

## RESEARCH ARTICLE

# Contrasting trends in biodiversity of birds and trees during succession following cacao agroforest abandonment

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## Abstract

1. Understanding how transformed habitats act as reservoirs of biodiversity is a key challenge at a time when ecosystems are under unprecedented pressure. Here we compare tree and bird biodiversity in actively cultivated and abandoned cacao agroforests, and use a space for time approach to ask how this diversity has changed over 100 years of succession.
2. Tree and bird communities were surveyed in cacao agroforests, secondary forests at different stages of succession and primary forests in the Northern Range of Trinidad, West Indies, to test the prediction that there are consistent temporal trends in alpha and beta-diversity across taxa.
3. Temporal alpha-diversity was taxon dependent. We found that tree alpha-diversity increased with forest age. In contrast, there was no temporal trend in bird alpha-diversity. Tree and bird species richness were negatively correlated.
4. Tree and bird composition varied with forest age and environmental distance. A greater proportion of native trees, and of highly forest-dependent and insectivorous birds were found in older forests.
5. Our analyses show that actively cultivated and young abandoned cacao agroforests can sustain high bird alpha-diversity, despite lower levels of tree alpha-diversity. Old secondary and primary forests have unique species compositions including more sensitive and specialist species. Compositional shifts with successional stage for both trees and birds produce a patchwork of habitats that contribute to regional gamma-diversity.
6. *Synthesis and applications.* Our research highlights the value of actively cultivated cacao agroforests and secondary forest alongside primary forests as reservoirs of biodiversity. By supporting both biodiversity and livelihoods, traditionally grown shade-cacao agroforests fall within a people and nature framework. Taken together, these results emphasise the contributions of secondary forests, which are often overlooked, to conservation.

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## KEYWORDS

bird diversity, cocoa, multi-taxa, people and nature, secondary forest succession, tree diversity, tropical forest biodiversity conservation

## 1 | INTRODUCTION

Growing anthropogenic pressures on ecosystems mean that global biodiversity is being threatened in ways that have no precedent in historical times (Blowes et al., 2019; Isbell et al., 2017; Magurran & Dornelas, 2010). Landscape transformation, including appropriating natural habitat for crop use, is viewed as a major contributor to this ongoing biodiversity crisis (Ehrlich & Pringle, 2008; Semper-Pascual et al., 2019).

Habitat transformation is not a single 'all or nothing' event, and the way in which converted land is exploited may change with fashions in food items or as a result of economic forces. For example, a widespread form of land conversion in the tropics has been the transformation of primary forest to cacao agroforest (Ruf & Schroth, 2004). While patterns of succession and biodiversity have been studied in other agricultural systems, cacao farming has received relatively little attention. Globally, many historic agroforests have been abandoned due to ecological change (such as pests, diseases or environmental factors), fluctuating market prices and competition from large-scale commercial agriculture (Bekele, 2004; Ruf & Schroth, 2004). Some abandoned cacao agroforests are now being reclaimed for non-intensive harvesting (Dreisinger, 2012) to meet a rising demand for ethically and sustainably sourced products (Hiscox et al., 2015).

A key conservation challenge is to find solutions that support both people and nature (Chazdon, Harvey, et al., 2009; Mace, 2014). Often conservation efforts focus on protecting untouched natural areas (Chazdon, 2014). While conserving these areas is important, they may be affected by land-use changes in the surrounding area, and represent only a small proportion of forest habitats. Secondary habitat and anthropogenically altered environments cover an increasingly large fraction of the Earth's surface, but also have the potential to contribute to conservation initiatives (Chazdon, 2014). Thus, there is a pressing need to understand how biodiversity conservation can be promoted, not as an alternative to human use of the environment, but as part of it. Planted and secondary forests (forest which has been mostly or entirely deforested in the past with evidence of the disturbance still apparent; Corlett, 1994), which account for 64% of all Earth's forests (MacDicken et al., 2016), have the potential to be important reservoirs of global biodiversity. However, in many parts of the world, particularly in the tropics, the contribution that transformed habitat makes to biodiversity is less well understood (Chazdon, 2014; Chazdon, Harvey, et al., 2009; Chazdon, Peres, et al., 2009; DeClerck et al., 2010). To better understand whether this form of habitat transformation could support biodiversity conservation within the 'people and nature' framework, we investigate abandoned and active cacao agroforests in Trinidad's

Northern Range. Specifically we ask how the conservation value of abandoned agroforests changes, with succession, over time.

Trinidad and Tobago is a Caribbean twin-island nation located in a prominent biodiversity hotspot (Hosein et al., 2017; Maunder et al., 2008). The forested Northern Range mountains of Trinidad are a mosaic of primary and secondary forest at different successional stages following agricultural abandonment and other disturbances (Helmer et al., 2012). Tropical forests cover the Northern Range. Despite extensive work by residence and visiting researchers, many gaps in our knowledge of the biodiversity of this area remain. Cacao farming has transformed parts of the Northern Range as many of the old agroforests were periodically abandoned and new ones started over time (Bekele, 2004; NATT, 2017). This pattern of transformation therefore provides an informative case study for understanding how Trinidad's history of cacao farming shapes patterns of biodiversity, and the potential contribution of actively managed and abandoned cacao agroforests to biodiversity conservation.

The aim of this study is to investigate the patterns of tree and bird diversity through cacao agroforest secondary forest succession in Trinidad (representing c. 100 years of change). We also examine the relationship between the biodiversity trends in these taxa. Insights from previous studies of tree (Derroire et al., 2016; Finegan, 1996) and bird (Arroyo-Rodríguez et al., 2017; Buechley et al., 2015; Calvo & Blake, 1998; DeGraaf et al., 1991; Keller et al., 2003; Rey-Benayas et al., 2010) biodiversity over secondary forest succession across different systems lead us to hypothesise that species richness and evenness will increase over time for both taxa, mainly during early stages of succession. Because trees are ecosystem engineers, forests with greater tree diversity should support a more diverse array of other taxa by providing a wide-range of habitat types, microclimates and resources (Díaz & Cabido, 2001; Petchey & Gaston, 2006; Weiher, 2011). It follows that trends in bird and tree diversity should be positively correlated. Finally, as a result of this secondary succession we expect species composition to change (turnover) over time for both trees and birds (Borges, 2007; de Souza Modena et al., 2013; Derroire et al., 2016).

We assess both temporal alpha and temporal beta-diversity. To do this we first quantify bird and tree alpha-diversity metrics (species richness, Shannon diversity and Simpson diversity, using the Hill number framework; Hill, 1973) in relation to the time since abandonment of cacao agroforests, and benchmark these patterns against data from active agroforests and primary forest while controlling for environmental variables. We then ask how compositional change (species turnover as measured by a Jaccard index) in both taxa (trees and birds) is linked to site age and environmental differences between sites.

## 2 | MATERIALS AND METHODS

### 2.1 | Location

The 28 sites in our study represent c. 100 years of secondary forest succession (Figure 1). Active cacao agroforests (Appendix S1), secondary forest regenerating from abandoned cacao agroforests and primary forest (areas with no indication of disturbance or human modification) were surveyed across the southern slopes of the Northern Range in Trinidad (one active agroforest being just south of the Northern Range, but managed similarly to the other active sites). Sites were chosen based on expert opinion to control for variability in environmental variables including land history, forest and matrix habitat type, altitude and land gradient as much as possible. We also ensured that similarly aged sites were not geographically clustered, and that the sites were spread latitudinally across the Northern Range. Site choice was influenced by our ability to obtain reliable ages, information on land-use history, and where we had permission to survey. The minimum distance between sites was approximately 0.8 km (QGIS Development Team, 2020). Sites were all 1–5 ha, with trees over 5 m tall and over 50% canopy cover. The successional age and land history of each site was estimated from local knowledge and historic records.

The number of years since each cacao agroforest site was abandoned was used as a proxy for successional time. This chronosequence approach assumes that the active and abandoned cacao agroforests were all managed similarly, and that the secondary forest sites are transitioning through succession at a similar rate. This approach also assumes that patterns of biodiversity are driven by forest age rather than by environmental factors. These factors were controlled for where possible through site choice. Historical records, including those held at the National Archives Trinidad and Tobago, and local knowledge confirm that the active and secondary cacao agroforests underwent similar management (Appendices S1 and S2).

Boundaries of secondary forest sites and active cacao agroforests were determined from local knowledge and landmarks, such as the crotons (usually *Cordyline fruticosa*) commonly used as boundary markers. Sites were situated in valleys on the southern slopes of the Northern Range, in lower montane seasonal evergreen forest ( $\leq 250$  m altitude, with some higher altitude sites; Appendix S2; Kenefick et al., 2013). Each site was predominantly surrounded by similar habitat. Historically, agricultural estates in Trinidad used to be larger than they are today, and often included many adjacent patches of cacao agroforest (De

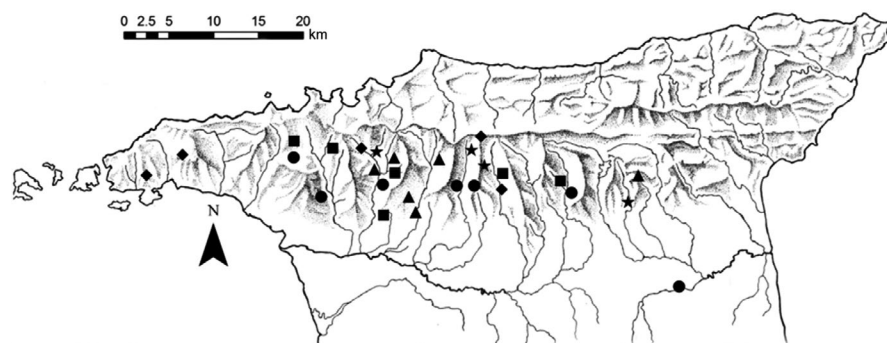
Verteuil, 2000). Because of this, the patches of abandoned cacao agroforest in this study were largely surrounded by other patches of abandoned cacao agroforest that were originally part of the same estate. The active cacao agroforests were all surrounded by other active cacao agroforests that belonged to different land owners. The primary forest sites were squares situated within a larger tract of primary forest; the size and shape being chosen so that it would be comparable with the active cacao agroforest and secondary forest sites.

Active cacao agroforests were planted predominantly with cacao *Theobroma cacao* trees and some shade trees such as mountain immortelle *Erythrina poeppigiana*. Most sites also included other tree species such as mango *Mangifera indica*, citrus *Citrus* sp. and coconut *Cocos nucifera*. Secondary forest sites ranged from c. 20 to 100 years old. Primary forest sites, which had no evidence or record of disturbance and had not been disturbed in local memory, were surveyed as a baseline for beta-diversity comparisons. These sites were given a conservative age estimate of 200 years old. All but two sites were directly connected on at least one edge to a neighbouring forested area, and all sites were within 140 m of a larger tract of forest (QGIS Development Team, 2020). All sites were surrounded by similarly aged and managed forests.

### 2.2 | Data collection

#### 2.2.1 | Trees

All trees (woody vegetation  $>6$  cm DBH and  $>3$  m tall) within five metres of a 50 m transect line were identified to species level. Transects were randomly placed and oriented within the site using a random number table. If the transect line reached a boundary or impassable obstacle, the path was reoriented by 90 degrees. Samples and photographs were taken of trees, and the species submitted to the National Herbarium of Trinidad and Tobago where necessary to confirm identifications. Topographic and environmental data collected on site included altitude using a calibrated GPS, land gradient using an inclinometer and canopy cover using a spherical densiometer. Distance to nearest water source, matrix habitat and weather conditions were recorded at the start of each transect. The geographical distances between site pairs, and of each site from neighbouring forest and from areas of human habitation ( $>5$  houses and a paved road) were measured using QGIS (QGIS Development Team, 2020).



**FIGURE 1** Site locations in the Northern Range of Trinidad ( $n = 28$ ). There were seven active sites (circles), six 25–50 yo (diamonds), seven 60–80 yo (triangles), 4  $> 100$  yo (squares) secondary forests and four primary forest sites (stars)

## 2.2.2 | Birds

To survey birds, a single transect was placed through each site using QGIS in the longest orientation given the forest shape (QGIS Development Team, 2020). Transects were set at least 50 m from the site edge to maximise area coverage, and to avoid double counting birds or counting birds outside the site. At each site the transect was surveyed three times, 20 min apart, at a consistent walking speed between repetitions and between sites (estimated using a GPS). The first transect was used in the analysis for this paper, and the subsequent repetitions were used to assess the repeatability of the bird surveys (Appendix S3). Bird surveys were conducted in the early morning (7 a.m. to 9 a.m.) when birds are more active, and the same three experienced surveyors jointly conducted every bird survey (DJ, HA and Nicholas Manchouck). All birds seen or heard on either side of the transect line (up to 200 m) within the survey period were identified to species level (binoculars were used, and sound recordings taken; for discussion on detectability see Appendix S4). Domesticated captive birds (*Numida meleagris* and *Gallus* species) were not included in these analyses. The method and order of detection (seen, heard or both) was noted, as well as bird behaviour (flying over, flying low, perched, on the ground, eating, nesting etc.) and whether a bird was directly interacting with the site (perched, nesting, feeding within or flying low through the site). Surveys were not conducted in extreme weather conditions (wind, fog or rain). Surveys were conducted between late April and early August (2019), coinciding with the start of the wet season and the main bird breeding season (ffrench, 1985; Kenefick et al., 2013; Snow & Snow, 1963).

## 2.3 | Analysis

### 2.3.1 | Environmental variables

Annual precipitation, average altitude, average land gradient and distance to nearest settlement (measured as distance to the nearest settlement with >5 houses and a paved road using QGIS) were used in the environmental analysis. Environmental distance was quantified using multi-dimensional scaling (MDS); this provided a measure of the (pairwise) environmental distance between sites in multidimensional Euclidean space. Annual precipitation information was obtained from Fick and Hijmans (2017) WorldClim v2 supplemented with information from global climate models, digital elevation models and local weather stations (Spiers et al., 2018).

### 2.3.2 | Alpha-diversity

Alpha-diversity was assessed by quantifying Hill numbers of the order  $q$  (species richness [ $q = 0$ ], Shannon diversity [ $q = 1$ ] and Simpson diversity [ $q = 2$ ]; Hill, 1973) estimates from extrapolated rarefaction curves for trees and birds in each site using the iNEXT

package (Chao et al., 2014; Appendix S11). In all cases we estimated diversity values for a sample size of 100 individual trees and 50 individual birds. At these sample sizes the extrapolated rarefaction curves for each site and order approached an asymptote while the confidence intervals remained small (Appendix S11). This approach allows us to make fair comparisons across sites, even when using metrics such as species richness and Shannon diversity which are strongly influenced by sample size (Chao et al., 2014). It also has the advantage of presenting results in a coherent statistical framework.

While we controlled for differences in altitude as much as possible through our choice of sites, older sites tended to be at higher altitudes for historical reasons (Appendix S6). Altitude was not included in the alpha-diversity analyses, however, because altitude was collinear with forest age which was the main interest of this study (Zuur & Ieno, 2016). The total altitudinal range between the sites is small (<550 m; Appendix S6).

### 2.3.3 | Beta-diversity

The Chao-Jaccard index was used to quantify compositional dissimilarity between sites (dis.chao function, COMMecol package). The Chao-Jaccard index corrects for under-sampling and unseen species by weighting for rare species shared between two sites (Chao et al., 2005). A quantile regression (50th quantile; Koenker, 2013) was then used to relate Chao-Jaccard compositional dissimilarity to age difference and environmental distance in pairwise comparisons for both the tree and bird assemblages. Quantile regressions were chosen because they are more robust to outliers and unequal variance (heteroscedasticity) than standard linear regressions (Cade & Noon, 2003; John, 2015).

Compositional change was further analysed by testing for changes in the proportion of native trees over succession. Information on tree species native ranges was collated from Quesnel and Farrell (2005) and POWO (2019). Compositional change in the bird community was evaluated by testing for shifts in the proportion of birds with high, medium and low forest dependence with forest age. Information on bird forest dependence was obtained from BirdLife International (BirdLife International, 2020). In addition, we assessed changes in the proportion of birds assigned to the feeding guilds: granivores (seeds, nuts and dry fruits), insectivores (invertebrates), omnivores (generalist diet including animal and plant foods), predators and scavengers (meat and carrion) and pollinators and seed dispersers (fruits and nectar; information from Acevedo-Charry & Aide, 2019; Wilman et al., 2014).

### 2.3.4 | Concordance in diversity patterns across taxa

We used a Spearman test to examine whether trees and birds exhibit correlated trends in alpha-diversity (Revelle, 2015). To further visualise the compositional relationships between sites we also performed a cluster analysis for both trees and birds,

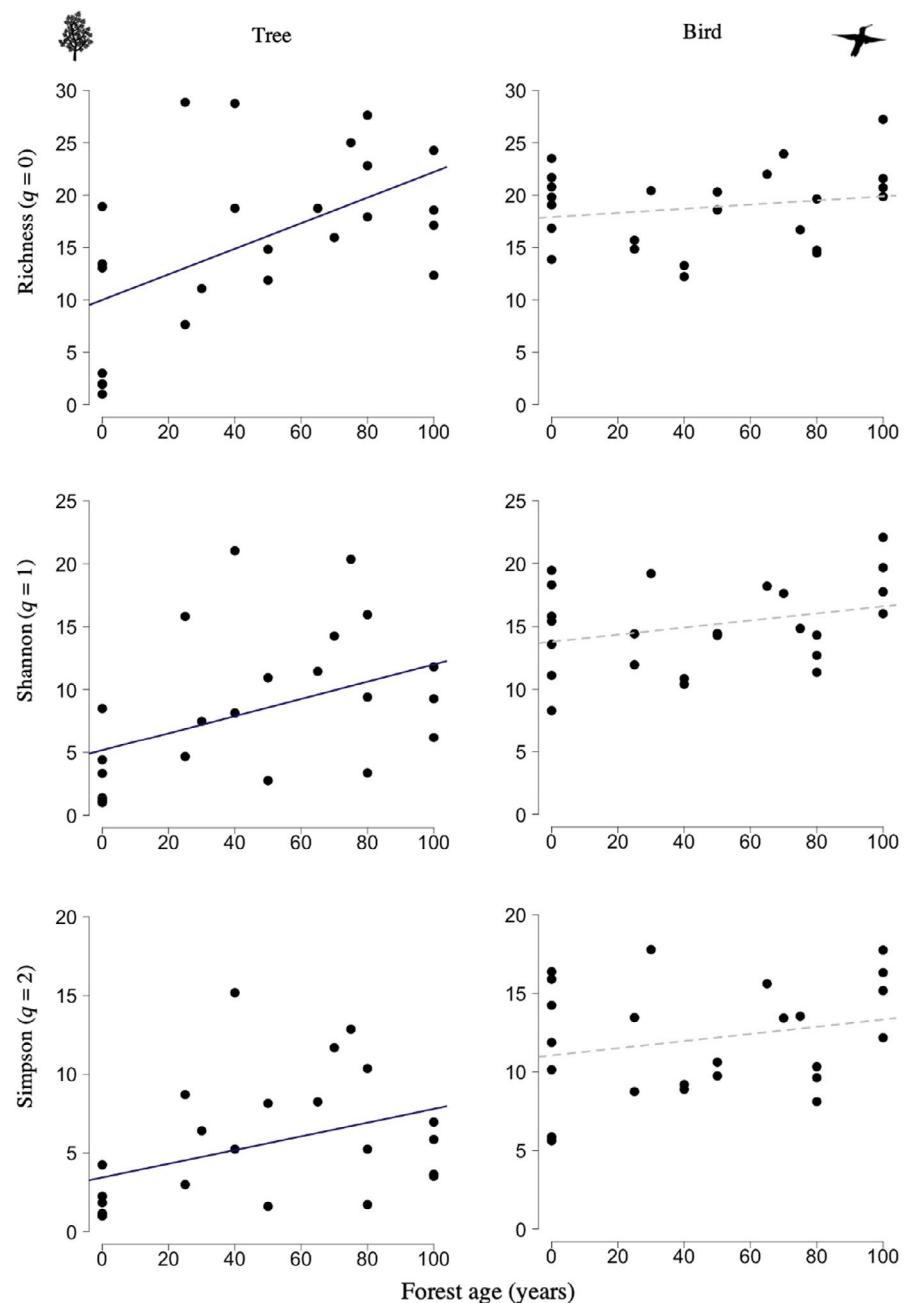
and then used a tanglegram to explore the congruence between dendrograms to understand the extent of agreement in species composition change across taxa. The cluster analyses employed Euclidean distances and the Ward's minimum variance method, and the tanglegram was constructed using the *DENEXTEND* package (Galili, 2015); a cophenetic correlation coefficient (*cor\_cophenetic* function R; Spearman) evaluated the alignment between tree and bird dendrograms. A null model allowed us to ask if the alignment of these dendrograms differed from what would be expected by chance. In this model, the site names for the tree community were randomly reshuffled to produce a new dendrogram; the (cophenetic) correlation between this and the dendrogram produced by the unshuffled bird sites was then computed. This process was repeated 200 times to generate a null distribution

of the cophenetic correlation coefficients against which the observed alignment value could be compared (Galili, 2015; Gotelli & Entsminger, 2003).

### 3 | RESULTS

#### 3.1 | Alpha-diversity

A total of 1,492 trees (representing 135 species), and 1,172 birds (representing 83 species) were recorded. Linear models were used to assess the relationship between the diversity measures and forest age (excluding primary forest sites; Appendix S5). Species richness estimates were log transformed as species richness scales



**FIGURE 2** Hill numbers of the order  $q$  ( $q = 0$  species richness,  $q = 1$  Shannon diversity and  $q = 2$  Simpson diversity) estimates from extrapolated rarefaction curves over forest age for tree and bird assemblages excluding primary sites (for  $n = 100$  trees and  $n = 50$  birds). Tree diversity ( $q = 0, 1$  and  $2$ ) increased significantly with forest age, but there was no change in bird diversity ( $q = 0, 1$ , and  $2$ ). Statistically significant trend lines are shown as continuous lines, non-significant trends are shown as dashed grey lines



nonlinearly with effort, and to better fit the model assumptions of normal distribution.

GLMs of tree Hill numbers for each order  $q$  ( $q = 0$  species richness,  $q = 1$  Shannon diversity and  $q = 2$  Simpson diversity) found a significant increase in tree species richness ( $F_{(1,22)} = 12.24$ ,  $R^2 = 0.33$ ,  $p < 0.01$ ), Shannon diversity ( $F_{(1,22)} = 5.17$ ,  $R^2 = 0.15$ ,  $p = 0.03$ ) and Simpson diversity with forest age ( $F_{(1,22)} = 4.26$ ,  $R^2 = 0.12$ ,  $p = 0.05$ ). In contrast to this, there was no change in bird species richness ( $F_{(1,22)} = 0.74$ ,  $R^2 = -0.01$ ,  $p = 0.40$ ), Shannon diversity ( $F_{(1,22)} = 2.29$ ,  $R^2 = 0.05$ ,  $p = 0.15$ ) or Simpson diversity with forest age ( $F_{(1,22)} = 1.36$ ,  $R^2 = 0.02$ ,  $p = 0.26$ ; Figure 2). Lastly, we found that tree and bird species richness were negatively correlated ( $r_s = -0.38$ ; Appendix S8).

### 3.2 | Beta-diversity

A 0.5 quantile regression found a significant increase in Chao-Jaccard compositional dissimilarity between tree assemblages with increasing age distance between site pairs ( $F_{(2,375)} = 74.86$ ,  $R^2 = 0.28$ ,  $p < 0.001$ ) and with greater environmental distance ( $p = 0.01$ ; Figure 3; SCATTERPLOT3D package R; Ligges & Mächler, 2003).

For the bird community, a 0.5 quantile regression uncovered a significant increase in Chao-Jaccard compositional dissimilarity with greater age difference between site pairs ( $F_{(2,375)} = 13.37$ ,  $R^2 = 0.06$ ,  $p < 0.001$ ). There was no change in compositional dissimilarity with environmental distance ( $p = 0.1$ ; Figure 4; SCATTERPLOT3D package R Ligges & Mächler, 2003).

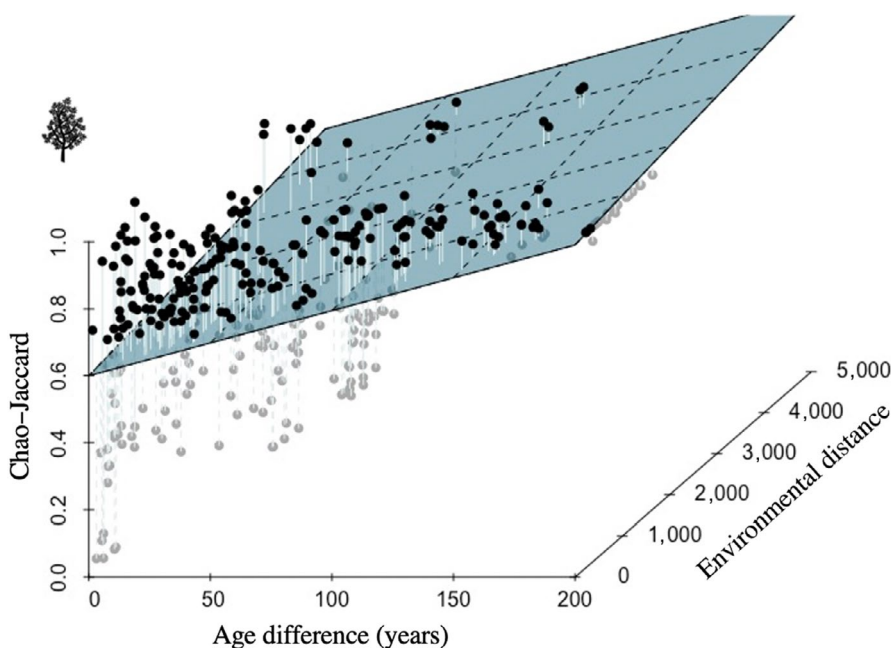
To further investigate tree compositional change, we assessed changes in the proportion of native trees using a linear regression (POWO, 2019; Quesnel & Farrell, 2005) and found there was a significant increase in the proportion of native trees with forest age ( $F_{(1,26)} = 30.44$ ,  $R^2 = -0.52$ ,  $p < 0.01$ ; Figure 5a).

To further assess bird compositional change, we assessed changes in the proportion of forest-dependent bird species with information on forest dependence from BirdLife international (BirdLife International, 2020). A linear regression was used to assess changes in the proportion of forest-dependent species (high, medium and low dependence) with forest age. A linear regression revealed a significant increase in the proportion of high forest-dependent birds with forest age ( $F_{(1,26)} = 10.39$ ,  $R^2 = 0.26$ ,  $p < 0.01$ ; Figure 5b). There was no significant change in the proportion of medium ( $F_{(1,26)} = 1.23$ ,  $R^2 = 0.01$ ,  $p = 0.28$ ) or low forest-dependent birds ( $F_{(1,26)} = 0.38$ ,  $R^2 = -0.02$ ,  $p = 0.54$ ) with forest age.

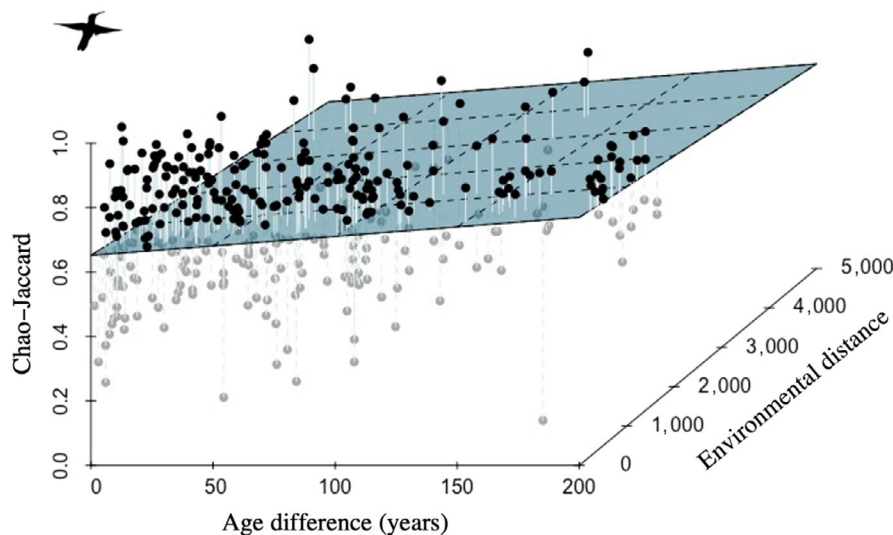
Lastly, we tested for changes in the proportion of trophic guilds using linear regressions: granivores (seeds, nuts and dry fruits), insectivores (invertebrates), omnivores (generalist diet including animal and plant foods), predators and scavengers (meat and carrion) and pollinators and seed dispersers (fruits and nectar; information from Acevedo-Charry & Aide, 2019; Wilman et al., 2014). There was a significant decrease in the proportion of omnivorous birds ( $F_{(1,26)} = 7.30$ ,  $R^2 = 0.19$ ,  $p = 0.01$ ; Figure 5c), and a significant increase in the proportion of insectivorous birds with forest age ( $F_{(1,26)} = 6.46$ ,  $R^2 = 0.17$ ,  $p = 0.02$ ; Figure 5d). There was no change in the proportion of granivores ( $F_{(1,26)} = 0.46$ ,  $R^2 = -0.02$ ,  $p = 0.50$ ), predators and scavengers ( $F_{(1,26)} = 0.02$ ,  $R^2 = -0.04$ ,  $p = 0.89$ ), or pollinators and seed dispersers ( $F_{(1,26)} = 0.46$ ,  $R^2 = -0.02$ ,  $p = 0.50$ ) with forest age.

### 3.3 | Site clustering

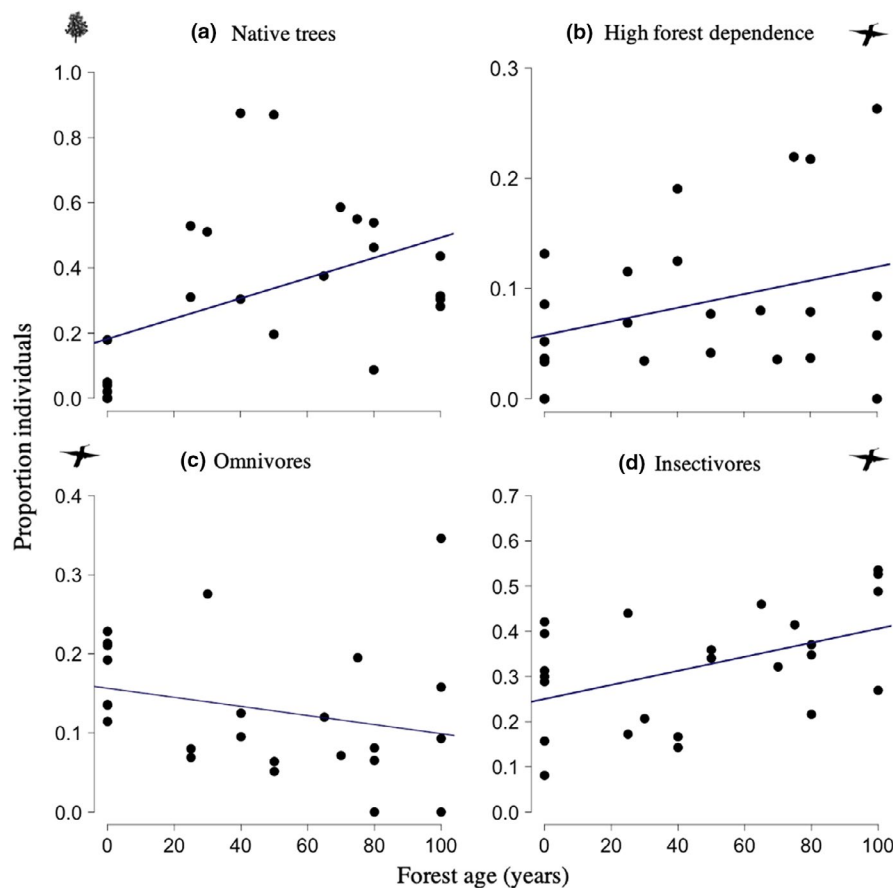
Hierarchical clustering of the forest sites according to tree and bird composition visually demonstrates that sites of similar age were often grouped as more compositionally similar to each other for both trees and birds (Figure 6). Results from a null model indicate that the tree and bird dendrograms are significantly more aligned than would be



**FIGURE 3** Tree compositional dissimilarity (Chao-corrected Jaccard) according to the age and environmental distance between site pairs. Age difference is the pairwise difference in age between sites, and environmental distance is the pairwise distance between sites in Euclidean space built using the environmental factors: annual precipitation, average site altitude, distance to the nearest settlement and average land gradient. A 0.5 quantile regression found there was a significant increase in tree compositional dissimilarity with greater age distance and environmental distance



**FIGURE 4** Bird compositional dissimilarity (Chao-corrected Jaccard) according to the age and environmental distance between site pairs. Age difference is the pairwise difference in age between sites, and environmental distance is the pairwise distance between sites in Euclidean space built using the environmental factors: annual precipitation, average site altitude, distance to the nearest settlement and average land gradient. A 0.5 quantile regression found there was a significant increase in bird compositional dissimilarity with greater age distance, but not with environmental distance between sites



**FIGURE 5** Compositional change in the tree and bird communities. (a) The proportion of native trees significantly increased with forest age. (b) The proportion of highly forest-dependent birds significantly increased over succession. (c and d) There was a significant increase in the proportion (total individuals) of insectivorous (invertebrates) birds, and a significant decrease in omnivorous (generalist diet including animal and plant foods) birds over succession

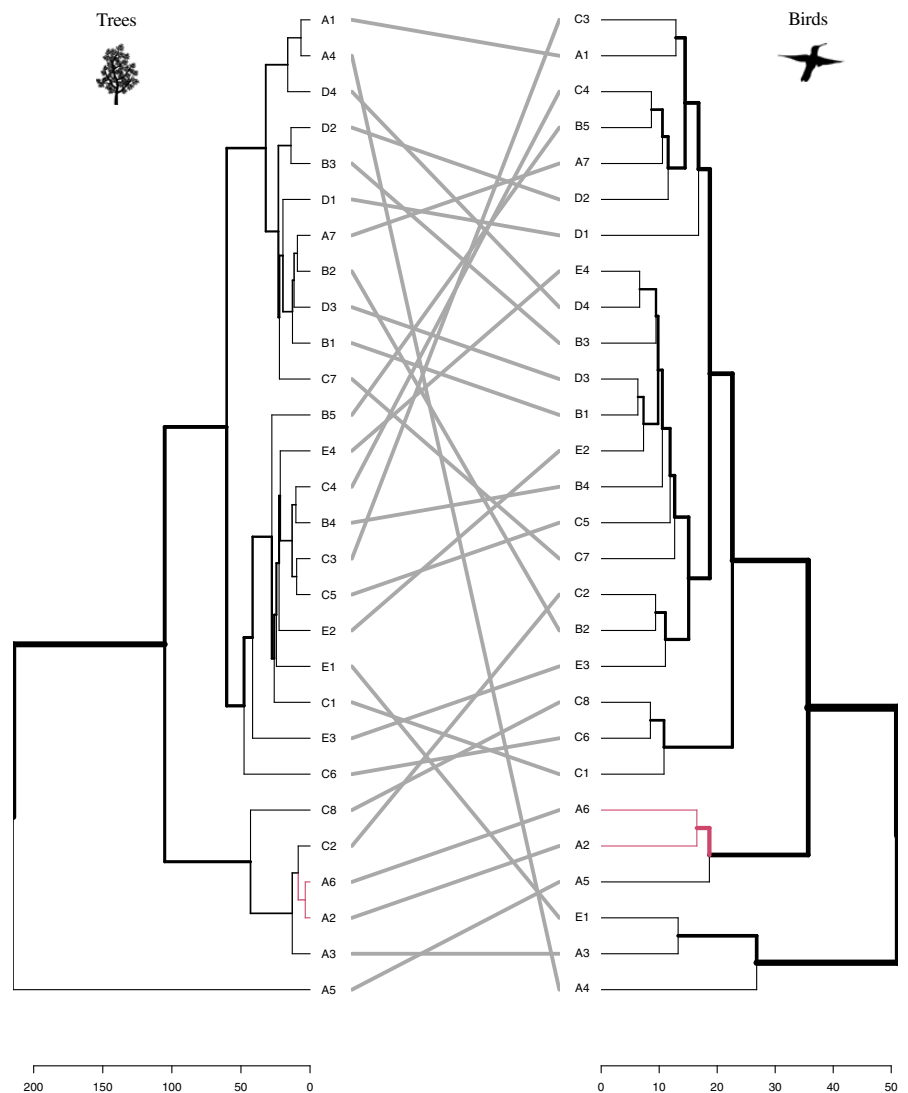
expected by chance (Appendix S10). The observed cophenetic correlation coefficient (Spearman) was outside the 95% confidence limits of the null distribution, in the direction of a higher correlation, indicating that patterns of compositional change between taxa are concordant.

## 4 | DISCUSSION

We found that tree species alpha-diversity increased over time in abandoned cacao agroforests in Trinidad's Northern Range. In

contrast, bird alpha-diversity did not change with forest age. In line with these divergent trends, tree and bird alpha-diversity were negatively correlated. Although older sites did tend to be at higher altitudes, we argue that altitude is not a major contributor to patterns of alpha-diversity because the study design takes account of potential changes with altitude across successional stages, the altitudinal gradient between sites is small, and all sites lie below 1,000 m, the point at which reductions in alpha-diversity might be expected in these types of communities (Appendix S6; Herzog et al., 2005; Sanders & Rahbek, 2012). Both tree and bird composition changed with forest

**FIGURE 6** Tanglegram comparing the hierarchical clustering of sites based on bird (left) and tree (right) species composition. Red lines indicate common branches between the two trees. Sites labelled 'A' are actively cultivated cacao agroforests, 'B' are 25–50 years, 'C' are 51–80 years, 'D' are 81–100 years and 'E' are primary forest. The horizontal axes represent the distance between sites or clusters of sites



age, and there was some concordance in how sites were clustered on the basis of tree and bird composition. To understand the implications of these results, we first discuss temporal alpha-diversity then temporal beta-diversity, and finish by considering the implications of our results within a 'people and nature' framework.

#### 4.1 | Alpha-diversity

As we predicted, tree species alpha-diversity increased significantly with forest age. While other studies have found tree species richness recovers early in succession (approximately 4–40 years; Derroire et al., 2016; Finegan, 1996), our results reveal that in this system species richness continues to increase over c. 100 years of succession. Contrary to expectation, bird species alpha-diversity did not change with forest age. Other studies have shown that bird species richness can increase with forest age, especially early in succession (DeGraaf et al., 1991; Keller et al., 2003; Rey-Benayas et al., 2010). The consistency of bird alpha-diversity over time in this study may be because basic functions and structural characteristics of a forest

can recover quickly and be sustained with few tree species (Derroire et al., 2016), and so the established trees in cacao agroforests could be maintaining core structural elements such as providing shade, shelter, perches and some nesting sites. Also contrary to expectation, tree and bird species richness were negatively correlated. We suggest that this result arises because bird alpha-diversity is high even in active and recently abandoned agroforests, where tree diversity is substantially lower.

#### 4.2 | Beta-diversity

Compositional dissimilarity increased significantly as the age gap between sites grew, and compositional dissimilarity increased more with age difference than with environmental distance for both trees and birds. The proportion of native trees significantly increased over time, which is expected as non-cultivated species naturally colonise abandoned agroforests and gradually replace the planted crop trees which are often introduced species. In this study, active and young secondary cacao agroforests were primarily composed of cacao, mountain



immortelle, citrus, mango, breadfruit *Artocarpus altilis* and coconut. Older secondary and primary forests had a greater proportion of native forest species such as sandbox *Hura crepitans*, angelin *Andira inermis*, cooperhoop *Brownea coccinea*, white mahoe *Heliocarpus trichopodus*, roughleaf *Curtella americana*, toporite *Hernandia sonora* and mature stranglers including *Ficus* and *Clusia* species.

As with trees, turnover within bird assemblages significantly increased with greater age difference between sites, but not with environmental distance between sites. Other studies have found that bird diversity changes along a human-modified landscape continuum, and factors such as distance to urban centres, forest patch size and isolation, and matrix habitat conditions (largely controlled for in this study) can influence bird assemblages (Brotons & Herrando, 2001; Rey-Benayas et al., 2010). For birds, common species such as the palm tanager *Thraupis palmarum*, blue-grey tanager *Thraupis episcopus*, bananaquit *Coereba flaveola* and spectacled thrush *Turdus nudigenis* were abundant, especially in active agroforests and young secondary forests. Species such as the long-billed gnatwren *Ramphocaenus melanurus*, rufous-breasted hermit *Glaucis hirsutus*, red-eyed vireo *Vireo olivaceus* and the white-bearded manakin *Manacus manacus* were more common in secondary and older forests. Results from the tanglegram showed that sites were ranked similarly according to tree and bird composition, meaning the amount of compositional change between sites is concordant for trees and birds.

These results also demonstrate that, although bird alpha-diversity remained constant, bird species composition changed significantly with forest age. This is a pattern of temporal biodiversity change which has been reported across biomes and taxa (Dornelas et al., 2014; Pandolfi & Lovelock, 2014). Our observation that the proportion of highly forest-dependent and insectivorous bird species significantly increases with forest age indicates that, although active cacao agroforests and young secondary forests have species-rich bird assemblages, not all sensitive forest-dependent species or specialist feeders such as insectivores can be supported in these environments. Other studies have found that sensitive and closed-canopy specialist bird species, which are most at risk, are dependent on old-growth forests in mainland South America (Lennox et al., 2018). It could be that this pattern does not occur in Trinidad because there are relatively few specialist bird species.

#### 4.2.1 | Synthesis and applications

Conservation has historically focused on preserving pristine natural areas and protecting charismatic species (Barlow et al., 2007; Barnosky et al., 2017; Chazdon, Harvey, et al., 2009; Gardner et al., 2009). However, the proportion of secondary forests and transformed landscapes is rising relative to old-growth forests and unaltered environments (Arroyo-Rodríguez et al., 2017; Derroire et al., 2016; Lebrija-Trejos et al., 2008; Martin et al., 2013). Thus, understanding the dynamics and recognising the potential value of altered ecosystems is increasingly needed to maximise conservation

efforts (Chazdon, 2014; Chazdon, Harvey, et al., 2009; Chazdon, Peres, et al., 2009; DeClerck et al., 2010). Such knowledge can inform key decisions faced in managing biodiversity, including: which areas to conserve; when and how to implement restoration initiatives; how populations or ecosystems are likely to respond to perturbation; and how to measure ecosystem health.

### 4.3 | Biodiversity trends across taxa

The divergent patterns of tree and bird alpha-diversity in this study highlight how focusing on one taxonomic group, or using species alpha-diversity alone, may not be sufficient to assess the wellbeing and conservation value of habitats. Other studies have shown that spatial biodiversity patterns can be uncorrelated across different taxa (Mandl et al., 2010; Pärt & Söderström, 1999; Wolters et al., 2006), with the result that one taxon cannot necessarily be used as a surrogate of others when comparing alpha-diversity between sites. Our work shows that this is also true for temporal biodiversity patterns (Magurran et al., 2018). This illustrates that not all taxa will respond similarly to environmental changes.

#### 4.3.1 | People and nature: shade-cacao and biodiversity conservation

Our study also shows that young secondary forests and actively managed agroforests can be valuable for sustaining biodiversity. While tree species alpha-diversity increased significantly with forest age overall, the active cacao agroforests and young secondary forests, sustained high levels of tree alpha-diversity. Furthermore, the habitat heterogeneity generated from the long history of cacao farming in Trinidad can increase the collective landscape-level diversity (gamma-diversity) when habitat patches support different species (Fischer & Lindenmayer, 2005; Peintinger et al., 2003; Socolar et al., 2016; Tschardt et al., 2002, 2012). We have shown that there is considerable turnover in species composition between forest patches, and thus the patchwork mosaic of forest types making up the Northern Range is contributing to the overall richness of the species pool and maintenance of gamma-diversity.

Traditionally managed shade-cacao offers two canopy layers and a wealth of flowering and fruiting plants, and so could provide useful habitat for birds despite being human-managed and heavily dominated by cacao trees. Research on coffee agroforests, which are managed similarly, has found that 'shade-coffee' agroforests can provide valuable habitat for birds and can sustain diverse bird assemblages, especially in polyculture plantations and when traditional low-intensity farming practices are used (Arroyo-Rodríguez et al., 2017; Buechley et al., 2015; Calvo & Blake, 1998).

There is an ongoing debate over the best farming methods for cacao, which could lead to a shift away from traditional shade-farming methods, towards intensive monoculture systems without

shade trees (sun-plantations; Waldron et al., 2012). All but one of the active cacao agroforests surveyed in our research were shade-plantations. Sun-plantations can seem attractive economically as the cacao trees mature more rapidly and may produce higher yields, but cacao trees in shade-agroforests live longer, may be less susceptible to pests (Jezeer et al., 2017; Ruf & Schroth, 2004), and shade trees can contribute towards supporting greater species richness (Araújo-Santos et al., 2021; Jezeer et al., 2017; Waldron et al., 2012). There is a growing market for ethical and environmentally responsible cacao (Poelmans & Rousseau, 2016), and traditional shade-cacao agroforests can be more profitable despite lower yields as the cacao can be sold for higher prices (Jezeer et al., 2017). Shade trees and other crop trees can provide additional income as well. Finding agricultural and agroforestry systems such as cacao which can support biodiversity, has utility in reconciling our need to provide local income and to produce enough food and goods to meet demand, with our need to protect biodiversity and important ecosystem functions.

In this study, primary forests were distinctive in tree species composition, even when compared to the oldest secondary forest sites. This result agrees with other studies that suggest it can take centuries for species composition within secondary forests to converge with that of old-growth forests (Derroire et al., 2016; Finegan, 1996; Rozendaal et al., 2019). It is clearly important to protect primary forests due to their slow recovery. However, our findings emphasise the potential value of agroforests and secondary forests in sustaining species-rich assemblages. These habitats not only play an important role in enriching regional biodiversity but can also provide conservation solutions that support both people and nature.

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## AUTHORS' CONTRIBUTIONS

H.A. developed the project in consultation with A.E.M. and A.E.D.; Fieldwork and analysis were done by H.A. and D.J. in consultation with all authors, and all authors contributed to the manuscript,

contributed critically to the drafts and gave their final approval for publication.

## DATA AVAILABILITY STATEMENT

Data available via the University of St Andrews' PURE database <https://doi.org/10.17630/4c8d8124-4e87-4d95-91e3-544a06eb-6cdb> (Arnold et al., 2021).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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