forest recovery to evaluate whether predictable differences among species can be explained by niche position, niche breadth and functional traits. Evaluating how non-random reforestation may differentially favour species across environmental gradients may help provide a framework for understanding ecological 'winners' and 'losers' during forest transitions.

2 | Methods

2.1 | Study Area

The island of Puerto Rico (~9000 km^2) encompasses six Holdridge life zones (Holdridge 1947), with climate zones ranging from subtropical dry forest to subtropical lower montane rain forest (Brandeis et al. 2007). The island is characterized by steep environmental gradients with mean annual precipitation ranging from ca. 700 to 4500 mm year, and diverse geological substrates including extrusive and intrusive volcanic, limestone, alluvial, no-carbon sedimentary and ultramafic bedrock (Krushensky 1995). The island experiences periodic natural disturbance by hurricanes which can cause spatially heterogeneous and sometimes severe damage to forests across the island (Hall et al. 2020; Helmer et al. 2023a; Uriarte et al. 2023; Vargas et al. 2025).

Particularly in the last century, the forests of Puerto Rico have been subject to extensive anthropogenic disturbance via land-cover change. In the mid-1900s, forest cover on the island had been reduced to ~18% due to land clearing for agriculture (Kennaway and Helmer 2007), with some estimates as low as 6% (Birdsey and Weaver 1987). A variety of political and socio-economic changes led to the widespread abandonment of agricultural land and the subsequent natural regeneration of forests (Aide et al. 1995; Brandeis et al. 2007; Grau et al. 2003; Yackulic et al. 2011). Forest cover on the island was estimated to have increased to ~45% in the early 2000's (Kennaway and Helmer 2007), and to even as high as ~55% as of 2022 (Martinuzzi et al. 2022).

2.2 | Habitat Suitability Models, Niche Position and Niche Breadth

To characterize species-specific suitable habitat for each species, we built species distribution models (SDMs) with Maxent v 3.4.1 (Phillips et al. 2017) using the R Package ENMeval v 2.0 (Kass et al. 2021; Muscarella, Galante, et al. 2014). We used a data set of 54,732 total occurrence records for 645 tree species in Puerto Rico consisting of observations from the online databases GBIF (GBIF.org 2026), four herbaria (UPRRP, MAPR, NY, US) and georeferenced records from previously published studies (e.g., Aide et al. 1995), as well as our own observations. We excluded records from GBIF with spatial issues or with coordinates identical to records from other data

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sources. For distribution modelling, we focused on a subset of 549 species with ≥10 occurrence records. For these species, the mean (±sd) number of occurrence records per species was 84.9 (±107.0). We used the 'target-group' background approach to account for spatial sampling bias in our occurrence dataset (Anderson 2003). Specifically, when building an SDM for a given species, we used records of all other species as background points. We used four abiotic covariates in our SDMs that are relevant for the growth and survival of trees: log-transformed precipitation in the driest month (mm), an index of precipitation seasonality (Feng et al. 2013), temperature in the hottest month (°C) and a categorical map of geological substrate (Krushensky 1995). The seasonality index is based on entropy and is at a minimum when an equal amount of total annual rainfall is evenly distributed across all 12 months (Barbaros and Baran 2025; Feng et al. 2013). We downloaded temperature and precipitation data (climatological averages from 1963 to 1995) at 450 m resolution from the PRISM Climate Group (http://prism.oregonstate.edu). We used species occurrence records from 1900 to 2026 to fit SDMs. Despite a temporal mismatch with the climate normals from 1963 to 1995 used as predictors, we consider this approach justified because it maximizes representation of species–environment relationships in a landscape characterized by substantial land-use change. Moreover, climatic conditions in the study area have changed relatively little outside the period represented by the climate data (Willig et al. 2019), and thus the temporal mismatch is likely minor relative to the broad climatic gradients encompassed by species' island-wide distributions. Information about number of occurrence records and mean environmental conditions per species is provided in Table S1.

We fit a series of Maxent models using all pairwise combinations of five regularization multipliers (1–5) and four feature class combinations ('L', 'LQ', 'LQP', 'LQPT') (i.e., a total of 20 models per species) and we evaluated the performance of these SDMs using spatial cross-validation. Specifically, we partitioned the data using the 'checkerboard2' partitioning method (Radosavljevic and Anderson 2014) with an aggregation factor of 5 implemented in ENMeval v 2.0 (Kass et al. 2021; Muscarella, Galante, et al. 2014). Among the 20 models fitted per species, we selected the best model using sequential criteria of the lowest value of omission rate at the 10 percentile of predicted occurrence and then the highest value of AUC. We provide the ODMAP protocol for the SDMs as Table S2.

In downstream analyses, we primarily used continuous predicted values from the SDMs. However, for analyses of habitat fragmentation and potential species richness (see next section), we converted continuous SDM predictions to binary maps of suitable vs. non-suitable habitat based on a species-specific threshold value that maximized the True Skill Statistic (TSS) (Allouche et al. 2006). We used the 'ecospat.max.tss' function of the ecospat v 4.4.1 R package (Broennimann et al. 2024) to compute the threshold TSS value for each species. While we consider the TSS threshold most suitable for our study, it is important to note that other options are available which may lead to different results (Scherrer et al. 2018).

We used habitat suitability maps (spatial predictions of SDMs) to compute metrics of niche position and breadth for each species (Figure 1). To do so, we first centered and scaled each environmental variable included in the SDMs across the island. Next, we computed the median value of each variable among grid cells that were classified as forest regrowth (i.e., non-forest in 1950 and forest in 2000). For each species, we computed the median value of each environmental variable across grid cells with the highest modelled suitability for that species. We then computed 'niche position' as the average difference between the median environmental values in reforested grid cells and in grid cells with highest suitability. To compute niche breadth, we binned each (scaled) environmental variable into 100 bins and found the maximum predicted suitability across grid cells in each bin. We then computed the area under the curve and expressed this as a proportion of the potential area if a species had maximum habitat suitability across the full range of the environmental variable. In other words, a niche breadth value of one would indicate that the species has its maximum predicted habitat suitability across all environmental conditions.

2.3 | Habitat Amount and Connectivity

We used maps of land cover from 1951 to 2000 (Helmer et al. 2023a, 2023b; Kennaway and Helmer 2007) to estimate the amount and configuration of climatically-suitable and available (i.e., forested) habitat through time for each species. These prior works had defined forested habitat as areas with >25% tree cover, a category that can include some managed systems such as shade coffee and other forms of woody agriculture (Kennaway and Helmer 2007; Lee et al. 2025). We focus on this period because the vast majority of forest change occurred during these years, with forest cover remaining mostly stable from 2000 to the present (Marcano-Vega 2023). Full details on land-cover classification maps can be found in (Helmer et al. 2023a, 2023b; Kennaway and Helmer 2007). Briefly, the forest cover map from 1951 (original scale 1:120,000 or ~1200 m) was based on aerial photos. The 2000 map was derived from Landsat TM/ETM images with 30 m pixels. The spatial resolution of the downloaded datasets was 30 m, whereas the climate data used for SDMs was ~450 m. To match the spatial resolution of these datasets, we aggregated the landcover maps to match the coarser resolution climate data using the 'resample' function of the terra R package v. 1.8-70 (Hijmans 2025). Although we acknowledge this spatial aggregation could obscure effects of fine-scale environmental heterogeneity, our study focuses on macroclimate and broad scale edaphic conditions.

To estimate changes in the amount of suitable habitat that was forested (i.e., 'potential habitat'), we masked the suitability maps (i.e., SDM output for each species) with the forest cover maps from 1951 and from 2000. Then, for each species, we summed values of predicted habitat suitability across all forested grid cells. We calculated the change in potential habitat amount as the difference of the total weighted potential forest habitat for each species from 1951 to 2000. Units of potential habitat change as presented are thus in map pixels weighted by modelled habitat suitability rather than units of area, per se.

To assess habitat fragmentation at each time point, we computed the mean of Euclidean nearest-neighbour distance

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(km) between habitat patches in 1951 and 2000 for each species using the TSS thresholded maps and the 'lsm_l_enn_mn' function of the Landscape Metrics v. 2.0 R package (Hesselbarth et al. 2019). We chose this metric to reflect how the connectivity of potential habitat patches changed through the study period. Figure S1 provides a schematic overview of the workflow described above.

2.4 | Functional Traits

We used data on five functional traits that represent life-history strategies expanded from previously published work (Muscarella and Uriarte 2016). Specifically, we considered: wood density (WD g cm $^{-3}$), tree maximum height (m), leaf thickness (mm), leaf area (mm^2), leaf specific area (SLA g mm^2 g^{-1}) and seed dry mass (g). For seed dry mass, we obtained data from the Seed Information Database (SID) (https://ser-sid.org/) and Swenson and Umaña (2015). For other traits, we used measurements from 334 species across 12 forest plots representing the climatic and environmental gradient in Puerto Rico. This combined data set included a total of 1736 (53%) missing measurements across the six traits included. We used phylogenetic imputation to fill gaps in trait data with the R package Rphylopars (Goolsby et al. 2017) and using the phylogeny of Puerto Rican trees published by (Muscarella, Uriarte, et al. 2014). Prior to imputation, the trait values were scaled and centered by subtracting the mean and dividing by standard deviation. After trait imputation, we performed a principal component analysis (PCA) including all traits, and we used the first principal component axis (PC1) as a multivariate trait to represent the acquisitive-conservative continuum of life history strategies. Based on this process, we were able to include 459 species in the analyses using functional traits.

2.5 | Statistical Analyses

To answer our first question about how the amount and connectivity of suitable habitat changed for Puerto Rican tree species from 1951 to 2000, we compared the changes in potential habitat amount and connectivity with the respective values in 1951. To address our second question about potential species richness in reforested areas of Puerto Rico, we summed the thresholded SDM predictions across the island. Finally, we used multiple linear regression to answer our third question about the associations between changes in potential habitat (or connectivity) and niche breadth, niche position and species traits:

$$Y_{sp} \sim NB_{sp} + NP_{sp} + T_{sp} + e \quad (1)$$

where Y_{sp} is either the change in potential habitat or connectivity for species *sp*; NB is niche breadth, NP is niche position, T is the PCA Axis 1 of functional traits and e is a normally distributed error term. Prior to this analysis, we centered and scaled values of niche position, niche breadth and PC1 to facilitate direct comparison of the effect size of each term. All statistical analyses were conducted in R version 4.5.2 (R Core Team 2025).

3 | Results

Based on maps from Helmer et al. (2002) and Kennaway and Helmer (2007), Puerto Rico as a whole gained about 10 times as much forest as it lost between 1951 and 2000 (Figure 2). During this period, the largest gains of forest cover occurred in the two largest Holdridge life zones on the island (subtropical moist and subtropical wet forest), which represent a total of 85% of the island's land area (Table 1; Figure 2). Proportionally, the subtropical wet forest life zone gained the most forest cover with nearly 50% of its spatial extent transitioning to forest cover. Subtropical and lower montane rain forest (the two life zones with smallest total land area) had very little change in land cover, with the vast majority remaining as stable forest. It is worth noting that these two zones correspond with El Yunque National Forest, a protected area which was established in 1903. At the whole island scale, the average area of individual forest patches increased, while the total number of forest patches and nearest neighbour distance between patches decreased from 1951 to 2000 (Figure 2C–E).

In general, SDMs provided good explanatory power of the observed occurrence records. Across species, the mean ± SD of AUC for SDMs was 0.79 ± 0.09 and the mean ± SD omission rate for the 10th percentile of test values (OR10) was 0.14 ± 0.08. The first two axes of the principal component analysis of traits explained 65% of the total variation (Figure 3A). In general, PC1 (which explained 43% of the total variation) was associated with the leaf economic spectrum; higher values represented relatively acquisitive traits (e.g., thin leaves and high SLA). PC2 (which explained an additional 22% of the variation) was most strongly related to wood density and leaf area; species with higher values of PC2 tended to have relatively small leaves and high density wood.

Across species, the amount of potential suitable habitat gained via reforestation was 1–14 times more than the amount of suitable habitat lost (median ± SD = 6.7 ± 2.7). Tree species with relatively more suitable and available habitat in 1951 also had relatively larger gains in potential suitable habitat from 1951 to 2000 (Figure 3B). Across the island, reforested patches represented suitable habitat for 53–259 species (Figure 4). Predicted species richness in reforested patches was highest in the relatively dry southwestern parts of the island and the eastern parts of the Cordillera Central.

Metrics of niche position, niche breadth and traits were weakly but significantly correlated across species (Figure S2). Niche breadth and niche position were negatively correlated (Pearson's $r = -0.16$, $p < 0.001$) indicating species that occupy more marginal habitats compared to the most common conditions in reforested areas also tend to have relatively smaller niche breadths. There was also a weak negative relationship between niche position and PC1 (Pearson's $r = -0.10$, $p < 0.001$), indicating that species with relatively acquisitive traits (higher values of PC1) tend to occur in relatively similar habitats compared to the conditions in reforested sites. Finally, there was a weak positive relationship (Pearson's $r = 0.29$, $p < 0.001$) between trait PC1 and niche breadth, indicating that species with more acquisitive traits tend to occur across a broader range of environmental conditions.

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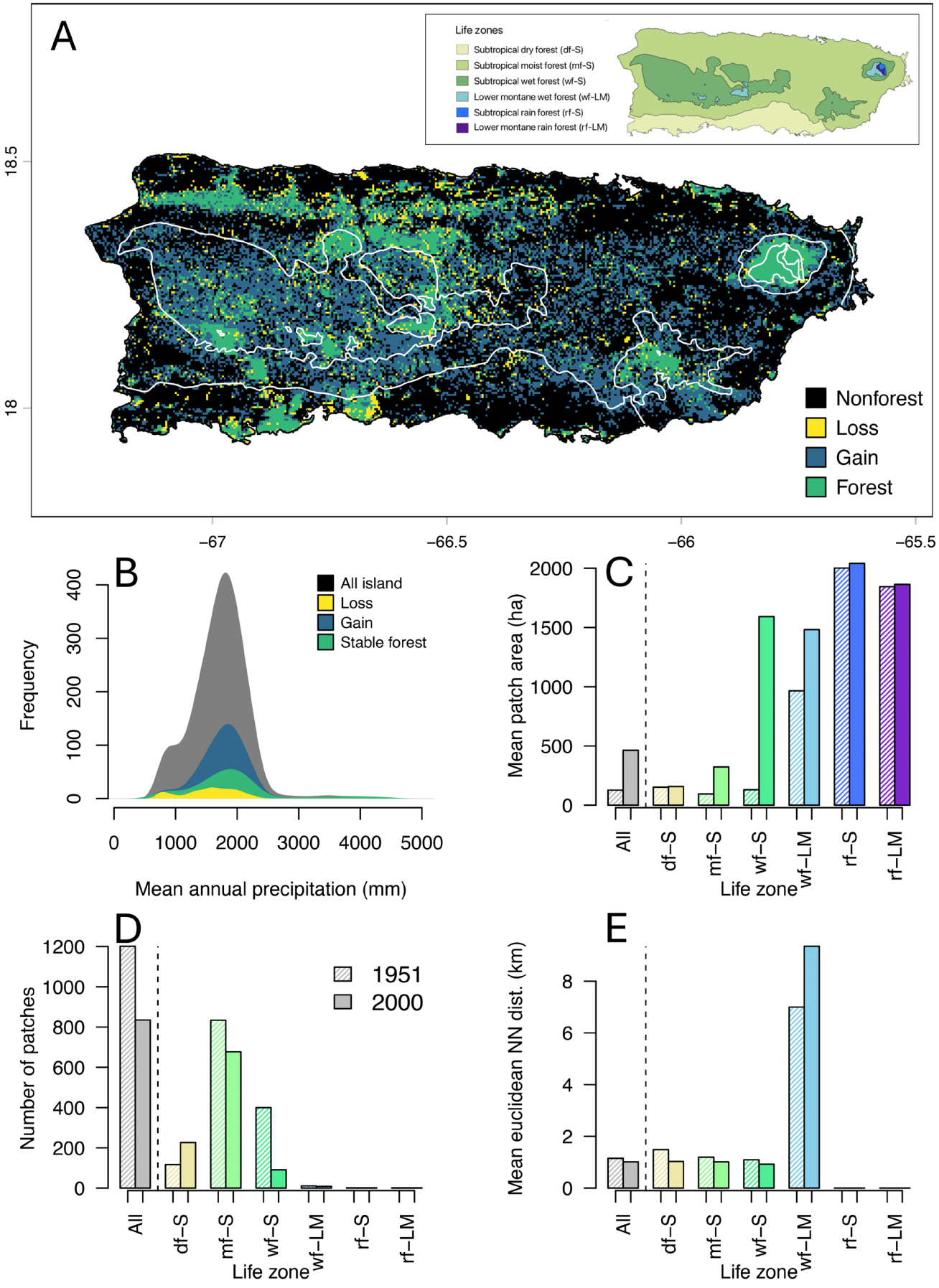

FIGURE 2 | Legend on next page.

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FIGURE 2 | (A) Forest change map with persistent non-forest, forest lost from 1951 to 2000, forest gained from 1951 to 2000, persistent forest. White lines show delineations of Holdridge life zones, as shown in the inset. (B) Density of grid cells along a gradient of mean annual precipitation for the different categories of LULCC in (A). Across the entire island (grey bars) and within each life zone (coloured bars) in 1951 (hatched bars) and in 2000 (solid bars), (C) shows the mean forest patch areas (ha), (D) shows the total number of forest patches and (E) shows the mean euclidean distance (km) between neighbour forest patches. Bar colours in C–E correspond to the colours of Panel (A) inset.

TABLE 1 | The percentage of the total area in mainland Puerto Rico classified into six different Holdridge life zones (Daly et al. 2003), as well as the proportion of each life zone in different land cover change categories based on maps of land cover in 1951 and 2000 (Helmer et al. 2002; Kennaway and Helmer 2007).

		Change class (proportion)				
Holdridge life zone	Area (%)	Stable non-forest	Forest loss	Forest gain	Stable forest	Net change forest area (km^2)
Subtropical dry	13.9	0.66	0.05	0.20	0.09	+179
Subtropical moist	61.7	0.56	0.05	0.30	0.10	+1391
Subtropical wet	22.9	0.28	0.05	0.47	0.19	+924
Lower montane wet	1.2	0.04	0.03	0.22	0.70	+27
Subtropical rain	0.2	0.00	0.03	0.05	0.93	+0.4
Lower montane rain	0.1	0.00	0.00	0.01	0.99	+0.2

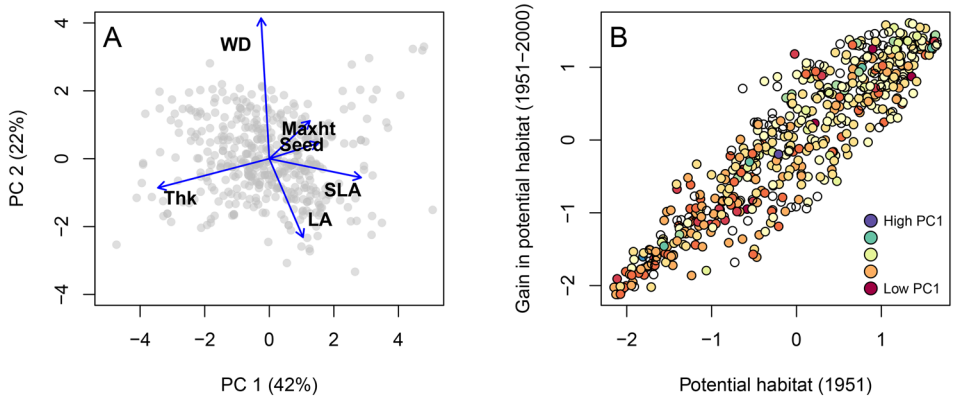

FIGURE 3 | (A) Principal component Axis 1 and 2 of the trait ordination analysis. Grey points are species scores; arrows show loadings of individual traits. The traits shown are wood density (WD, g cm^{-3}), maximum height (Maxht, m), leaf thickness (Thk, mm), specific leaf area (g SLA, mm^2 g^{-1}) and seed dry mass (Seed, g). (B) The amount (centered and scaled) of potential habitat per species in 1951 (x-axis) versus the amount (centered and scaled) of increased potential habitat from 1951 to 2000 (y-axis). Each point represents a species, and point colours reflect species scores on PC1.

Niche position and niche breadth were significantly associated with the amount of potential habitat change from 1951 to 2000, with the combined linear model explaining 94% of the variation in the data (adjusted $R^2 = 0.94$, Table S3). As expected, species that occupy more marginal habitats relative to the environmental conditions in the reforested areas (i.e., larger values of niche position) gained relatively less climatically-suitable habitat during the study period ($p < 0.001$; Figure 5A). There was a stronger association between habitat gain and species niche breadth; species with broader niches had larger gains of suitable habitat ($p < 0.001$; Figure 5B). We did not find a significant relationship between species traits (PC1) and change of suitable habitat ($p = 0.1$; Figure 5C).

Reforestation also altered habitat connectivity—measured as nearest neighbour distance between potential habitat patches—differently across species but the combined model explained only ~3% of the total variation (Figure 5D–F, Table S3). The change in connectivity was not significantly related to niche position or trait axis PC1, but species with lower values of niche breadth had relatively large decreases in terms of nearest neighbour distance between potential habitat patches (i.e., larger gains of potential connectivity) ($p < 0.001$) (Figure 5E). Full data and scripts to repeat our analyses are provided in a FigShare repository (Muscarella et al. 2026).

4 | Discussion

By the mid-1900s, Puerto Rico had been largely converted to agriculture, leaving limited habitat for forest-dwelling species,

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including trees. With the widespread abandonment of agricultural land during the second half of the 20th century, tree cover generally increased but spatial patterns of reforestation were non-random with respect to environmental conditions across the island (Helmer et al. 2008). Our study on the species-specific changes in availability of potential suitable habitat (i.e., climatically-suitable and forested) from 1951 to 2000 showed: (1) The largest gains in potential habitat were realized by species with already large amounts of potential habitat in 1951; (2) Niche breadth (followed by niche position and species traits) was the strongest predictor for the amount of potential habitat gained during the study period and (3) Niche breadth was weakly associated with changes in connectivity among patches (as measured by nearest neighbour distance). We discuss our results in terms of the consequences of natural forest regeneration for tropical tree biodiversity.

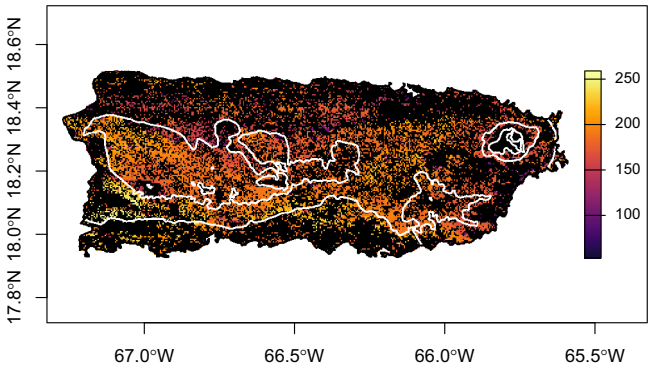

FIGURE 4 | Potential species richness in areas of forest regrowth (forest gained between 1951 and 2000) based on overlapping maps of thresholded species distribution models (based on maximizing TSS per species) and reforested pixels. White lines delineate Holdridge life zones as in the inset of Figure 2A.

4.1 | Forest Transitions

Global forest cover has expanded in recent decades, a trend that has been partly driven by agricultural abandonment (Rudel et al. 2009, 2020). In many instances, LULCC dynamics have occurred non-randomly across the landscape such that low-productivity and topographically rugged areas have been preferentially abandoned, leading to reforestation in these areas (Mather and Needle 1998). In Puerto Rico, the forest transition happened largely passively with selective abandonment of less-profitable lands in the steeper and wetter slopes of the central mountain, in rugged karst terrain and in other lands that are less arable or accessible (Helmer et al. 2008). In contrast, coastal plains remain largely used for agriculture and today are primary areas of urban development (Parés-Ramos et al. 2008). The spatial distribution of forests following these forest transitions is thus likely to systematically benefit some species over others, depending on environmental preferences.

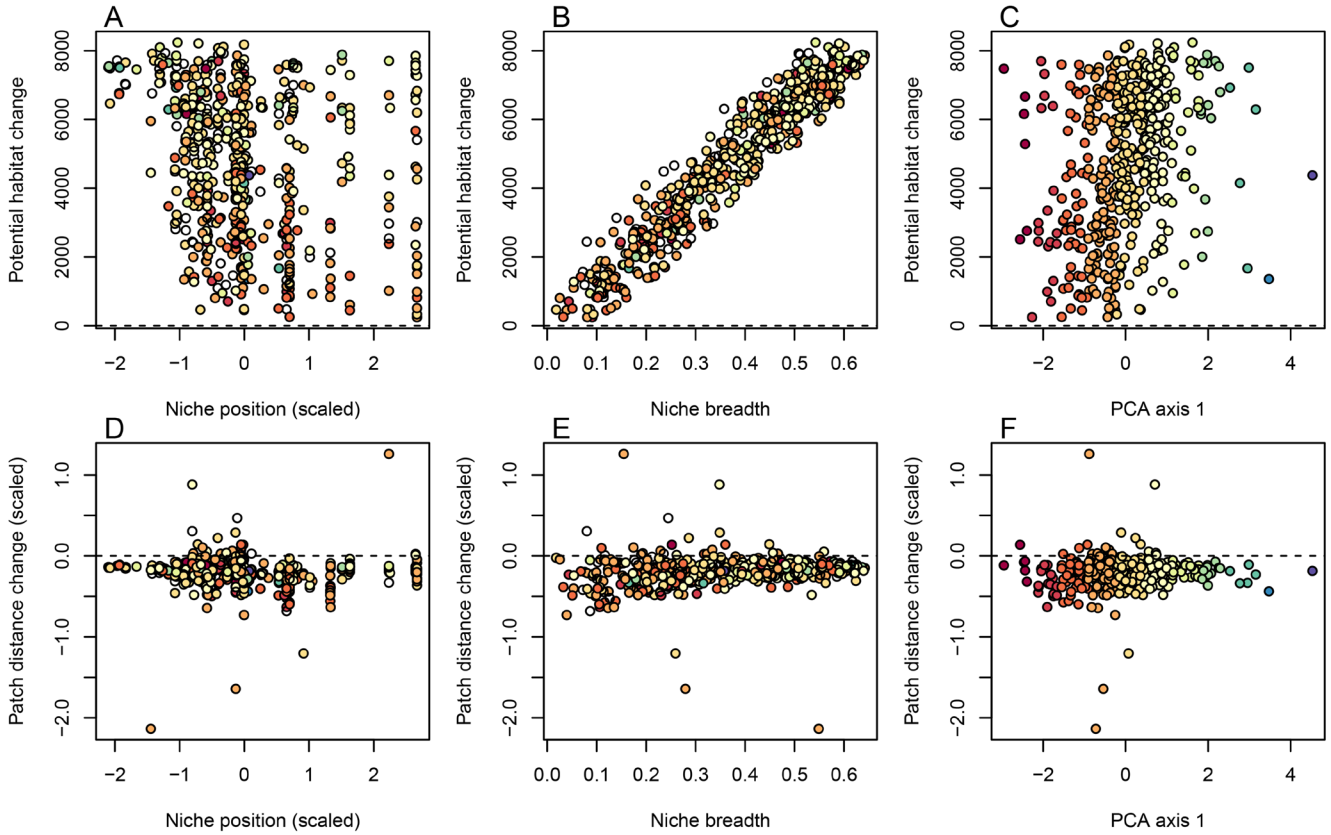

FIGURE 5 | Relationship between the change in the amount (A–C) and mean distance between patches (D–F) of potential habitat from 1951 to 2000 as a function of (A, D) centered and scaled niche position (i.e., 'marginality'), (B, E) niche breadth and (C, F) trait PCA for Puerto Rican tree species. Point colours are based on values of trait PC1 (see Figure 3). Units for potential habitat change (A-C) are pixels weighted by habitat suitability; units for patch distance change (D–F) are scaled and centered kilometres.

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Gains of forest habitat can carry a range of benefits for biodiversity and ecosystem services. For example, trees and other forest-dwelling species may generally benefit from larger populations, which buffer against local extinction and can help safeguard genetic diversity (Chazdon et al. 2009). From an ecosystem services perspective, natural reforestation can provide enormous benefits (e.g., carbon sequestration) (Chazdon et al. 2016; Poorter et al. 2016). Numerous studies have shown, however, that species composition of regenerating secondary forests in diverse tropical regions is hardly predictable (Norden et al. 2015). The effects in terms of species-specific habitat recovery in the context of natural forest regeneration are often overlooked, yet they could provide important information to guide conservation practices and predict the potential for biodiversity recovery. In the context of Puerto Rico, LULCC can shape how plant communities respond to natural disturbances such as hurricanes, influencing both the immediate effects of the disturbance and subsequent recovery, with lasting impacts on forest structure and composition (Uriarte et al. 2004).

4.2 | Species-Specific Consequences of Forest Regeneration

In our study, species exhibited a wide range of potential habitat gains. The amount of habitat gain was most strongly correlated to species niche breadth, where broader niche species (habitat generalists) showed the largest gains of potential habitat. Niche position was also significantly associated with habitat gain whereby species that occupy more marginal habitats with respect to the most common conditions in the reforested landscape gained relatively less potential habitat. Notably, niche breadth and niche position were weakly (negatively) correlated across species such that species with central niche positions also tended to have high values of niche breadth. While our model explains a large proportion of the variation, we interpret these strong associations with caution, acknowledging that the high explanatory power may partly reflect this collinearity rather than strictly independent effects. The largest increases in potential habitat gain between 1951 and 2000 were exhibited by species with central niche position and wide niche breadth. These results illustrate how natural forest regrowth can translate into relatively larger or smaller changes in potential habitat availability depending on species' climatic associations.

In Puerto Rico, most of the land area falls within the subtropical moist and wet life zones, with comparatively little area in dry forest and the (wetter) higher elevation lower montane climatic zone. The largest areas of reforestation have also occurred in the dominant, moist and wet life zones. As a result, forest regrowth favoured species whose niche positions more closely align with these dominant climatic conditions. Species with non-marginal niche positions tend to be more widespread and have higher occupancy rates and dispersal potential (Vela Díaz et al. 2020; Vleminckx et al. 2023). In our study system, species with niche positions closer to the conditions of the subtropical moist and wet life zones were more likely to become widespread during forest regeneration. As forest regrowth largely overlapped with their climatic optimum, these species showed a greater gain in potential habitat.

It is perhaps not surprising that species with broader niche breadths exhibited the largest gains of potential habitat. This result suggests that habitat generalists are expected to benefit most during forest regeneration. A positive association between niche breadth and geographic range size is well established; generalist species tend to occupy larger ranges and often become ecologically dominant and locally abundant (Morueta-Holme et al. 2013; Moulatlet et al. 2025; Sheth et al. 2020). In Puerto Rico, we observe a similar pattern, with broad-niche species exhibiting substantially greater gains in potential habitat. As generalists, these species can occupy a wide range of environmental conditions, allowing most forest expansion to provide suitable habitat.

In our study, species' traits were not significantly associated with potential habitat gain, although the direction of the relationship was consistent with expectations. The conservative–acquisitive plant economic spectrum, based on plant functional traits, is widely used to distinguish plant resource-use strategies (Wright et al. 2004) and can help predict recolonization and successional patterns after LULCC (Díaz 2025; Poorter et al. 2021). In our study, species with conservative traits were associated with more marginal habitats and had narrower niche breadths (also see Helmer et al. 2018). A similar pattern was reported at the global scale by Chen et al. (2025), who found that species with conservative leaf traits were generally associated with narrow niche breadths. Although not statistically significant, our results suggested a tendency for species with more acquisitive traits to gain more potential habitat than species with more conservative traits.

Besides total forest area, forest cover changes in Puerto Rico also affected landscape configuration. Between 1951 and 2000 mean patch area increased, and mean patch number and nearest neighbour distance between patches decreased. We interpret the change in these indices as a reduction in landscape fragmentation and an overall increase in landscape connectivity. A previous study examining habitat fragmentation changes in Puerto Rico between 1977 and 2000 found an increase in landscape aggregation of wetland habitats and a decrease in aggregation in forested habitats (Gao and Yu 2014). Specifically Gao and Yu (2014) found that deforestation between 1977 to 2000 was located in the forest interiors, while the reforested sites tend to be located along the edges of the forests.

We found only a weak relationship between niche position and increases in connectivity (reflected by changes in nearest-neighbour distance). Both species with marginal and non-marginal niche positions showed significant increases in connectivity, although the effect was stronger for species with non-marginal niche positions. Numerous studies highlight the crucial role of seed arrival in natural forest regeneration, suggesting that decreasing the distance between forest patches will facilitate dispersal and strongly influence the species composition of regenerating forest communities (Chazdon and Guariguata 2016; Reid et al. 2015). When forest regrowth provides an increase in the suitable habitat available, its spatial configuration becomes an important determinant of habitat availability. Conversely, if regrowth does not provide an increase in suitable habitat, its extent may matter less, though it can still facilitate movement across the landscape (Bowen et al. 2007;

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Fricke et al. 2025). Percolation theory predicts that once a habitat covers more than about 60% of a landscape, connectivity does not limit species dispersal (Keitt et al. 1997). The ~50% to 55% forest cover across Puerto Rico circa the year 2000 may mean that most habitat patches are relatively well-connected. It is also worth noting that our analyses of habitat connectivity could vary depending on the specific threshold value chosen.

Maps of potential species richness are commonly generated in macroecological studies and can be valuable for applied research, conservation and addressing fundamental questions about the processes governing spatial patterns of biodiversity (Conroy and Noon 1996; Graham and Hijmans 2006). We found a high degree of variation in potential species richness across reforested patches in Puerto Rico, ranging from 68 to 209 species per grid cell. This shows how reforestation has different potential to support biodiversity depending on where it takes place and which species are the main actors in the forest regrowth.

It is critical to note that our study focuses on quantifying the amount and arrangement of 'potential' habitat patches, as opposed to actually occupied habitat. This distinction is essential for considering the diverse consequences of LULCC for biodiversity and conservation. Individual species may be absent from high-quality patches for numerous reasons including, for example, dispersal limitation or priority effects. Additionally, the degree to which patches of climatically-suitable habitat are actually occupied by individual species also depends on highly local and dynamic conditions (e.g., understory light environment related to forest successional stage) that are not explicitly included in our distribution models. Thus, our estimates of potential suitable habitat could be further refined by considering how age (or age distribution) of suitability forest patches relates to successional associations for individual species. Moreover, tracking actual occupancy of forest patches through time across the island would provide additional insight to effects of LULCC on forest biodiversity. For example, early successional species can be very abundant across Puerto Rico shortly after hurricane disturbances but will decline as succession proceeds. More shade-tolerant species with conservative traits can show the opposite pattern over time (Helmer et al. 2023a).

Natural forest regeneration has enormous potential to support biodiversity. Investigating the species-specific consequences of natural regeneration, and how it affects changes in potential habitat amount and configuration, can help predict and understand the trajectories of natural forest recovery and inform species conservation practices (Smith and Levine 2025). In Puerto Rico, even though forest regrowth resulted in an overall increase in the amount and connectivity of potential habitat for all tree species, the magnitude of potential habitat gain varied widely among species. In the context of LULCC and natural forest regeneration, some species tend to consistently be the 'winners' in terms of habitat gain. This could become even more evident when examining the combined effects of climate change and LULCC. Sweeney and Jarzyna (2022) found that habitat generalists are more resilient to environmental change and benefit from natural regeneration at the expense of habitat specialists. Consequently, rare and endemic species likely have geographically restricted ranges, relatively small population sizes and narrow niche breadths (Rabinowitz 1981). Species exhibiting these forms of rarity may derive limited benefits from passive forest regeneration. For these vulnerable groups, active assisted regeneration practices may be necessary to ensure their persistence. These findings indicate that forests regenerating after clearing or other disturbances may have a community that is shifted toward acquisitive and generalist species, highlighting the importance of monitoring and supporting specialist, rare and conservative species as forests recover.

5 | Conclusions

In Puerto Rico, the increase in forest cover over a 50-year period led to a large increase in potential habitat for tree species, suggesting a substantial 'win' in terms of forest conservation and restoration. The largest gains were realized by species occupying habitats similar to those of reforested areas, species with relatively wide niche breadths and species with relatively acquisitive functional traits. Importantly, our findings illustrate how the benefits of forest regeneration are not distributed evenly across species, and that landscape context and species functional characteristics strongly influence regeneration outcomes. For forest management and restoration, maintaining heterogeneous forest mosaics and promoting a diversity of environmental conditions may help support species with narrower habitat associations and less acquisitive trait strategies that benefit less from natural regrowth alone. These results suggest that although passive forest regeneration can substantially expand habitat availability, targeted restoration may still be needed to conserve functionally or ecologically specialized species.

Author Contributions

R.M., L.M. and P.M. conceptualized the study; R.M., L.M. and M.U. collected and curated data; R.M., P.M. and M.U. acquired funding; R.M. and L.M. conducted analyses; R.M. and L.M. wrote the manuscript with input from all authors.

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Conflicts of Interest

The findings and conclusions in this publication are those of the authors and should not be construed to represent any official USDA or U.S. Government determination or policy.

Data Availability Statement

Original land cover maps for Puerto Rico in 1951 and 2000 can be obtained from Helmer et al. (2023b) and Kennaway and Helmer (2023). Full data and scripts to repeat our analyses, including outputs from species distribution models described in the text and species mean traits,

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are provided in a FigShare repository (Muscarella et al. 2026), DOI: https://doi.org/10.6084/m9.figshare.32336394.

Peer Review

For transparency, the peer review documents associated with this article are available at https://doi.org/10.1111/ddi.70263.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Schematic diagram of the data used in this study. Panels A–D illustrate input data for the study. (A) Environmental conditions and species occurrence records are used for species distribution models. For illustration, the map background shows precipitation in the driest month (mm) and the white points represent occurrence records of an example species, *Coccoloba venosa*. (B) Continuous output of species distribution model for *C. venosa*; higher values (lighter colours) indicate higher modelled habitat suitability. (C, D) Maps of forest cover in 1951 and 2000, respectively. Panels E-J show derived maps used for analysis. (E, F) Maps of environmental conditions [e.g., precipitation in the driest month (mm)] in areas classified as forest. (G, H) Maps of modelled habitat suitability for *C. venosa* restricted to areas classified as forest (i.e., 'Potential suitable habitat'). Potential suitable habitat amount is computed based on the sum of grid cells in these maps for each species. (I, J) Maps of thresholded potential suitable habitat for *C. venosa*. Connectivity index (nearest patch distance) is based on thresholded maps. **Figure S2:** Correlations between niche breadth, niche position and functional trait PCA Axis 1.

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Point colours correspond to species values along PCA Axis 1 (see legend in Panel B). **Table S1:** Summary statistics from multiple linear regression models. **Table S2:** Included as an .xlsx file. Number of occurrence records and median ± standard deviation of four environmental conditions at occurrence records for each study species. Top two rows, respectively, summarize these statistics across the full island and across grid cells classified as new forest (i.e., not forest in 1951 and forest in 2000). Metadata provided as a separate tab in the .xlsx file. **Table S3:** Included as an .csv file. ODMAP protocol for SDMs used in this study.

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