

Trade-offs between economic development and biodiversity conservation on a tropical island

Emilio Pagani-Núñez¹  | Yang Xu²  | Mingxiao Yan¹ | Jiekun He³  | Zifei Jiang¹ | Haisheng Jiang³ 

¹Department of Health and Environmental Sciences, Xi'an Jiaotong-Liverpool University, Suzhou, China

²Environmental Horticulture Research Institute, Guangdong Academy of Agricultural Sciences, Guangzhou, China

³Spatial Ecology Lab, School of Life Sciences, South China Normal University, Guangzhou, China

Correspondence

Haisheng Jiang, Spatial Ecology Lab, School of Life Sciences, South China Normal University, No. 55, West of Zhongshan Avenue, Tianhe District, Guangzhou 510631, China.
Email: jhs@scnu.edu.cn

Article impact statement: Economic development may have detrimental effects for biodiversity conservation even in a context of enhanced environmental protection.

Funding information

Guangdong Academy of Agricultural Sciences, Grant/Award Number: 201917; National Natural Science Foundation of China, Grant/Award Number: 32001164

Abstract

Resolving trade-offs between economic development and biodiversity conservation needs is crucial in currently developing countries and in particularly sensitive systems harboring high biodiversity. Yet, such a task is challenging because human activities have complex effects on biodiversity. We assessed the effects of intense economic development on Hainan Island (southern China) on different components of biodiversity. This highly biodiverse tropical island has undergone extensive economic development and conversion of forest to agriculture and urban area. We identified 3 main transformation areas (low, medium, and high transformation) based on land-use, local-climate, and economic changes across 145 grids (10 × 10 km), and estimated changes in avian biodiversity from 1998 to 2013. We recorded ongoing taxonomic biotic homogenization throughout the island. Differences between traditional and directional alpha diversity decreased by 5%. Phylogenetically clustering increased by 0.5 points ($W = 7928, p < 0.01$), and functional overdispersion increased by 1 point ($W = 16,411, p < 0.01$). Initial taxonomic, phylogenetic, and functional scores correlated negatively with changes in these scores across all transformation areas (all $ps < 0.01$). At the local scale, economic and environmental indicators showed complex and divergent effects across transformation areas and biodiversity components. These effects were only partially ameliorated in an ecological function conservation area in the mountainous central part of the island. We found complex effects of economic development on different biodiversity dimensions in different areas with different land uses and protection regimes and between local and regional spatial scales. Profound ecosystem damage associated with economic development was partially averted, probably due to enhanced biodiversity conservation policies and law enforcement, but not without regional-scale biotic homogenization and local-scale biodiversity loss.

KEYWORDS

biodiversity loss, forest conversion, functional diversity, phylogenetic diversity, species richness, tropical islands, urbanization

Compensaciones entre el Desarrollo Económico y la Conservación de la Biodiversidad en una Isla Tropical

Resumen: Es muy importante resolver las compensaciones entre el desarrollo económico y la conservación de la biodiversidad en los países que actualmente se encuentran en desarrollo y en los sistemas particularmente sensibles que albergan una gran biodiversidad. Sin embargo, dicha labor es un reto porque las actividades humanas tienen efectos complejos sobre la biodiversidad. Analizamos los efectos del desarrollo económico intenso en la isla de Hainan (sur de China) sobre diferentes elementos de la biodiversidad. Esta isla tropical con una gran biodiversidad ha sufrido un desarrollo económico extenso y la conversión forestal a campos agrícolas y áreas urbanas. Identificamos tres áreas principales de

transformación (baja, media y alta) con base en cambios en el uso de suelo, clima local y en la economía a lo largo de 145 cuadrantes (10×10 km) y estimamos los cambios en la diversidad de aves desde 1998 hasta 2013. Registramos la homogenización biótica continua de los taxones en la isla. La diferencia entre la diversidad alfa tradicional y direccional disminuyó 5%. Las agrupaciones filogenéticas incrementaron 0.5 puntos ($W = 7928, p < 0.01$) y la sobredispersión funcional incrementó un punto ($W = 16411, p < 0.01$). Los puntajes taxonómicos, filogenéticos y funcionales iniciales estuvieron correlacionados negativamente con los cambios en estos puntajes en todas las áreas de transformación (todas $p < 0.01$). En la escala local, los indicadores económicos y ambientales mostraron efectos complejos y divergentes en las áreas de transformación y los elementos de la biodiversidad. Estos efectos sólo mejoraron parcialmente en un área de conservación con función ecológica en la parte montañosa al centro de la isla. Descubrimos que el desarrollo económico tiene efectos complejos sobre diferentes dimensiones de la biodiversidad en diferentes áreas con usos de suelo y sistemas de protección diferentes y entre las escalas espaciales local y regional. El daño profundo al ecosistema asociado con el desarrollo económico pudo evitarse parcialmente, probablemente debido a la mejora en las políticas de conservación de la biodiversidad y la aplicación de la ley, pero no sin sufrir pérdidas de la biodiversidad a escala local y una homogenización biótica a escala regional.

PALABRAS CLAVE

conversión forestal, diversidad filogenética, diversidad funcional, islas tropicales, pérdida de la biodiversidad, riqueza de especies, urbanización

摘要

权衡经济发展和生物多样性保护之间的关系是发展中国家目前面临的重要问题,尤其是对那些生物多样性丰富、生态系统敏感的发展中国家而言。然而,由于人类活动对生物多样性的影响十分复杂,这样的任务非常具有挑战性。本研究中,我们在中国的海南岛探讨了经济的快速发展是如何影响生物多样性不同组分的。作为生物多样性极高的热带岛屿,海南岛在过去几十年经济快速发展,土地利用剧烈改变(如,大面积的森林变成农田,并城市化)。我们基于145个 10×10 公里网格的土地利用、气候和经济变化将海南岛分为3种主要的栖息地变化模式,并分析了这三类模式中鸟类多样性在1998-2013年的变化。结果显示,鸟类群落在传统和定向的 α 多样性之间的差异下降了5%,反映了海南岛正处于物种分类上的同质化过程。鸟类群落的谱系聚集程度上升了0.5 ($W = 7928, p < 0.01$),功能性状发散上升了1 ($W = 16411, p < 0.01$)。在所有的栖息地变化模式中,群落的物种分类、系统发育和功能结构的变化程度均与它们的初始状态呈负相关 ($P < 0.01$)。在局域尺度,经济发展和环境因素对不同栖息地变化模式和生物多样性组分具有复杂且不同的影响。这些影响仅在海南岛中部山区新建的生态功能保护区内得到部分优化。我们的研究发现了经济发展对热带岛屿不同区域、不同土地利用和保护策略以及不同生物多样性维度在局域和区域尺度上的复杂影响。生物多样性保护政策和执法的强化,似乎可以避免经济发展导致的部分生态系统退化,但仍难以避免区域尺度上的生物同质化和局域尺度上的生态多样性丧失。权衡热带岛屿的经济发展与生物多样性保护

生物多样性丧失, 森林丧失, 功能多样性, 谱系多样性, 物种多样性, 热带岛屿, 城市化

INTRODUCTION

Intense landscape transformation can reduce biodiversity up to 75% (Díaz et al., 2019; Haddad et al., 2015), strongly constraining ecological processes in remaining patches of natural habitat (Chase et al., 2020). Agricultural intensification drives biodiversity loss by consuming primary productivity through forest to agriculture conversion (Otero et al., 2020). Similarly,

urbanization leads to an equivalent loss of 500 million years of avian evolutionary history (Sol et al., 2017). This situation has stimulated the incorporation of environmental protection in the international political agenda, yet biodiversity conservation targets have only been partially reached (Sutherland et al., 2021). To achieve these targets, a comprehensive assessment of the impacts of economic development on biodiversity in developing countries and especially in sensitive systems is long overdue.

Large-scale economic and land-use changes can affect multiple facets of biodiversity and interact with local climatic changes (Jetz et al., 2007). These changes reduce species richness where human-driven impacts are especially intense, such as in heavily transformed landscapes (Díaz et al., 2019; Pimm et al., 2014), and species variability in nearby landscapes (generally referred to as biotic homogenization) (Devictor et al., 2008; McKinney, 2006). These changes also affect different components of species diversity, such as taxonomic (TD), functional (FD), and phylogenetic diversity (PD) (Baiser & Lockwood, 2011; Georgiev et al., 2020; Graham & Fine, 2008). Yet, in highly biodiverse systems, heterogeneous agricultural landscapes can sustain relatively high species richness (Fahrig, 2017) within and between sites (Ranganathan et al., 2008; Sreekar et al., 2021; Tscharrntke et al., 2008). Biodiversity changes are mediated by priority (i.e., historical contingency) effects, namely, initial community structure and historical land uses (Dallimer et al., 2015; Fukami, 2015). Early community niche dynamics, if not assessed, may act as a confounding factor simulating apparent randomness—species' composition changes that are difficult to attribute to specific factors.

Hainan Island (People's Republic of China) is one of the world's largest tropical islands and represents a highly suitable model to investigate the combined effects of economic growth and enhanced environmental protection. Since the early 2000s, Hainan has undergone intense economic development, leading to unregulated urban development (Gu & Wall, 2007), decreased area of natural tropical forests (Lin et al., 2017), and declines of native avian species (Xu et al., 2017). In 2010, the establishment of an ecological function conservation area (EFCA) aimed at regulating ecosystem services, such as carbon sequestration and water provision, may have helped ameliorate these negative effects by restricting land-use changes in this special protection zone (Sun et al., 2020; Zhai et al., 2018). Promoting human development and ecosystem stability and resilience through ecosystem restoration and ecofriendly agroforestry are key strategies to achieve sustainable economic growth (Li et al., 2020; Zheng et al., 2019). However, there is a lack of detailed assessments of how these profound economic changes are affecting biodiversity (Mi et al., 2021).

We conducted an integrated assessment of changes in the economy, climate, land use, and avian biodiversity over 15 years on Hainan Island (18°10'–20°10'N and 108°37'–111°03'E). We carried out our analyses at the local (10 × 10 km grid) and regional (entire island) scales. We expected apparent random drift, broadscale biodiversity changes, and biotic homogenization due to the magnitude of the changes. Nonetheless, we expected biodiversity to be less affected by changes and more diverse and communities to be more resilient inside than outside the EFCA. We expected divergent effects of these changes on TD, PD, and FD in natural, rural, and urban areas.

METHODS

A flowchart of our method is in Appendix S1.

Study area

Hainan Island is one of the world's largest tropical islands (rank of 42) and the southernmost and largest island of the People's Republic of China. It has an area of about 35,400 km² and a population of over 10 million people in 2020 (National Bureau of Statistics, 2021). It is dominated by a tropical wet savanna climate with very mild winters and hot and rainy summers (Köppen classification). It is a remarkably biodiverse island. It has over 400 avian species and is part of the Indo-Burma biodiversity hotspot (Myers et al., 2000). Biodiversity conservation efforts have significantly improved in recent years, and as a result there are 32 protected areas covering >7% of the island's area (Xu et al., 2017).

The EFCA, a large special protection zone established in 2010 in the mountainous central part of the island, while focusing on ecosystem service provision might also benefit biodiversity conservation (Li et al., 2020; Zheng et al., 2019) (Figure 1a). The EFCA aims to balance the trade-off between provisioning and regulating services (i.e., economic development and ecosystem functions) (Zheng et al., 2019). These aims are achieved by restricting and regulating land-use changes, such as the expansion of rubber plantations in the EFCA and promoting ecosystem restoration to recover previously degraded areas.

Avian diversity data

We focused on avian biodiversity because birds are often used as indicators of biodiversity (Kati et al., 2004) and because the data we used had sufficient resolution to conduct a comprehensive analysis from local to regional scales. We conducted surveys to assess long-term changes in avian diversity in Hainan. Surveys were conducted along line transects by pairs of trained ornithologists in 172 10 × 10 km grids from 1997 to 1998 (total 2232.5 km of transects, mean [SD] = 12,980 m [14,429]) and 2012 to 2013 (total 4080.4 km of transects, mean [SD] = 23,723 m [21,503]), mostly between March and October throughout the island. At least 1 member of each observer pair participated in both survey periods. Species identities and number of individuals were recorded. We recorded 5894 individuals from 191 species in 1998 and 8141 individuals from 215 species in 2013, for a total of 256 avian species. All statistical analyses were conducted in R 3.6.1 (R Core Team, 2021).

Two strategies were employed to overcome uneven sampling effort among grids. First, we used the rarefy function in the vegan package (Oksanen et al., 2020) to compute rarefied richness at the grid level by setting a minimum threshold of 5 observed individuals in each grid (Zou et al., 2020). This was our TD metric. Grids with fewer than 5 observed individuals were excluded from further analyses, reducing the sample from 172 to 152 grids. Results with a 5-individual threshold were compared with a 20-individual threshold. We obtained a strong positive correlation for both periods (1997–1998, $R^2 = 0.96$; 2012–2013, $R^2 = 0.89$) (Appendix S2), suggesting that this procedure was appropriate to obtain an accurate representation of species richness in the different grids. Second, to compute PD and FD (see below), we applied a Wisconsin transformation

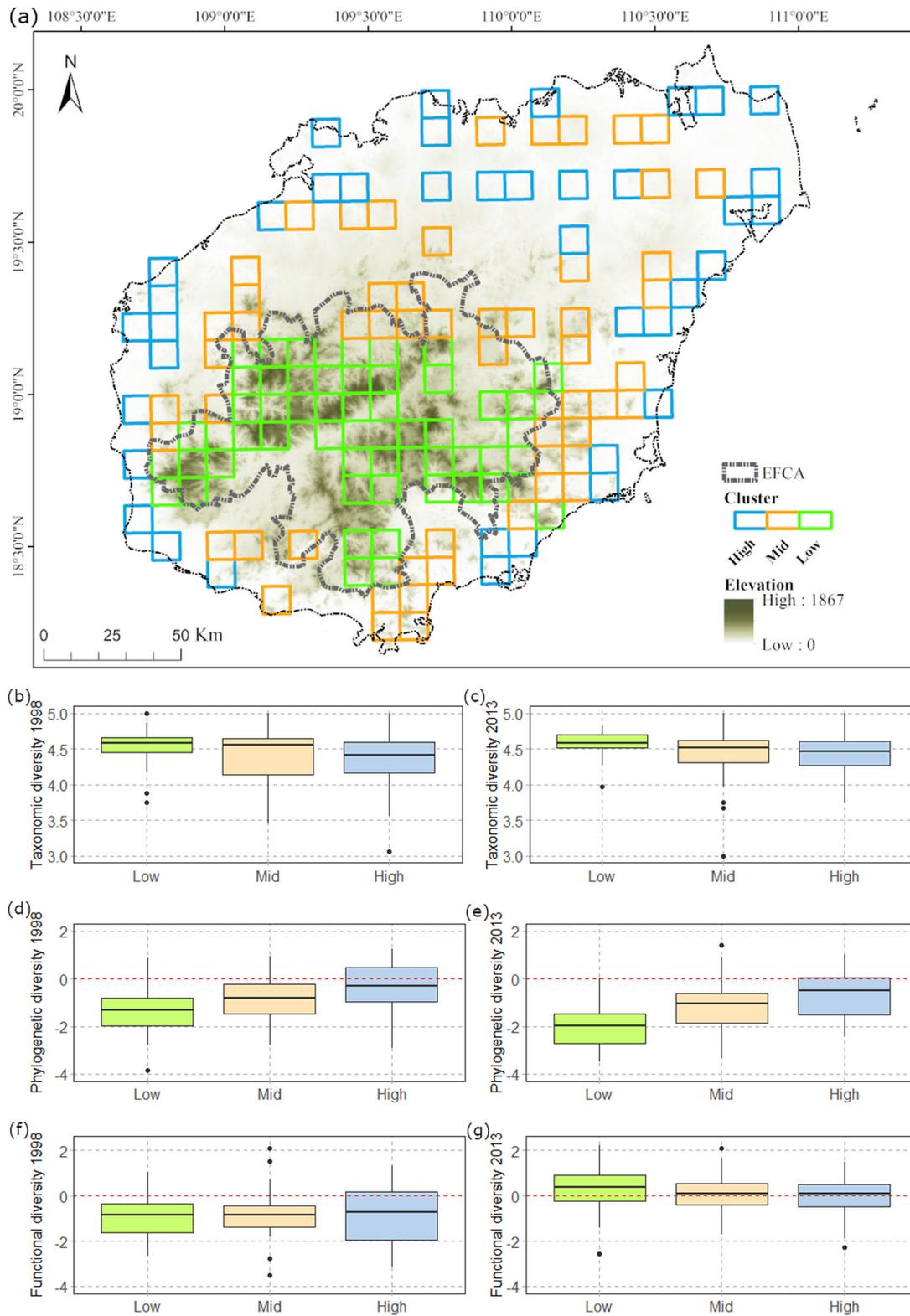


FIGURE 1 On Hainan Island (People's Republic of China), (a) 145 grid areas (10 × 10 km) classified according to land use into low, middle (mid), and high transformation areas (EFCAs, boundaries of the ecological function conservation area) and (b–g) differences in taxonomic, phylogenetic, and functional diversity in 1998 and 2013 between low, mid, and high transformation areas

(i.e., each grid was first divided by the species maximum number and then by the grid total) to these community data with the decostand function in vegan (Oksanen et al., 2020).

Phylogenetic and functional diversity

We extracted 1000 phylogenetic trees, including the 256 avian species we recorded, from a comprehensive phylogeny of global birds (9993 species) (Jetz et al., 2012). We constructed a consensus phylogenetic tree with the functions consensus.edges in the phytools package (Revell, 2012) and multi2di in the ape package (Paradis et al., 2004) to resolve multichotomies. We used this consensus phylogenetic tree in further calculations. We also curated a trait database for the 256 avian species, including information on diet, foraging substrate, body morphology, and clutch size. We used these traits because habitat transformation, and particularly urbanization, filters species according to these characteristics (Callaghan et al., 2019; Sepp et al., 2018). Diet and foraging information was obtained from a commonly used foraging traits' database (Wilman et al., 2014). Diet was expressed as the proportion of 10 food types per species (invertebrate, vertebrate endotherm, vertebrate ectotherm, vertebrate fish, scavenger, fruit, etc.). Foraging substrate was also expressed as the proportion of 8 types (water below surface, water around surface, ground, understory, etc.). Body morphology included body mass (taken from the abovementioned database) and body length, beak culmen length, wing length, tail length, and tarsus length, which were taken from the China Animal Scientific Database (<http://www.zoology.csdb.cn>). When data from both sexes were available, we computed the average. We also took information on clutch size from this database. Brood parasites were assigned a score of 1 for clutch size. We then scaled trait data and built a dendrogram through a hierarchical clustering analysis with the function hclust, which was later converted into a phylo object.

We used the package picante to compute PD and FD (Kembel et al., 2010). We estimated phylogenetic diversity by computing standardized effects sizes of Faith's phylogenetic diversity with the function ses.pd, which allowed us to control for the effect of unequal richness across communities. We estimated functional diversity with the same function. Given the lack of independence between PD and FD (Cadotte et al., 2019), rather than simply using observed values, we compared these values against 999 null models constructed by shuffling all taxa labels across the tips of the phylogenies. In doing so, we were able to assess significant changes in observed values against a null model based on this randomization. We standardized PD and FD values against the null models by deducting the random mean from the observed value and dividing these values by the standard deviance of the random values. We computed these scores for 1998 and 2013.

Land-use data

All spatial analyses and calculations were performed using ArcMap 10.3 (ESRI, Redlands, California), particularly the

Zonal tool to estimate land-use values per grid. Land-use data were obtained from the Data Centre for Resource and Environmental Sciences of the Chinese Academy of Science (RESDC) (<https://www.resdc.cn>), which is based on Landsat TM/ETM remote sensing images. The downloaded data have a resolution of 1 km². We used data from 2000 to match 1997–1998 avian diversity data and averaged data from 2012 and 2013 to match 2012–2013 avian biodiversity data. Hereinafter, we refer to these periods as 1998 and 2013. We used grids of 10 × 10 km as the unit for analysis (Anderson et al., 2009; Luoto et al., 2007). Information on the 21 land-use categories we used, which we grouped into 7 categories (urban, agricultural, forest, water, grassland, coastal, and water), is in Appendix S3. This information is available in Chinese from <https://www.resdc.cn/data.aspx?DATAID=335>. The boundary of the EFCA was delineated from available sources (Li et al., 2020), and the area of each grid in the EFCA was computed.

Habitat, climate, and economic data

We also downloaded data on habitat productivity (NDVI), climate, population density, gross domestic product (GDP), and light pollution from the same source (RESDC). Annual NDVI was based on SPOT/VEGETATION and MODIS remote sensing images; maximum monthly NDVI values from January to December at 1 km² resolution were combined. Original values were divided into 9 levels with the Jenks (1967) natural breaks method (1, 0.00–0.04; 2, 0.05–0.17; 3, 0.18–0.36; 4, 0.37–0.48; 5, 0.49–0.58; 6, 0.59–0.65; 7, 0.66–0.69; 8, 0.70–0.81; 9, 0.82–1.0) and reclassified as low (0.00–0.36), mid (0.37–0.65), and high (0.66–1.00). The number of pixels in each class were counted for each grid. Unfortunately, these scores simply provided an estimate of habitat productivity and did not allow us to determine specific vegetation classes or to discriminate between natural forests and plantations. Still, in combination with land-use data, we were able to determine which areas could sustain high biodiversity. Digital elevation model data are based on SRTM (Shuttle Radar Topography Mission) at a 90-m cell resolution, and precipitation and temperature data are based on daily observations from over 2400 meteorological stations across China. Precipitation and temperature data were generated by sorting, calculation, and spatial interpolation. The units of precipitation and of temperature were 0.1 mm and 0.1°C, respectively.

We used population and economic growth (Clausen & York, 2008; Jha & Bawa, 2006; Pergams et al., 2004), particularly GDP per capita, as indicators of economic change in Hainan because social processes may have a strong effect on biodiversity (Bragina et al., 2015). County-level population density and GDP data were transformed to the grid scale by weighting the area of each county in each grid. The unit of population density was number of people per square kilometer, and GDP was 10,000 yuan per km². Light pollution data (watts per square centimeter per steradian per micrometer) were based on the Operational Linescan Sensor (OLS) onboard DMSP (Defense Meteorological Satellite Program) at 1-km² resolution. Light

pollution data were computed for each grid with the same method as for NDVI. For further analyses, we used the area in square kilometer of the 3 NDVI classes (low, mid, or high), mean precipitation and SD per grid, mean temperature and SD per grid, mean elevation and range per grid, grid area, total population and GDP per grid, and area of the 3 light pollution classes (low, mid, or high) for 1998 and 2013.

Habitat classification and environmental change

We aimed to characterize broadscale habitat transformation initial conditions (i.e., in 1998) throughout the island. To do this, we followed a sequential iteration procedure based on land-use classification reliability to produce several meaningful clusters (Carrier et al., 2021). We used the 7 relevant land-use categories (urban, agricultural, grasslands, forests, water, coastal, and barren [square kilometers per grid]), EFCA area (square kilometers per grid), climatic variables (mean and SE precipitation and temperature), and elevation mean and range (meters per grid) to aid the classification process. All the variables were scaled, which strongly improved clustering performance. We ran a principal component analysis (PCA) on these variables and then applied a hierarchical clustering procedure on the obtained components with the HCPC function FactoMineR (Lê et al., 2008). We performed a multiresponse permutation procedure (MRPP) to assess the homogeneity of the different groups (mrpp function of vegan package [Oksanen et al., 2020]). An MRPP A score >0.4 is desirable (Peck, 2010). We obtained a score of $A = 0.24$, so we had to remove less important variables (with the lowest η^2 values). Following this criterion, we removed area, water, barren, coastal, grassland, and precipitation mean. We also excluded low NDVI, which provided redundant information with the other 2 NDVI categories. We retained 11 descriptive variables for an MRPP A score of 0.41 and produced 3 balanced and meaningful groups according to the level of transformation (low transformation area [LTA], $n = 43$; mid transformation area [MTA], $n = 57$; high transformation area [HTA], $n = 51$) (see RESULTS). We preferred to use these acronyms rather than natural, rural, and urban because these broad land-use categories were present in each of the transformation areas.

We were also interested in characterizing land-use, local-climate, and economic changes between the 2 study periods. To do this, we ran 3 different PCAs for each group of factors, focusing on variables that were relevant in the hierarchical clustering analysis or that have potential to explain biodiversity changes. We used differences between 1998 and 2013 in urbanization, agriculture, forest cover, mid NDVI, and high NDVI area per grid as quantitative variables characterizing land-use changes. We used differences between 2013 and 1998 in precipitation mean and SD, temperature mean and SD, and elevation mean and range per grid as quantitative variables to characterize local-climate changes. We used differences between 2013 and 1998 in low, mid, and high light pollution, population density, and GDP per grid to quantify economic changes. All variables were scaled. We excluded grids that produced scores with

>6 SDs from the mean. This resulted in 6 additional grids being excluded. We also excluded a grid with anomalous rarefied richness scores (close to 0). This reduced our sample to 145 grids.

Statistical analyses

After obtaining 3 main transformation areas and characterizing land-use, local-climate, and economic changes for the Island, we compared alpha and beta diversity between 1998 and 2013 and determined the importance of its spatial component. In doing so, we determined the extent of biodiversity homogenization at the regional scale (Devictor et al., 2008). We used the Rarefy package to estimate directional (spatially explicit) and nondirectional rarefied species accumulation curves and beta diversity accumulation curves (Ricotta et al., 2019). We ran the same analysis with the 21 raw land-use categories in 1998 and 2013 to assess potential landscape homogenization. We then ran a Wilcoxon rank sum test to determine differences in alpha and beta directional and nondirectional diversity between 1998 and 2013. Also using a Wilcoxon Test, we determined whether there were differences in TD, PD, and FD between these 2 periods.

We investigated differences in TD, PD, and FD among LTA, MTA, and HTA. To do this, we used linear mixed-effects modeling in the function lme of the nlme package (Pinheiro et al., 2007). We used a mock random factor and latitude and longitude as linear correlation structure to account for spatial autocorrelation effects (Dormann et al., 2007). We were thus able to construct spatially explicit models to assess the relationships between biodiversity patterns and transformation areas. We used TD as dependent variable and the 3 transformation areas as factors. We alternatively used LTA and MTA as references and showed results for all the potential interactions. We did the same with PD and FD as dependent variables.

We determined the magnitude of historical contingency effects on biodiversity changes from 1998 to 2013 (Fukami, 2015). We constructed linear mixed-effects models following the procedure described above with a focus on biodiversity score changes between periods. We ran a model with TD changes as dependent variable and the interaction between initial TD, PD, and FD scores (in 1998) and transformation areas as independent variables. We did the same with PD and FD changes as dependent variables. We also assessed whether there were differences in biodiversity changes (for TD, PD, and FD) between transformation areas.

Finally, we assessed the relationships between land-use, local-climate, and economic changes and biodiversity changes across transformation areas. We followed the statistical approach described above. Changes in TD was the dependent variable and the interaction between the 3 components of the PCA characterizing land-use changes and transformation areas were the predictors. We repeated this procedure to assess the interaction among the 3 components of local-climate change and with the 2 components of economic change across the 3 transformation areas and repeated this procedure with PD and FD as dependent variables.

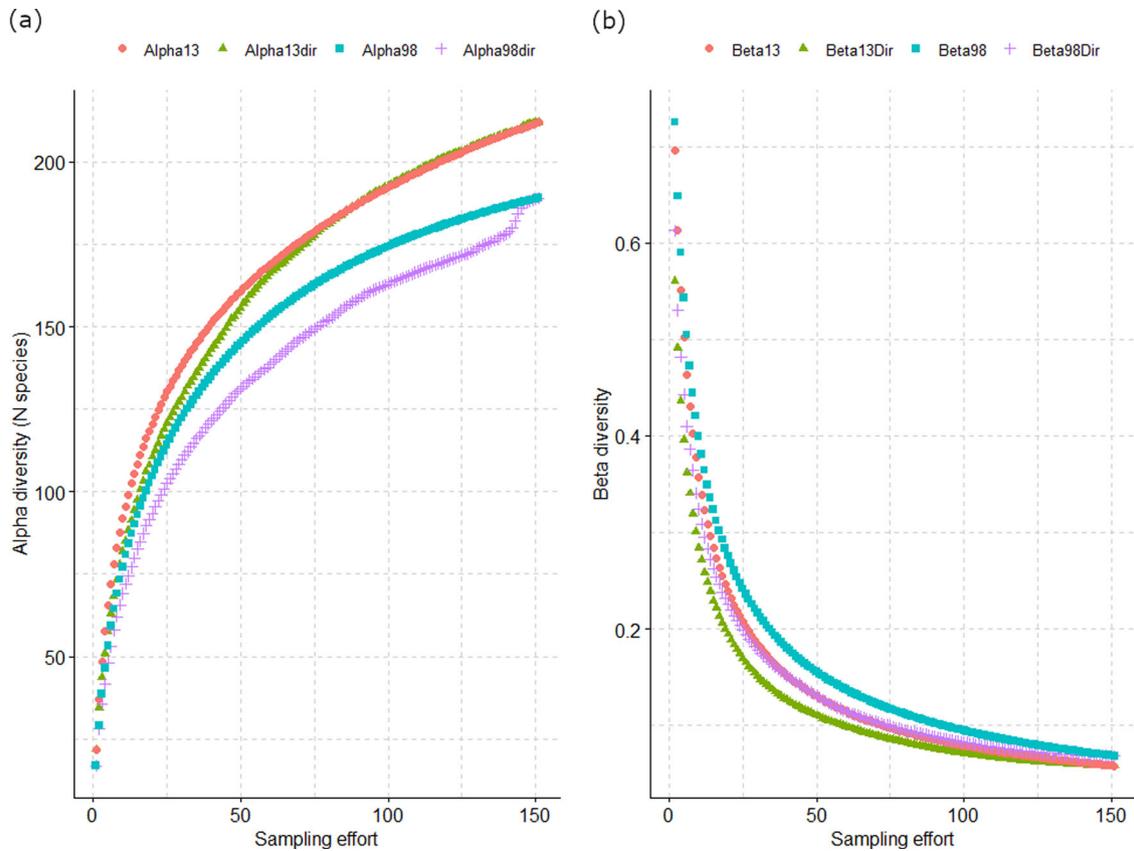


FIGURE 2 On Hainan Island (People's Republic of China), (a) traditional (alpha) and directional (alpha dir) alpha diversity species accumulation curves for 1998 (98) and 2013 (13) and (b) traditional (beta) and directional (beta dir) beta diversity species accumulation curves for 1998 (98) and 2013 (13)

RESULTS

Land-use classification and biodiversity scores

Based on land-use and climatic variables from 1998, we classified 145 grid cells as LTA, MTA, or HTA (Figure 1a & Appendix S4). The LTA grids were mainly in the EFCA (5373 km², 37% of grid sample), which showed high precipitation and temperature variability and high habitat productivity (NDVI). The MTA grids were dominated by highly thermic and productive agricultural land, mainly in lowland areas outside the EFCA. The HTA grids were in thermic but less productive lowland areas outside the EFCA and were dominated by urban and agricultural land uses and low levels of forest cover.

Between 1998 and 2013, the directional (namely spatial) component of taxonomic diversity variation decreased in importance within and between grids (namely, alpha and beta diversity), suggesting ongoing biotic homogenization (traditional alpha diversity 1998 vs. 2013, $W = 15,235$, $p < 0.01$; directional alpha diversity 1998 vs. 2013, $W = 16,220$, $p < 0.01$; traditional beta diversity 1998 vs. 2013, $W = 8818$, $p < 0.01$; directional beta diversity 1998 vs. 2013, $W = 8643$, $p < 0.01$) (Figure 2a,b). Conversely, we recorded no significant differences in directionality regarding land uses between the 2 periods (nondirectional β : $W = 10,084$, $p = 0.12$, directional β : $W = 10,205$, $p = 0.16$, both cases $n = 145$

grids), suggesting that landscapes did not become significantly more homogeneous. Taxonomic diversity did not change in grids across this period ($W = 11,072$, $p = 0.43$), whereas phylogenetic diversity decreased ($W = 7928$, $p < 0.01$) and functional diversity increased ($W = 16,411$, $p < 0.01$) (Figure 1b–g).

Transformation areas showed marked differences in their biodiversity scores. In 1998, communities in LTA were taxonomically more diverse than in HTA and marginally significantly more diverse than in MTA. Communities were more diverse from an evolutionary point of view in LTA than in MTA and HTA and in MTA than in HTA. There were no significant differences in functional diversity between transformation areas (Table 1 & Figure 1b,d,f). There were subtle differences between 1998 and 2013 biodiversity scores. The MTA became phylogenetically overdispersed when compared with HTA, whereas LTA showed higher taxonomic diversity than MTA and tended to be functionally overdispersed in comparison with HTA (Table 1 & Figure 1c,e,g).

Community and land-use priority effects

We recorded strong effects of initial taxonomic, phylogenetic, and functional scores (i.e., scores from 1998) on biodiversity changes (Appendix S5). Initial taxonomic, phylogenetic, and

TABLE 1 Spatially explicit, linear, mixed-effects models fit by restricted maximum likelihood used to assess biodiversity differences over time (1998–2013) in 145 100-km² grids throughout Hainan Island (People's Republic of China) with taxonomic,^a phylogenetic,^b and functional^c diversity measures (1998–2013) as dependent variables and transformation area (low, middle [mid], or high), product of an agglomerative hierarchical clustering on 145 grids, as a predictor

Diversity component and year		β	SE	<i>t</i>	<i>p</i>
Taxonomic	1998				
	intercept	4.55	0.05	87.96	<0.01
	low-mid	-0.14	0.07	-2.00	0.05
	low-high	-0.23	0.08	-3.02	<0.01
	mid-high ^d	-0.09	0.07	-1.23	0.22
	2013				
	intercept	4.58	0.07	62.03	<0.01
	low-mid	-0.13	0.05	-2.40	0.02
Phylogenetic	1998				
	intercept	-1.30	0.25	-5.09	<0.01
	low-mid	0.45	0.19	2.37	0.02
	low-high	0.85	0.21	4.12	<0.01
	mid-high	0.40	0.20	1.98	0.05
	2013				
	intercept	-2.03	0.25	-8.16	<0.01
	low-mid	0.80	0.19	4.26	<0.01
Functional	1998				
	intercept	-0.95	0.26	-3.65	<0.01
	low-mid	0.11	0.20	0.57	0.57
	low-high	0.16	0.22	0.73	0.46
	mid-high	0.04	0.21	0.21	0.83
	2013				
	intercept	0.26	0.23	1.11	0.27
	low-mid	-0.17	0.18	-0.95	0.35
low-high	-0.38	0.19	-1.99	0.05	
mid-high	-0.21	0.18	-1.15	0.25	

^aRarefied richness.

^bStandardized effect size of Faith's phylogenetic diversity versus null communities.

^cStandardized effect size of Faith's functional diversity versus null communities (based on a trait dendrogram instead of a phylogenetic tree).

^dWe alternatively set low and mid transformation levels as reference and show results of all possible interactions.

functional scores showed significant negative relationships with changes in its respective component across the 3 transformation areas. This means that communities with the lowest scores showed the largest increases and communities with the highest scores showed the largest decreases in these scores. Moreover, we recorded several nonsignificant tendencies in LTA, with taxonomically poorer communities displaying larger increases in phylogenetic diversity and phylogenetically and functionally poorer communities displaying larger increases in functional diversity.

We found no significant differences in the magnitude of the changes for the 3 components of biodiversity among the 3

transformation areas (Appendix S6). We recorded a nonsignificant tendency of LTA to experience smaller increases in phylogenetic diversity and larger increases in functional diversity than HTA. Thus, overall, initial land-use conditions had a relatively weak effect on biodiversity changes.

Economic development effects on biodiversity

Three sets of indicators described land-use, local-climatic, and economic changes (Figure 3a & Appendix S7). Land-use changes were characterized by decreasing productivity

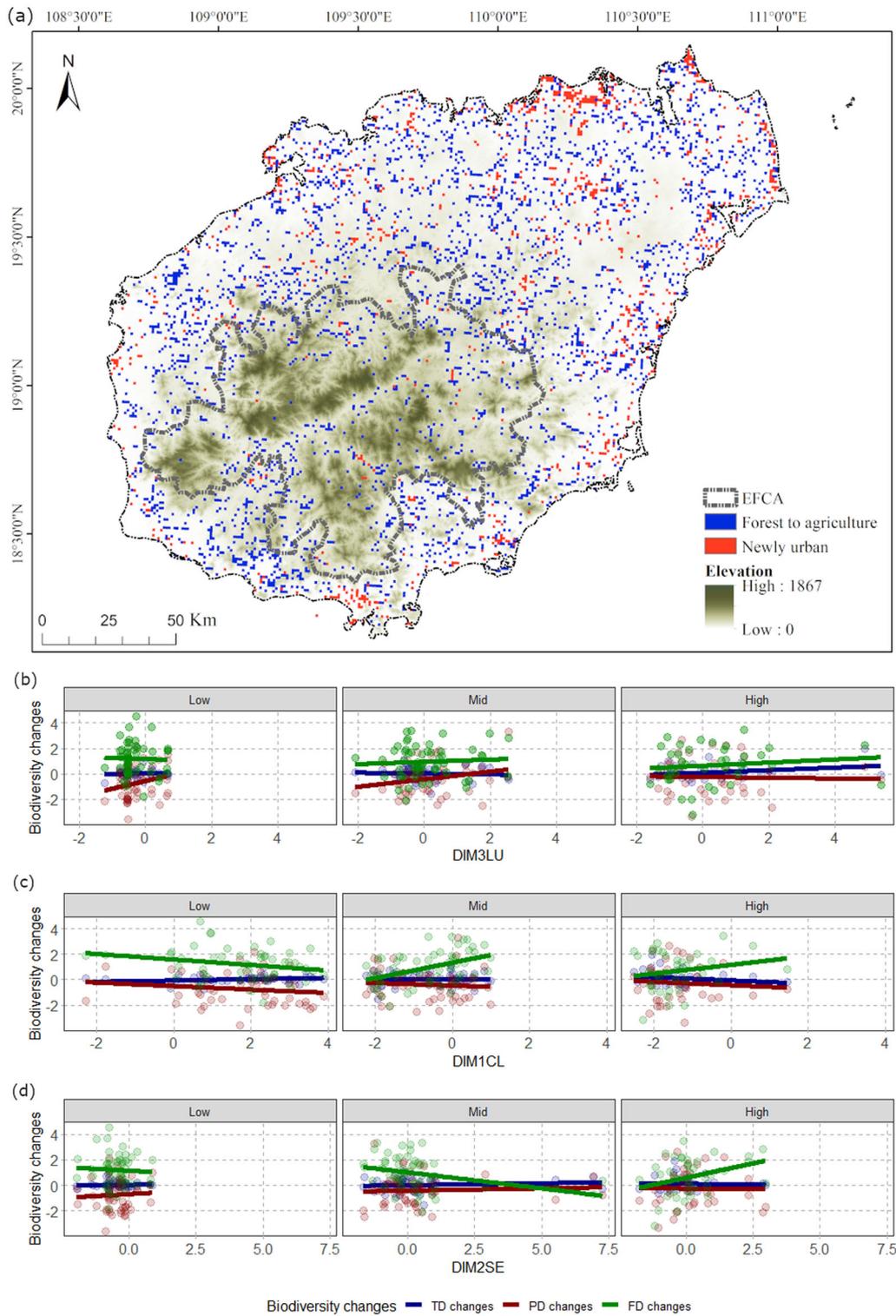


FIGURE 3 On Hainan Island (People’s Republic of China) from 1998 to 2013, (a) 1 × 1 km pixels showing the dominant land-use changes urbanization (newly urban) and forest to agriculture conversion (EFCAs, ecological function conservation area), (b) relationship between taxonomic (TD), phylogenetic (PD), and functional diversity (FD) change and the component DIM3LU (landscape urbanization index) that characterizes land-use changes, (c) relationship between TD, PD, and FD change and the component DIM1CL (high elevation climate index [i.e., increased precipitation variability and decreased temperature in high-elevation areas]) that characterizes local-climate changes, and (d) relationships between TD, PD, and FD change and the component DIM2SE (economic growth index [i.e., changes in population and gross domestic product]) that characterizes economic changes (low, mid, or high) in spatial classification according to transformation areas

index (NDVI) (DIM1LU), forest to agriculture conversion index (DIM2LU), and landscape urbanization index (DIM3LU). These changes represented an overall decrease of about 50 km² in highly productive areas, an increase of about 100 km² in urban areas (at the expense of forest cover), and 100 km² of forest converted agriculture. Changes in local climatic conditions were characterized by high elevation climate index (namely, increasing precipitation variability and decreasing temperature in high elevation areas) (DIM1CL), precipitation and temperature index (DIM2CL), and temperature variability index (DIM3CL). Overall, local climatic conditions were characterized by a 500-ml average increase in precipitation and a 2°C decrease in temperature. Economic changes were characterized by light pollution index (DIM1SE) and economic growth index (DIM2SE). There was an average population increase of 3551 people/100 km² and an average GDP increase of over 589,569 RMB/100km², in addition to an expansion of 372 km² of high-intensity light pollution.

Regarding land-use changes, the landscape urbanization index correlated positively with taxonomic diversity changes in HTA and phylogenetic diversity changes in LTA (Table 2 & Figure 3b). Thus, increasingly urbanized grids showed increases in taxonomic diversity in urban areas and increases in evolutionary diversity in natural areas. We also recorded a nonsignificant positive effect on phylogenetic diversity changes in MTA. Decreasing productivity index correlated positively with functional diversity changes in LTA (i.e., in response to decreasing habitat productivity, communities became functionally overdispersed in natural areas).

Changes in local climatic conditions also affected different components of biodiversity. High elevation climate index correlated positively with functional diversity changes in MTA and HTA and showed a nonsignificant negative effect on taxonomic diversity changes in HTA (Table 2 & Figure 3c). Thus, increasing precipitation variability and decreasing temperature in high elevation areas were related to functional overdispersion in transformed habitats. The temperature variability index correlated negatively with functional diversity changes in MTA and HTA, yet was only marginally significant in the former, suggesting that increasing temperature variability was linked to functional clustering in rural areas.

Regarding economic changes, the light pollution index showed parallel (positive) effects with landscape urbanization on taxonomic diversity changes in HTA (Table 2). This suggests that increasing human activities indicated by light pollution were indistinguishable from landscape urbanization. Finally, economic growth index correlated negatively with functional diversity changes in MTA and positively in HTA (Figure 3d). Thus, increasing population density and economic wealth produced divergent effect in rural (functional clustering) and urban habitats (functional overdispersion).

DISCUSSION

We recorded avian biodiversity changes on a tropical island with high biodiversity on which enhanced biodiversity conservation

policies are being established and where rapid economic growth and increasing ecological footprints are occurring (Dong et al., 2019). Biodiversity may experience changes in response to economic development and broadscale land use that may be difficult to attribute to specific factors because these responses are complex and divergent across spatial scales (Jarzyna & Jetz, 2018). As such, there may be ubiquitous regional-scale biodiversity changes due to extensive ecosystem degradation and local effects that can be attributed to specific factors, such as land use and climate change (Chase et al., 2020; Newbold et al., 2015). This complexity was apparent in our study area. We recorded evidence of regional-scale spatial biotic homogenization, phylogenetic clustering and functional overdispersion, and habitat-dependent biodiversity responses. Our results contribute to identifying the drivers of these changes and hence inform conservation policies and sustainable development plans aiming to harmonize environmental protection and economic growth.

Our data show that large-scale habitat transformation resulted in decreased spatial variability of taxonomic diversity (Magurran et al., 2015). Because differences in taxonomic diversity were relatively constant between transformation areas, this result might be a consequence of changes in other components of biodiversity. Increasing regional-scale phylogenetic clustering and functional overdispersion and the fact that communities that were more diverse taxonomically, phylogenetically, and functionally showed decreases in each of these components suggest there was a considerable reorganization of communities in response to human-driven changes. This result is in line with previous studies showing functional changes but no net biodiversity losses across time series (Dornelas et al., 2014; Vellend et al., 2013; see also Jarzyna & Jetz, 2018). Our results are novel in showing that communities responded to an intensification of human activities by becoming less diverse in terms of their evolutionary origins but more diverse in terms of their life-history traits. Human activities may have driven the extinction of less human-tolerant species (Sol et al., 2014). However, our results are in contrast with other studies showing steep decreases in functional diversity in response to habitat transformation at global scales (Sol et al., 2020). Our study was conducted at local to regional scales; thus, results are in line with works investigating similar geographical ranges in which the matrix can harbor relatively high functional diversity (Pagani-Núñez et al., 2019; Sreekar et al., 2021).

An interesting aspect of our results is that initial community structure determined changes in biodiversity metrics to a greater extent than land-use transformation. Intrinsic community dynamics had more weight in shaping these responses than extrinsic habitat features. Probably, human-driven environmental filters prevented community recolonization by native specialists (Xu et al., 2017) and promoted rapid colonization by a relatively high diversity of disturbance-tolerant species (Jarzyna & Jetz, 2018). This could be the result of niche preemption caused by species competition, with human-tolerant species outcompeting specialists in combination with niche modification caused by human activities (Fukami, 2015). Enhanced environmental protection averted to some extent human-driven

TABLE 2 Spatially explicit, linear, mixed-effects models fit by restricted maximum likelihood used to assess biodiversity changes over time (1998–2013) (dependent variables: Taxonomic,^a phylogenetic,^b and functional^c changes) and the interactions among habitat transformation levels (low, mid [middle], or high), product of an agglomerative hierarchical clustering on 145 100-km² grids from Hainan Province (People’s Republic of China), and land-use,^d local-climate,^e and economic changes,^f represented, by 3 sets of principal component analyses

Type of change across transformation area		β	SE	<i>t</i>	<i>p</i>
Land use	taxonomic				
	intercept	0.05	0.11	0.46	0.65
	low:DIM1LU	0.05	0.21	0.26	0.80
	mid:DIM1LU	0.03	0.04	0.71	0.48
	high:DIM1LU	0.05	0.04	1.27	0.20
	low:DIM2LU	-0.02	0.09	-0.20	0.85
	mid:DIM2LU	0.01	0.05	0.25	0.80
	high:DIM2LU	-0.02	0.06	-0.41	0.68
	low:DIM3LU	0.05	0.17	0.29	0.77
	mid:DIM3LU	-0.04	0.06	-0.64	0.52
	high:DIM3LU	0.10	0.05	2.00	0.05
	phylogenetic				
	intercept	-0.35	0.31	-1.14	0.26
	low:DIM1LU	0.02	0.60	0.03	0.98
	mid:DIM1LU	-0.04	0.11	-0.38	0.70
	high:DIM1LU	-0.08	0.11	-0.69	0.49
	low:DIM2LU	-0.23	0.26	-0.87	0.39
	mid:DIM2LU	-0.12	0.13	-0.94	0.35
	high:DIM2LU	-0.06	0.16	-0.38	0.71
	low:DIM3LU	1.08	0.49	2.22	0.03
	mid:DIM3LU	0.34	0.19	1.79	0.08
	high:DIM3LU	-0.05	0.15	-0.31	0.75
	functional				
	intercept	0.88	0.33	2.72	0.01
	low:DIM1LU	-0.58	0.63	-0.91	0.36
	mid:DIM1LU	0.01	0.12	0.05	0.96
	high:DIM1LU	0.28	0.12	2.38	0.02
	low:DIM2LU	0.08	0.28	0.28	0.78
	mid:DIM2LU	0.00	0.14	-0.03	0.97
	high:DIM2LU	0.26	0.17	1.51	0.13
	low:DIM3LU	-0.31	0.51	-0.59	0.55
	mid:DIM3LU	0.08	0.20	0.42	0.67
	high:DIM3LU	0.20	0.15	1.32	0.19
Local climate	taxonomic				
	intercept	<0.01	0.06	-0.05	0.96
	low:DIM1CL	0.03	0.04	0.96	0.34
	mid:DIM1CL	-0.02	0.06	-0.24	0.81
	high:DIM1CL	-0.10	0.05	-1.80	0.07
	low:DIM2CL	-0.05	0.06	-0.80	0.42
mid:DIM2CL	-0.04	0.05	-0.91	0.37	

(Continues)

TABLE 2 (Continued)

Type of change across transformation area	β	SE	<i>t</i>	<i>p</i>
high:DIM2CL	0.03	0.06	0.49	0.62
low:DIM3CL	-0.06	0.06	-0.90	0.37
mid:DIM3CL	0.00	0.05	-0.07	0.95
high:DIM3CL	-0.12	0.09	-1.26	0.21
phylogenetic				
intercept	-0.54	0.33	-1.64	0.10
low:DIM1CL	-0.13	0.10	-1.23	0.22
mid:DIM1CL	-0.17	0.19	-0.92	0.36
high:DIM1CL	-0.16	0.16	-1.03	0.30
low:DIM2CL	0.07	0.17	0.41	0.68
mid:DIM2CL	-0.02	0.14	-0.14	0.89
high:DIM2CL	-0.08	0.17	-0.49	0.63
low:DIM3CL	0.05	0.18	0.26	0.80
mid:DIM3CL	-0.21	0.15	-1.35	0.18
high:DIM3CL	-0.41	0.27	-1.53	0.13
functional				
intercept	1.34	0.30	4.44	<0.01
low:DIM1CL	-0.13	0.10	-1.27	0.21
mid:DIM1CL	0.57	0.18	3.15	<0.01
high:DIM1CL	0.47	0.15	3.16	<0.01
low:DIM2CL	0.05	0.16	0.30	0.76
mid:DIM2CL	<0.01	0.13	0.02	0.98
high:DIM2CL	0.05	0.16	0.29	0.77
low:DIM3CL	-0.20	0.17	-1.14	0.26
mid:DIM3CL	-0.28	0.15	-1.88	0.06
high:DIM3CL	-0.73	0.26	-2.78	0.01
Economic				
taxonomic				
intercept	0.02	0.11	0.17	0.87
low:DIM1SE	-0.04	0.10	-0.40	0.69
mid:DIM1SE	0.01	0.04	0.31	0.76
high:DIM1SE	0.10	0.03	3.10	<0.01
low:DIM2SE	0.05	0.11	0.41	0.68
mid:DIM2SE	0.03	0.03	0.78	0.44
high:DIM2SE	0.05	0.07	0.77	0.44
phylogenetic				
intercept	-0.34	0.32	-1.06	0.29
low:DIM1SE	0.36	0.30	1.20	0.23
mid:DIM1SE	-0.02	0.10	-0.17	0.86
high:DIM1SE	-0.07	0.10	-0.66	0.51
low:DIM2SE	0.15	0.32	0.47	0.64
mid:DIM2SE	0.03	0.10	0.29	0.77

(Continues)

TABLE 2 (Continued)

Type of change across transformation area	β	SE	<i>t</i>	<i>p</i>
high:DIM2SE	-0.05	0.21	-0.24	0.81
functional				
intercept	0.85	0.32	2.69	0.01
low:DIM1SE	-0.29	0.30	-0.98	0.33
mid:DIM1SE	0.14	0.10	1.32	0.19
high:DIM1SE	0.01	0.10	0.15	0.88
low:DIM2SE	-0.16	0.32	-0.50	0.62
mid:DIM2SE	-0.24	0.10	-2.36	0.02
high:DIM2SE	0.42	0.21	2.03	0.04

^aRarefied richness.

^bStandardized effect size of Faith's phylogenetic diversity versus null communities.

^cStandardized effect size of Faith's functional diversity versus null communities (based on a trait dendrogram instead of a phylogenetic tree).

^dAbbreviations: DIM1LU, decreasing productivity index; DIM2LU, forest to agriculture conversion index; DIM3LU, landscape urbanization index.

^eAbbreviations: DIM1CL, high elevation climate index (namely increased precipitation variability and decreased temperature in high elevation areas); DIM2CL, precipitation and temperature index; DIM3CL, temperature variability index.

^fAbbreviations: DIM1SE, light pollution index; DIM2SE, economic growth index.

impacts on biodiversity, primarily by preventing drastic land-use changes, such as the indiscriminate expansion of rubber monocultures occurring outside protected areas (Zhai et al., 2018; Zheng et al., 2019). Yet, negative broadscale effects on biodiversity were widespread, although a lack of stronger positive effects on biodiversity may be due to the limited time of implementation of the EFCA (only 3 out of 15 years studied here) and that its focus is on ecological services rather than on biodiversity conservation (Li et al., 2020; Zheng et al., 2019).

Land-use changes and human activities are often direct drivers of biodiversity change and loss (e.g., Sambell et al., 2019; Smith et al., 2012; Sol et al., 2014), yet there are also examples of how these processes can result in enhanced biodiversity at moderate disturbance levels (McKinney, 2008), affect different biodiversity components (Knapp et al., 2017; Sreekar et al., 2021), or show no effect on biodiversity (Korányi et al., 2021). Our study helps disentangle the diverging effects of different aspects of human activities on different biodiversity metrics. For instance, economic growth had a positive effect on taxonomic diversity that was only apparent in HTA. Landscape urbanization was linked only to increasing phylogenetic overdispersion in LTA. Regional-scale functional diversity overdispersion was apparently driven by many factors, including changes in local climatic conditions, landscape urbanization, and economic growth. Economic growth was linked to functional clustering in MTA and to functional overdispersion in HTA. These local-scale effects were more prevalent in MTA and HTA (7 significant effects) than in LTA (1 significant effect) (Figure 3b–d).

We acknowledge certain limitations of our approach. For instance, we were unable to discriminate between forest types with our data and did not examine in detail the performance of strictly protected natural reserves. Moreover, we focused on avian biodiversity responses to human activities, which might differ from other taxa due to their high mobility and plasticity, and the status of some species may have changed in the

last decade. Our research is significant in presenting evidence that environmental protection can minimize negative impacts of economic growth (Anderson & Mammides, 2020; Juutinen et al., 2019; Sandker et al., 2012), yet pervasive regional-scale negative effects can overcome local-scale positive effects (Jarzyna & Jetz, 2018). Less diverse communities would benefit from enhanced environmental protection, but more diverse communities would require highly focused protection measures. Therefore, conservation policies, while having broad benefits on biodiversity, may require focused actions targeting natural habitats and specialist species. Our results illustrate how economic growth and biodiversity conservation can be complementary but at the likely cost of broadscale biotic homogenization and local-scale biodiversity loss. Further research could investigate this issue at broader spatial scales and incorporate different taxa to determine whether these patterns are consistent at continental scales and in other climates. Moreover, it would be interesting to pinpoint which aspects of economic activities contribute most to biodiversity responses and to study the effects of diverging economic trajectories on different biodiversity metrics.

ACKNOWLEDGMENTS

We are very grateful to H. Yang, H Wang, and Y Pan for their help curating the trait database and to Y Zou, L Li, and L Xiao for their constructive comments on an earlier draft. We are also very grateful to 2 anonymous reviewers for their constructive comments. Y.X. acknowledges support from the National Natural Science Foundation of China (grant 32001164) and Foundation Project of President of Guangdong Academy of Agricultural Sciences (grant 201917).

ORCID

Emilio Pagani-Núñez  <https://orcid.org/0000-0001-8839-4005>

Yang Xu  <https://orcid.org/0000-0003-3244-264X>

Jiekun He  <https://orcid.org/0000-0001-9401-4208>

Haisbeng Jiang  <https://orcid.org/0000-0002-4793-1924>

REFERENCES

- Anderson, B. J., Armsworth, P. R., Eigenbrod, F., Thomas, C. D., Gillings, S., Heinemeyer, A., Roy, D. B., & Gaston, K. J. (2009). Spatial covariance between biodiversity and other ecosystem service priorities. *Journal of Applied Ecology*, *46*, 888–896.
- Anderson, E., & Mammides, C. (2020). The role of protected areas in mitigating human impact in the world's last wilderness areas. *Ambio*, *49*, 434–441.
- Baiser, B., & Lockwood, J. L. (2011). The relationship between functional and taxonomic homogenization: Functional and taxonomic homogenization. *Global Ecology and Biogeography*, *20*, 134–144.
- Bragina, E. V., Ives, A. R., Pidgeon, A. M., Kuemmerle, T., Baskin, L. M., Gubar, Y. P., Piquer-Rodríguez, M., Keuler, N. S., Petrosyan, V. G., & Radeloff, V. C. (2015). Rapid declines of large mammal populations after the collapse of the Soviet Union. *Conservation Biology*, *29*, 844–853.
- Cadotte, M. W., Carboni, M., Si, X., & Tatsumi, S. (2019). Do traits and phylogeny support congruent community diversity patterns and assembly inferences? *Journal of Ecology*, *107*, 2065–2077.
- Callaghan, C. T., Benedetti, Y., Wilshire, J., & Morelli, F. (2019). Avian trait specialization is negatively associated with urban tolerance. *Oikos*, *129*, 1541–1551.
- Carlier, J., Doyle, M., Finn, J. A., Ó hUallacháin, D., & Moran, J. (2021). A landscape classification map of Ireland and its potential use in national land use monitoring. *Journal of Environmental Management*, *289*, 112498.
- Ceballos, G., Ehrlich, P. R., & Raven, P. H. (2020). Vertebrates on the brink as indicators of biological annihilation and the sixth mass extinction. *Proceedings of the National Academy of Sciences of the United States of America*, *117*, 13596–13602.
- Chase, J. M., Blowes, S. A., Knight, T. M., Gerstner, K., & May, F. (2020). Ecosystem decay exacerbates biodiversity loss with habitat loss. *Nature*, *584*, 238–243.
- Clausen, R., & York, R. (2008). Economic growth and marine biodiversity: Influence of human social structure on decline of marine trophic levels. *Conservation Biology*, *22*, 458–466.
- Dallimer, M., Davies, Z. G., Diaz-Porras, D. F., Irvine, K. N., Maltby, L., Warren, P. H., Armsworth, P. R., & Gaston, K. J. (2015). Historical influences on the current provision of multiple ecosystem services. *Global Environmental Change*, *31*, 307–317.
- Devictor, V., Julliard, R., Clavel, J., Jiguet, F., Lee, A., & Couvet, D. (2008). Functional biotic homogenization of bird communities in disturbed landscapes. *Global Ecology and Biogeography*, *17*, 252–261.
- Diaz, S., Settele, J., Brondizio, E. S., Ngo, H. T., Agard, J., Arneith, A., Balvanera, P., Brauman, K. A., Butchart, S. H. M., Chan, K. M. A., Garibaldi, L. A., Ichii, K., Liu, J., Subramanian, S. M., Midgley, G. F., Miloslavich, P., Molnár, Z., Obura, D., Pfaff, A., ... Zayas, C. N. (2019). Pervasive human-driven decline of life on Earth points to the need for transformative change. *Science*, *366*, eaax3100.
- Dong, H., Li, P., Feng, Z., Yang, Y., You, Z., & Li, Q. (2019). Natural capital utilization on an international tourism island based on a three-dimensional ecological footprint model: A case study of Hainan Province, China. *Ecological Indicators*, *104*, 479–488.
- Dormann, C. F., McPherson, J. M., Araújo, M. B., Bivand, R., Bolliger, J., Carl, G., Davies, R. G., Hirzel, A., Jetz, W., Kissling, W. D., Kühn, I., Ohlemüller, R., Peres-Neto, P. R., Reineking, B., Schröder, B., Schurr, F. M., & Wilson, R. (2007). Methods to account for spatial autocorrelation in the analysis of species distributional data: A review. *Ecography*, *30*, 609–628.
- Dornelas, M., Gotelli, N. J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C., & Magurran, A. E. (2014). Assemblage time series reveal biodiversity change but not systematic loss. *Science*, *344*, 296–299.
- Ellis, E. C., Gauthier, N., Goldewijk, K. K., Bird, R. B., Boivin, N., Díaz, S., Fuller, D. Q., Gill, J. L., Kaplan, J. O., & Kingston, N. (2021). People have shaped most of terrestrial nature for at least 12,000 years. *Proceedings of the National Academy of Sciences of the United States of America*, *118*, e2023483118.
- Fahrig, L. (2017). Ecological responses to habitat fragmentation per se. *Annual Review of Ecology, Evolution, and Systematics*, *48*, 1–23.
- Fukami, T. (2015). Historical contingency in community assembly: Integrating niches, species pools, and priority effects. *Annual Review of Ecology, Evolution, and Systematics*, *46*, 1–23.
- Georgiev, K. B., Chao, A., Castro, J., Chen, Y., Choi, C., Fontaine, J. B., Hutto, R. L., Lee, E., Müller, J., Rost, J., Zmihorski, M., & Thorn, S. (2020). Salvage logging changes the taxonomic, phylogenetic and functional successional trajectories of forest bird communities. *Journal of Applied Ecology*, *57*, 1103–1112.
- Graham, C. H., & Fine, P. V. A. (2008). Phylogenetic beta diversity: Linking ecological and evolutionary processes across space in time. *Ecology Letters*, *11*, 1265–1277.
- Gu, K., & Wall, G. (2007). Rapid urbanization in a transitional economy in China: The case of Hainan Island. *Singapore Journal of Tropical Geography*, *28*, 158–170.
- Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., Lovejoy, T. E., Sexton, J. O., Austin, M. P., Collins, C. D., Cook, W. M., Damschen, E. I., Ewers, R. M., Foster, B. L., Jenkins, C. N., King, A. J., Laurance, W. F., Levey, D. J., Margules, C. R., ... Townshend, J. R. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, *1*, e1500052.
- Jarzyna, M. A., & Jetz, W. (2018). Taxonomic and functional diversity change is scale dependent. *Nature Communications*, *9*, 2565.
- Jenks, G. F. (1967). The data model concept in statistical mapping. *International Yearbook of Cartography*, *7*, 186–190.
- Jetz, W., Wilcove, D. S., & Dobson, A. P. (2007). Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biology*, *5*, e157.
- Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., & Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature*, *491*, 444–448.
- Jha, S., & Bawa, K. S. (2006). Population growth, human development, and deforestation in biodiversity hotspots. *Conservation Biology*, *20*, 906–912.
- Juutinen, A., Saarimaa, M., Ojanen, P., Sarkkola, S., Haara, A., Karhu, J., Nieminen, M., Minkkinen, K., Penttilä, T., Laatikainen, M., & Tolvanen, A. (2019). Trade-offs between economic returns, biodiversity, and ecosystem services in the selection of energy peat production sites. *Ecosystem Services*, *40*, 101027.
- Kati, V., Devillers, P., Dufrêne, M., Legakis, A., Vokou, D., & Lebrun, P. (2004). Testing the value of six taxonomic groups as biodiversity indicators at a local scale. *Conservation Biology*, *18*, 667–675.
- Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., Blomberg, S. P., & Webb, C. O. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, *26*, 1463–1464.
- Knapp, S., Winter, M., & Klotz, S. (2017). Increasing species richness but decreasing phylogenetic richness and divergence over a 320-year period of urbanization. *Journal of Applied Ecology*, *54*, 1152–1160.
- Korányi, D., Gallé, R., Donkó, B., Chamberlain, D. E., & Batáry, P. (2021). Urbanization does not affect green space bird species richness in a mid-sized city. *Urban Ecosystems*, *24*, 789–800.
- Lê, S., Josse, J., & Husson, F. (2008). FactoMineR: An R package for multivariate analysis. *Journal of Statistical Software*, *25*, 1–18.
- Li, R., Zheng, H., Polasky, S., Hawthorne, P. L., O'Connor, P., Wang, L., Li, R., Xiao, Y., Wu, T., & Ouyang, Z. (2020). Ecosystem restoration on Hainan Island: Can we optimize for enhancing regulating services and poverty alleviation? *Environmental Research Letters*, *15*, 084039.
- Lin, S., Jiang, Y., He, J., Ma, G., Xu, Y., & Jiang, H. (2017). Changes in the spatial and temporal pattern of natural forest cover on Hainan Island from the 1950s to the 2010s: Implications for natural forest conservation and management. *PeerJ*, *5*, e3320.
- Luoto, M., Virkkala, R., & Heikkinen, R. K. (2007). The role of land cover in bioclimatic models depends on spatial resolution. *Global Ecology and Biogeography*, *16*, 34–42.
- Magurran, A. E., Dornelas, M., Moyes, F., Gotelli, N. J., & McGill, B. (2015). Rapid biotic homogenization of marine fish assemblages. *Nature Communications*, *6*, 8405.
- McKinney, M. L. (2006). Urbanization as a major cause of biotic homogenization. *Biological Conservation*, *127*, 247–260.
- McKinney, M. L. (2008). Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosystems*, *11*, 161–176.

- Mi, X., Feng, G., Hu, Y., Zhang, J., Chen, L., Corlett, R. T., Hughes, A. C., Pimm, S., Schmid, B., Shi, S., Svenning, J.-C., & Ma, K. (2021). The global significance of biodiversity science in China: An overview. *National Science Review*, 8, nwab032.
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403, 853–858.
- National Bureau of Statistics. (2021). *China statistical yearbook*. China Statistics Press. (in Chinese).
- Newbold, T., Hudson, L. N., Hill, S. L. L., Contu, S., Lysenko, I., Senior, R. A., Börger, L., Bennett, D. J., Choimes, A., Collen, B., Day, J., De Palma, A., Diaz, S., Echeverria-Londoño, S., Edgar, M. J., Feldman, A., Garon, M., Harrison, M. L. K., Alhussaini, T., ... Purvis, A. (2015). Global effects of land use on local terrestrial biodiversity. *Nature*, 520, 45–50.
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Henry, M., Stevens, H., Szoecs, E., & Wagner, H. (2020). *vegan: Community ecology package*. R package version 2.5-7. <https://CRAN.R-project.org/package=vegan>
- Otero, I., Farrell, K. N., Pueyo, S., Kallis, G., Kehoe, L., Haberl, H., Plutzer, C., Hobson, P., García-Márquez, J., Rodríguez-Labajos, B., Martin, J., Erb, K., Schindler, S., Nielsen, J., Skorin, T., Settele, J., Essl, F., Gómez-Baggethun, E., Brotons, L., ... Pe'er, G. (2020). Biodiversity policy beyond economic growth. *Conservation Letters*, 13, e12713.
- Pagani-Núñez, E., Liang, D., He, C., Zhou, X., Luo, X., Liu, Y., & Goodale, E. (2019). Niches in the Anthropocene: Passerine assemblages show niche expansion from natural to urban habitats. *Ecography*, 42, 1360–1369.
- Paradis, E., Claude, J., & Strimmer, K. (2004). APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics*, 20, 289–290.
- Peck, J. E. (2010). *Multivariate analysis for community ecologists*. MjM Software Design.
- Pergam, O. R. W., Czech, B., Haney, J. C., & Nyberg, D. (2004). Linkage of conservation activity to trends in the U.S. economy. *Conservation Biology*, 18, 1617–1623.
- Pimm, S. L., Jenkins, C. N., Abell, R., Brooks, T. M., Gittleman, J. L., Joppa, L. N., Raven, P. H., Roberts, C. M., & Sexton, J. O. (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, 344, 1246752.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & Team, R. C. (2007). *nlme: Linear and nonlinear mixed effects models*. R package version 3.1-152. <https://CRAN.R-project.org/package=nlme>
- R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Ranganathan, J., Daniels, R. J. R., Chandran, M. D. S., Ehrlich, P. R., & Daily, G. C. (2008). Sustaining biodiversity in ancient tropical countryside. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 17852–17854.
- Revell, L. J. (2012). phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, 3, 217–223.
- Ricotta, C., Acosta, A. T. R., Bacaro, G., Carboni, M., Chiarucci, A., Rocchini, D., & Pavoine, S. (2019). Rarefaction of beta diversity. *Ecological Indicators*, 107, 105606.
- Sambell, C. E., Holland, G. J., Haslem, A., & Bennett, A. F. (2019). Diverse land-uses shape new bird communities in a changing rural region. *Biodiversity and Conservation*, 28, 3479–3496.
- Sandker, M., Ruiz-Perez, M., & Campbell, B. M. (2012). Trade-offs between biodiversity conservation and economic development in five tropical forest landscapes. *Environmental Management*, 50, 633–644.
- Sepp, T., McGraw, K. J., Kaasik, A., & Giraudeau, M. (2018). A review of urban impacts on avian life-history evolution: Does city living lead to slower pace of life? *Global Change Biology*, 24, 1452–1469.
- Smith, F. P., Gordard, R., House, A. P. N., McIntyre, S., & Prober, S. M. (2012). Biodiversity and agriculture: Production frontiers as a framework for exploring trade-offs and evaluating policy. *Environmental Science & Policy*, 23, 85–94.
- Sol, D., Bartomeus, I., González-Lagos, C., & Pavoine, S. (2017). Urbanisation and the loss of phylogenetic diversity in birds. *Ecology Letters*, 20, 721–729.
- Sol, D., González-Lagos, C., Moreira, D., Maspons, J., & Lapedra, O. (2014). Urbanisation tolerance and the loss of avian diversity. *Ecology Letters*, 17, 942–950.
- Sol, D., Trisos, C., Múrria, C., Jeliakov, A., González-Lagos, C., Pigot, A. L., Ricotta, C., Swan, C. M., Tobias, J. A., & Pavoine, S. (2020). The worldwide impact of urbanisation on avian functional diversity. *Ecology Letters*, 23, 962–972.
- Sreekar, R., Si, X., Sam, K., Liu, J., Dayananda, S., Goodale, U., Kotagama, S., & Goodale, E. (2021). Land use and elevation interact to shape bird functional and phylogenetic diversity and structure: Implications for designing optimal agriculture landscapes. *Journal of Applied Ecology*, 58, 1738–1748.
- Sun, R., Wu, Z., Chen, B., Yang, C., Qi, D., Lan, G., & Fraedrich, K. (2020). Effects of land-use change on eco-environmental quality in Hainan Island, China. *Ecological Indicators*, 109, 105777.
- Sutherland, W. J., Atkinson, P. W., Broad, S., Brown, S., Clout, M., Dias, M. P., Dicks, L. V., Doran, H., Fleishman, E., Garratt, E. L., Gaston, K. J., Hughes, A. C., Le Roux, X., Lickorish, F. A., Maggs, L., Palardy, J. E., Peck, L. S., Pettorelli, N., Pretty, J., ... Thornton, A. (2021). A 2021 horizon scan of emerging global biological conservation issues. *Trends in Ecology & Evolution*, 36, 87–97.
- Tscharntke, T., Sekercioglu, C. H., Dietsch, T. V., Sodhi, N. S., Hoehn, P., & Tylianakis, J. M. (2008). Landscape constraints on functional diversity of birds and insects in tropical agroecosystems. *Ecology*, 89, 944–951.
- Vellend, M., Baeten, L., Myers-Smith, I. H., Elmendorf, S. C., Beausejour, R., Brown, C. D., De Frenne, P., Verheyen, K., & Wipf, S. (2013). Global meta-analysis reveals no net change in local-scale plant biodiversity over time. *Proceedings of the National Academy of Sciences of the United States of America*, 110, 19456–19459.
- Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M. M., & Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology*, 95, 2027–2027.
- Xu, Y., Lin, S., He, J., Xin, Y., Zhang, L., Jiang, H., & Li, Y. (2017). Tropical birds are declining in the Hainan Island of China. *Biological Conservation*, 210, 9–18.
- Zhai, J., Hou, P., Cao, W., Yang, M., Cai, M., & Li, J. (2018). Ecosystem assessment and protection effectiveness of a tropical rainforest region in Hainan Island, China. *Journal of Geographical Sciences*, 28, 415–428.
- Zheng, H., Wang, L., Peng, W., Zhang, C., Li, C., Robinson, B. E., Wu, X., Kong, L., Li, R., Xiao, Y., Xu, W., Ouyang, Z., & Daily, G. C. (2019). Realizing the values of natural capital for inclusive, sustainable development: Informing China's new ecological development strategy. *Proceedings of the National Academy of Sciences of the United States of America*, 116, 8623–8628.
- Zou, Y., Werf, W., Liu, Y., & Axmacher, J. C. (2020). Predictability of species diversity by family diversity across global terrestrial animal taxa. *Global Ecology and Biogeography*, 29, 629–644.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Pagani-Núñez, E., Xu, Y., Yan, M., He, J., Jiang, Z., & Jiang, H. (2022). Trade-offs between economic development and biodiversity conservation on a tropical island. *Conservation Biology*, e139121. <https://doi.org/10.1111/cobi.13912>