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Underlying and proximate drivers of biodiversity changes in Mesoamerican biosphere reserves

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Protected areas are of paramount relevance to conserving wildlife and ecosystem contributions to people. Yet, their conservation success is increasingly threatened by human activities including habitat loss, climate change, pollution, and species overexploitation. Thus, understanding the underlying and proximate drivers of anthropogenic threats is urgently needed to improve protected areas' effectiveness, especially in the biodiversity-rich tropics. We addressed this issue by analyzing expert-provided data on long-term biodiversity change (last three decades) over 14 biosphere reserves from the Mesoamerican Biodiversity Hotspot. Using multivariate analyses and structural equation modeling, we tested the influence of major socioeconomic drivers (demographic, economic, and political factors), spatial indicators of human activities (agriculture expansion and road extension), and forest landscape modifications (forest loss and isolation) as drivers of biodiversity change. We uncovered a significant proliferation of disturbance-tolerant guilds and the loss or decline of disturbance-sensitive guilds within reserves causing a "winner and loser" species replacement over time. Guild change was directly related to forest spatial changes promoted by the expansion of agriculture and roads within reserves. High human population density and low nonfarming occupation were identified as the main underlying drivers of biodiversity change. Our findings suggest that to mitigate anthropogenic threats to biodiversity within biosphere reserves, fostering human population well-being via sustainable, nonfarming livelihood opportunities around reserves is imperative.

anthropogenic disturbances | conservation success | deforestation | protected areas | species loss

Significance

Given the current biodiversity crisis, understanding the ability of protected areas to safeguard biodiversity has never been more important. We examined such potential in a sample of 14 Mesoamerican biosphere reserves, using expert-provided data. During the last 30 y, there was an overall impoverishment of biodiversity and a significant replacement of disturbance-sensitive plant and animal guilds with disturbance-tolerant guilds. Forest loss and isolation promoted by the expansion of agriculture and road networks drove biodiversity change. High human population density and low availability of nonfarming occupation around reserves were the main underlying drivers of biodiversity change. We posit that to mitigate anthropogenic threats to biodiversity within biosphere reserves, it is critical to promote nonfarming sustainable livelihood opportunities around reserves.

Forest loss has led to a global biodiversity crisis, negatively affecting ecosystem functions (1) and human well-being (2). This process is particularly acute in the tropics (3), where the remaining forest is highly fragmented (4). The effect of forest loss on biodiversity depends, however, on species' habitat requirements (5). Some species are highly sensitive to forest loss because they depend on forest resources for shelter, feeding, and breeding (6) or because they are adapted to the abiotic conditions prevailing within the forest (7). However, other species tolerate and even proliferate in human-disturbed habitats, such as agroforestry plantations, forest edges, and pastures (8). Thus, forest cover changes can trigger a disturbance-sensitive/disturbance-tolerant species replacement (8, 9).

Protected areas represent one of the best options to conserve biodiversity (10). However, they are increasingly exposed to anthropic pressures that threaten the biodiversity they harbor. For example, almost one-third of the world's protected areas are under high human pressure (11), and nearly 30% do not reduce forest loss effectively (12). Other studies document that human activities are eroding biodiversity within protected areas worldwide (13, 14), but the mechanisms causing such erosion are still not fully understood. Therefore, understanding the underlying and proximate drivers of biodiversity degradation within protected areas is an urgent agenda to cope with the current biodiversity crisis (15).

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Among the factors that directly modify forest cover (16), the expansion of agricultural fields stands out as the main cause of forest loss in the tropics (17). Wood extraction and the extension of infrastructure, mainly road networks, are also important proximate drivers of forest loss and fragmentation (18). These proximate drivers are in turn influenced by demographic, economic, technological, political, and cultural factors, together known as indirect or underlying drivers of forest spatial change (16). For example, factors such as population growth (19), commercial demand for agricultural products (20), and low nonfarm occupation (21) are important drivers of forest loss because they promote agriculture expansion or infrastructure development.

Biodiversity changes in protected areas can be therefore caused by forest cover changes associated with human activities, which in turn are driven by the socioeconomic context. Previous studies have documented the drivers of forest loss in protected areas (22–24), and the biodiversity trends resulting from forest cover changes (25–27). However, important knowledge gaps remain regarding the underlying and proximate drivers of forest loss and their effects on biodiversity in protected areas, in particular biosphere reserves (described below). A comprehensive model of these potential cascading effects is still needed.

This study aims to help fill such knowledge gaps by testing a conceptual model summarized in Fig. 1. We used expert knowledge to document long-term temporal changes in the abundance and species richness of 31 biological guilds within 14 Mexican biosphere reserves from the Mesoamerican Biodiversity Hotspot. Expert knowledge is valuable in conservation science, especially when long-term empirical data are lacking (28). Biosphere reserves are recognized as earning places for sustainable development. Globally, they are designated under the Man and Biosphere program of UNESCO, but they are adapted to the conditions of each country. In Mexico, biosphere reserves are officially recognized as protected areas by law (29) and are often linked to research institutions in the Mexican modality of biosphere reserves (30). These reserves have two zones: 1) the core zone [strict protection IUCN category I, according to the World Database on Protected Areas (31)], where the only human activities allowed are ecosystem preservation, environmental education, research, and low-impact tourism, and 2) the buffer zone (IUCN category VI), where productive activities such as agriculture, agroforestry, ecotourism, and sustainable forest resource use are allowed (see details in *SI Appendix*, Tables S1 and S2). Within the spectrum of protected areas in Mexico, biosphere reserves stand out with the largest expanse under protection. They are established in key biogeographic sites, where ecosystems have minimal modification or have been altered and now require preservation and restoration because of their biological relevance (30). Additionally, biosphere reserves possess one of the lengthiest research legacies and have been demonstrated effective in avoiding forest loss (21) even when compared to stricter protected areas (32).

First, we assessed biodiversity (represented by different invertebrates, vertebrates, and plant guilds) changes occurring in the reserves over the last three decades (1990 to 2020) as a whole and separating disturbance-sensitive guilds from disturbance-tolerant ones (Table 1). Second, using multivariable analyses and structural equation modeling (SEM), we tested our conceptual framework assessing the effects of underlying (demographic, economic, and political) and proximate drivers (road network extension and agricultural expansion) on forest spatial changes and, ultimately, on biodiversity changes. Following the habitat amount hypothesis (34), we predicted a decrease in the abundance and richness of forest-dependent guilds and an increase of disturbance-tolerant guilds in response to forest cover loss. Also, we predicted that biodiversity changes are mostly driven by agriculture and road expansion (proximate drivers), which, in turn, are fostered by the

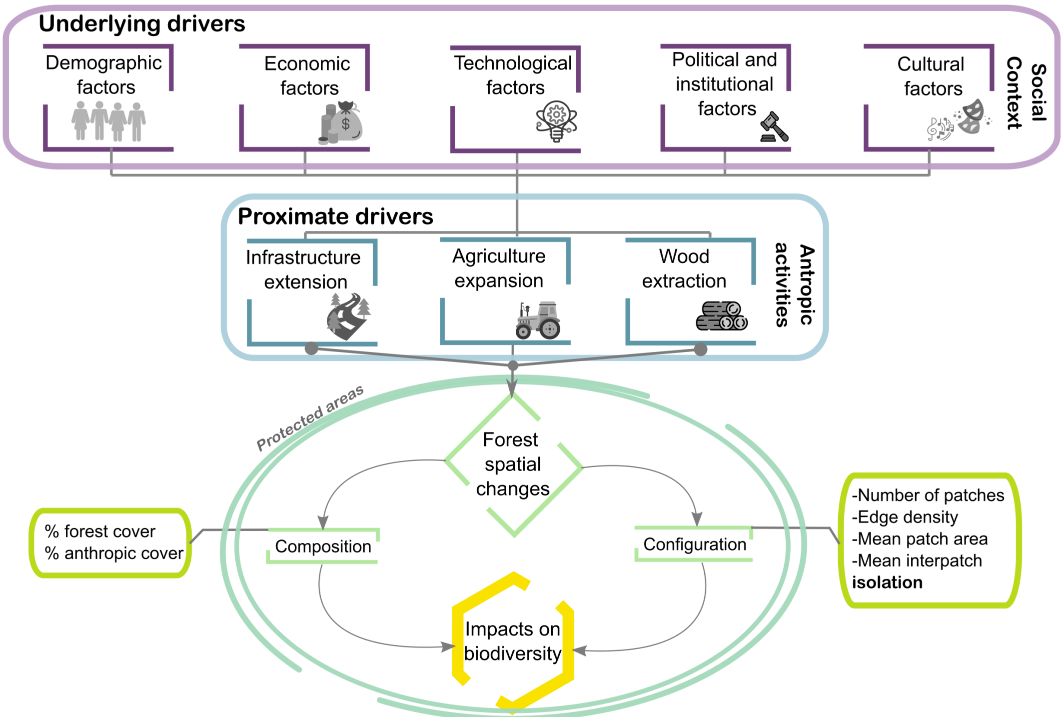

Fig. 1. Hypothetical relationships between underlying drivers, proximate drivers, forest spatial changes, and their impact on biodiversity in protected areas. The underlying drivers result in different proximate forces, such as wood extraction, infrastructure extension, and agricultural expansion, which can directly determine forest spatial changes (33). Such spatial changes can affect both the composition (e.g., forest cover) and configuration (e.g., number of patches) of the landscape surrounding each protected area, ultimately shaping biodiversity trends over time.

Table 1. Biodiversity guilds evaluated in the present study

Taxa	Guild	n	Disturbance response*
Mammals	Bats	18	
	Large, nonpredatory mammals	41	Sensitive
	Omnivorous/opportunistic mammals	39	Tolerant
	Primates	23	
	Rodents	18	Tolerant
	Top predators	38	Sensitive
Birds	Large frugivorous birds	19	
	Large game birds	25	Sensitive
	Raptors	20	
	Small nectarivorous birds	11	
	Understory birds	18	
Amphibians and reptiles	Lizards and large reptiles	19	
	Nonvenomous snakes	16	
	Stream-dwelling amphibians	15	
	Terrestrial amphibians	17	
	Venomous snakes	18	
Insects	Army ants	9	
	Disease-vectoring invertebrates	11	
	Dung beetles	8	
	Leaf-cutter ants	8	
	Light-loving butterflies	11	
Plants	Epiphytic plants	22	Sensitive
	Large-seeded species (shade-tolerant trees, climax species)	36	Sensitive
	Lianas/climbing vines	20	Tolerant
	Pioneer species	32	Tolerant
General groups	Ecological specialists	10	
	Exotic animals (non-native)	17	
	Exotic plants (non-native)	22	Tolerant
	Human diseases	7	
	Migratory species	11	
	Species dependent on tree cavities	16	

*The most frequent guilds were classified according to their hypothesized response to disturbance (i.e., disturbance-sensitive and disturbance-tolerant guilds).
We show the total number of surveys (n) that documented changes in abundance and richness in 10 Mexican biosphere reserves (see *Materials and Methods* for details).

demographic and economic dynamics (underlying factors) occurring in local human communities around reserves.

Results

Biodiversity Changes. The most representative taxa in our dataset were terrestrial mammals followed by plants and birds, with 177, 133, and 93 surveys, respectively. For insects, we compiled 50 surveys. The most representative functional guilds were large nonpredatory mammals, omnivorous/opportunistic mammals, and top predators, with nearly 40 surveys each, while army ants, leaf-cutter ants, and dung beetles were poorly covered, with less than nine surveys each (Table 1). Overall, abundance combining all guilds decreased over time (mean value = −0.33, 95%CI = −0.45 to −0.20, $P < 0.001$, Fig. 2*A*). This change resulted from a significant decrease in the abundance of disturbance-sensitive guilds (−0.88, CI −1.14 to −0.63, $P < 0.001$) despite an increase of disturbance-tolerant guilds (0.68, CI 0.43 to 0.93, $P < 0.001$, Fig. 2*B* and *SI Appendix*, Table S3). When assessing each guild separately, the abundance of large nonpredatory mammals, primates, top predators, large game birds, raptor birds, epiphytic plants, ecological specialists (foraging specialists and species with complex mutualisms), and large-seeded trees decreased over time (Fig. 3 and *SI Appendix*, Table S4). Interestingly, the abundance of most amphibian and reptile guilds, except venomous snakes, decreased. In contrast, the abundance of disease-vectoring invertebrates, lianas/climbing vines, pioneer species, exotic plants, and exotic animals increased over time (Fig. 3). Notably, in all these cases, species richness followed a similar pattern of change (*SI Appendix*, Fig. S1 and Table S5).

Drivers of Biodiversity Change. The goodness of fit of our Structural Equation Models was high (i.e., 40 to 81% of explained variance), indicating that our conceptual model properly explains the observed biodiversity changes in the studied biosphere reserves. Among the tested underlying drivers, only nonfarm occupation and population were included in the final model as they performed best as predictors (*SI Appendix*, Tables S6–S12). The reserves with lower nonfarm occupation experienced a higher agriculture expansion (a mean increase of 334.8 ± 799 ha SD), which caused a higher forest loss rate. Consequently, as predicted, these reserves underwent a reduction in biodiversity as a whole (*SI Appendix*. Fig. S2) and in the abundance and richness of the disturbance-sensitive species (Fig. 4*A*). In contrast, the abundance and richness of disturbance-tolerant species were not related to forest loss rate, but to temporal changes in interpatch isolation distance. Disturbance-tolerant guilds proliferated in biosphere reserves where the interpatch isolation distance decreased. In turn, such a

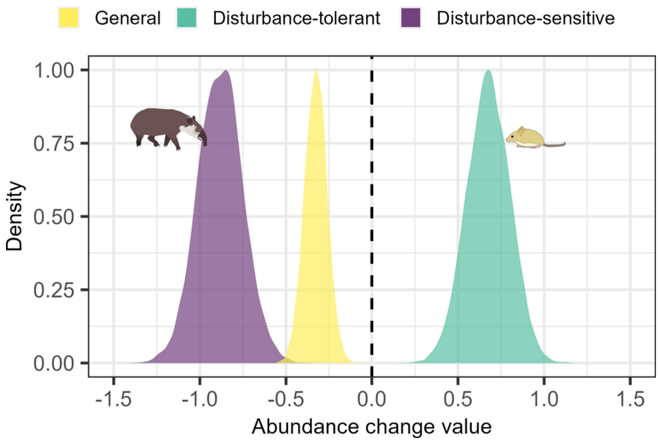

Fig. 2. Distribution of mean changes in abundance of all biodiversity guilds, disturbance-sensitive guilds, and disturbance-tolerant guilds during the last three decades in the studied Mexican biosphere reserves. The density plots resulted from bootstrap resampling with 10,000 iterations. The dashed line marks no change. In all cases, we found significant changes in abundance over time (estimated $\bar{x} \neq 0$, $P < 0.05$).

decrease was associated with increases in road density around and within reserves (an increase of 0.15 ± 0.07 $\mathrm{km/km^2}$), especially in those reserves where human population density was high (Fig. 4*B*). To understand the causes of such proliferation of disturbance-tolerant species, it is important to note that the reserves where the interpatch isolation distance decreased the most were reserves with lower forest cover and a greater number of relatively smaller forest patches (*SI Appendix*, Figs. S3 and S4).

Discussion

We found that over the last three decades, there has been a generalized biodiversity impoverishment across Mesoamerican biosphere reserves. This finding is consistent with the global pattern of biodiversity loss (35, 36), which is particularly acute in tropical forest reserves (15). However, our study adds to the very few that document long-term changes in biodiversity within tropical reserves (13) and goes further by documenting that such biodiversity erosion is strongly related to human pressures. We demonstrate that disturbance-tolerant guilds are replacing disturbance-sensitive ones and that such a winners–losers replacement (5, 8) was mainly driven by human demographic (population density) and socioeconomic (nonfarm occupation) factors within reserves. Thus, we provide insights into the causes of biodiversity changes within biosphere reserves, which can be highly valuable for improving management and biodiversity conservation strategies within and around reserves.

A general pattern of biodiversity loss is occurring in the studied Mesoamerican biosphere reserves. This parallels the biodiversity crisis facing the world in general (37), and also what has been documented in other protected areas. Laurance et al. (13) highlighted the deterioration of biodiversity in 60 tropical protected areas around the global tropics and identified some proximate anthropogenic activities involved. Gatiso et al. reported a recent decline in the abundance of mammals and birds in >75% of 114 European and African protected areas (38). Pollock et al. (14) documented a generalized decline of the bird community in Panama's protected areas. Studies documenting long-term changes in biodiversity are scarce but considering that many protected areas in the globe are under high anthropogenic pressure (11), it is likely that these patterns are consistent across multiple sites. Accordingly, around the world, only 28% of the protected areas remain free from deforestation (39). Yang et al. reported that about one-third of protected areas globally are inefficient in reducing forest loss (12). In other words, a biodiversity crisis is probably occurring not just in unprotected areas but also in protected areas (although presumably at a slower rate due to conservation efforts, see refs. (10) and (39)). However, the underlying causes of such a crisis have been poorly explored. Our study represents an advance in identifying the underlying drivers causing biodiversity impoverishment in reserves.

The biodiversity impoverishment is principally caused by a significant decrease in the abundance and richness of disturbance-sensitive species in more deforested biosphere reserves. This was the case of large-sized mammals and birds, apex predators, large-seeded trees, and epiphytic plants. However, we also found that primates and all amphibian and reptile guilds but one (venomous snakes) are decreasing in the studied reserves. This is unsurprising as all the former guilds comprise highly threatened forest-dependent species (40–42). Forest loss is known to eliminate tree species and associated plants (epiphytes) that constitute the structural and functional basis of old-growth forests (43, 44). Logically, removing trees, especially the largest ones, negatively impacts arboreal mammals, including primates and birds of prey (44). Similarly, ground mammals and birds highly dependent on forest resources, such as seed feeders, frugivorous, herbivorous, and insectivorous, are highly vulnerable to forest loss (27, 45–47). Large-sized vertebrates are particularly impacted because they require larger forest areas to maintain viable populations (48) due to their high energy requirements (49). This can explain why top predators and their relatively large-sized prey are declining in most biomes worldwide (50, 51)

Importantly, these biodiversity changes are mainly driven by agriculture expansion, which affected both the core and buffer zones of the reserves (*SI Appendix,* Table S13). This is an undesirable result, as land use change is prohibited within the core zone of biosphere reserves. However, the study reserves are inhabited by local communities whose economy depends strongly on subsistence agriculture (associated with slash-and-burn practices), which is a well-known driver of forest loss worldwide (52). What is not so well understood is the role of the local economy in driving forest spatial changes, and our findings indicate that promoting nonfarm occupation can prevent forest loss in biosphere reserves. This is consistent with previous findings. For example, forest loss rates seem to be lower in regions where economies are oriented to industrial (53) or touristic activities (54, 55). Similarly, there is evidence that in the absence of labor opportunities, local communities can develop agricultural activities with low revenues (mostly subsistence agriculture) (56). Under such circumstances, farmers are forced to increase the cultivated area to obtain profitable revenues, which promotes forest loss (57). In the study region, local communities with higher nonfarm occupation not only exert lower forest loss pressure on reserves but also have higher human welfare (21). Therefore, allocating higher resources to increasing nonfarm labor opportunities could potentially prevent forest loss and the extirpation of disturbance-sensitive species in forest reserves.

In contrast to disturbance-sensitive guilds, disturbance-tolerant ones are increasing their abundance and richness over time. This was the case of disease-vectoring invertebrates, lianas and climbing vines, pioneer trees, and exotic plants and animals—guilds that not only tolerate but can take advantage of the conditions prevailing in human-modified landscapes (58–61). Interestingly, these "winner" guilds proliferated principally in reserves where interpatch isolation distance decreased through time, and this change in landscape configuration was promoted by the expansion of

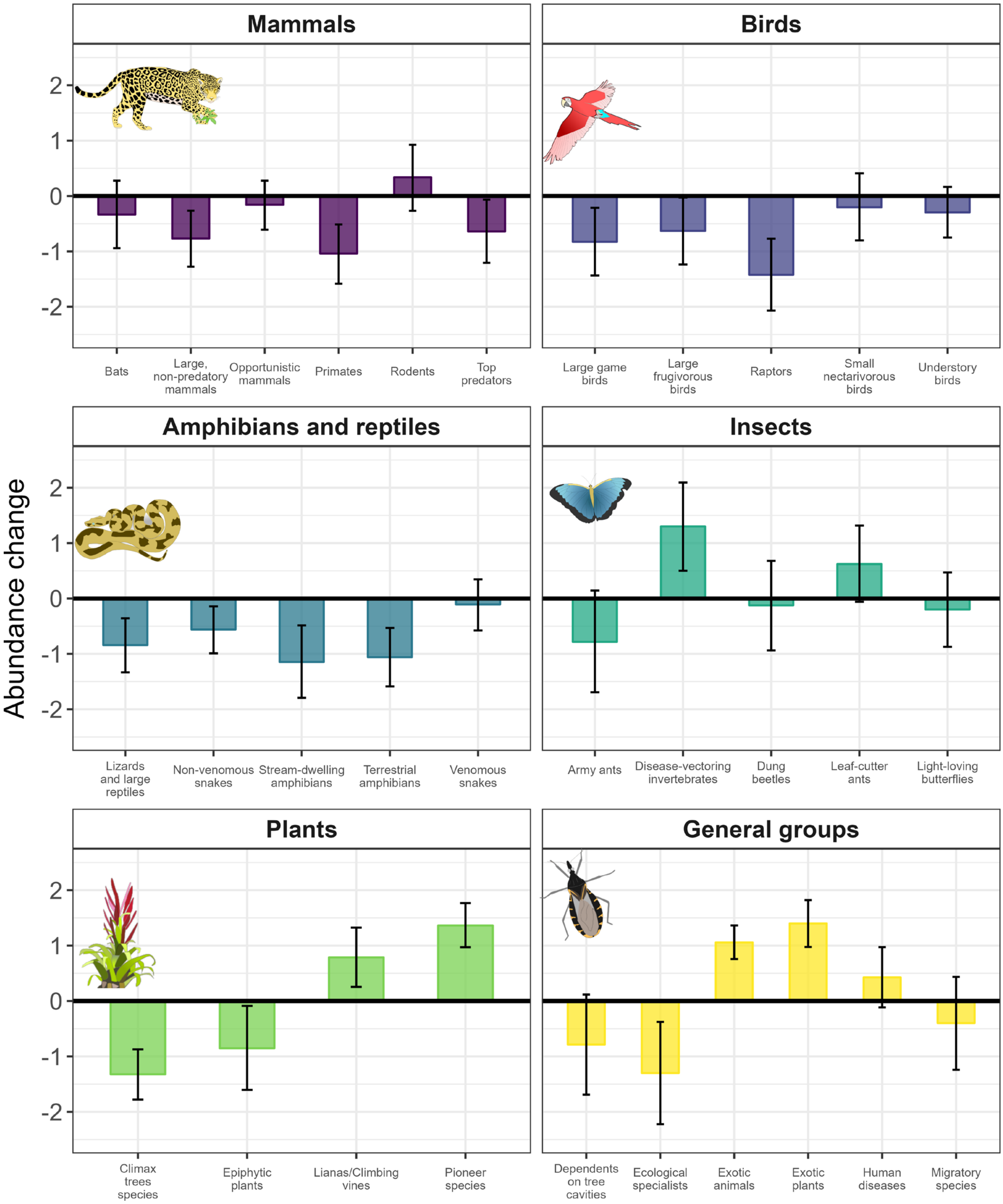

Fig. 3. Mean changes in abundance (±95% CI) of 31 biological guilds over the last 30 y in the studied Mexican biosphere reserves. The values derived from experts who provided information on relative changes of the biological guilds: 0, no change; 1, relative change <25%; 2, change ≥25% and <50%; and 3, changes ≥50% (see details in *Materials and Methods*). We used a bootstrap resampling with 10,000 iterations to estimate mean values and 95% CI. We considered that a change was significant if its 95% CI did not overlap zero (for details, see *SI Appendix, S1 Appendix*).

roads in reserves with higher population density. To understand the landscape context in which interpatch isolation decreased, it is important to note that isolation decreased mostly in less forested reserves composed of a high number of small patches, i.e., the higher the number of patches the lower the mean distance among them (*SI Appendix*, Figs. S3 and S4). Thus, on the one hand, the proliferation of disturbance-tolerant guilds could be related to a decrease in isolation, which can favor interpatch movements (e.g., seed dispersal and animal migration) and patch colonization (62). On the other hand, their proliferation could be also favored in reserves with many small and edge-affected patches, as forest edges are optimal environments for the recruitment of light-demanding pioneer plants (58, 63–65) and other winner species (8, 26). Whatever the causes of such a proliferation of winner species, our results indicate that there is an ongoing species replacement process in the studied reserves.

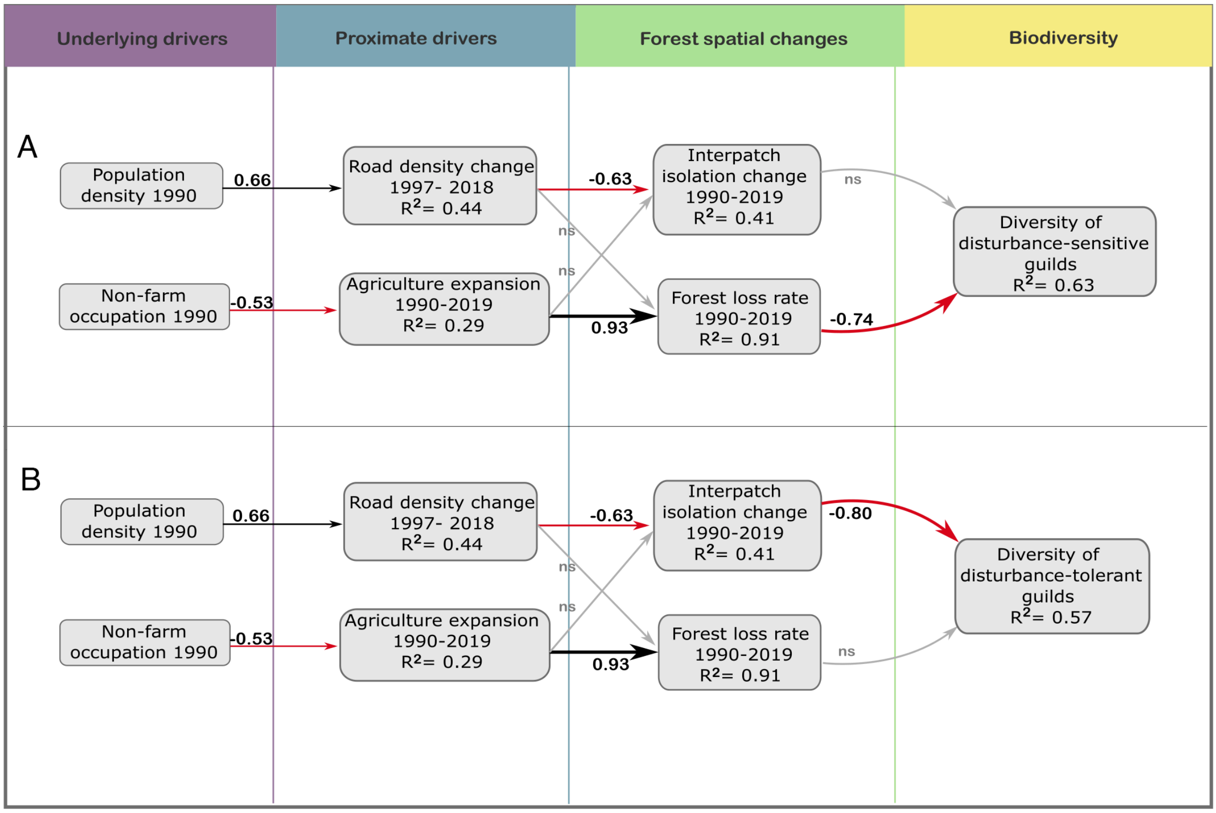

Fig. 4. Structural equation models (SEM) of the relationships between underlying and proximate drivers of forest spatial changes and their effects on the diversity (PCA scores of mean richness and abundance) of disturbance-sensitive (*A*) and disturbance-tolerant guilds (*B*). Significant positive and negative paths are indicated with black and red arrows ($P < 0.05$, thin arrows, $P < 0.01$ thick arrows), respectively, whereas gray arrows indicate nonsignificant relationships ($P > 0.05$). Values near the arrows correspond to standardized coefficients and indicate the direction (positive/negative) and strength of each path. Note that an increase in interpatch isolation change indicates that isolation decreased through time. Therefore, the negative effect of this variable on the diversity of disturbance-tolerant guilds (*B*) implies that these guilds proliferated in biosphere reserves where interpatch isolation decreased. Within the box of each response variable, we also show the R^2 value. The fitting of the models with the data was consistently good (model a: Fisher's C = 19.81, $P = 0.70$; model b: Fisher's C=15.93, $P = 0.89$).

This winners–losers replacement can potentially impact ecosystem functioning. Disturbance-sensitive and disturbance-tolerant species can play different roles in the ecosystem (8), so the replacement of the former by the latter could have strong ecological impacts. For example, long-lived, hard-wood, large-seeded, shade-tolerant tree species, typical of old-growth forests, have a much more important contribution to the aboveground biomass of the ecosystem than short-lived, soft-wood, light-demanding pioneer tree species (66). As carbon in tropical forests is mainly stored in the aboveground biomass (67), the replacement of shade-tolerant tree species by light-demanding pioneer species can significantly limit global carbon storage (68). Also, shade-tolerant tree species provide important resources for feeding and shelter to a plethora of invertebrate and vertebrate species (46, 69), which play critical ecological functions as pollinators, seed dispersers, primary and secondary consumers, and even as biological controls for small and medium-sized animal species associated with human-disturbed habitats (26). In addition, the depletion of top predator species (disturbance-sensitive species) triggers important cascading effects (46, 50), such as the increase of small-sized herbivore prey that in turn reduces the abundance of seedlings and juvenile trees (70). Therefore, the disappearance of disturbance-sensitive species can have strong negative consequences on the functionality of forest ecosystems (9, 71), and on the variety of contributions these ecosystems provide to people (72). This is a promising avenue for future research within biosphere reserves.

Biosphere reserves are known to be effective tools for preventing forest loss. However, our findings indicate that such a conservation effort has not prevented the impoverishment of biotic assemblages within several studied reserves (Fig. 2). A recent study has shown that socioeconomic context plays a significant role in the conservation of protected areas in Europe and Africa (38). This study suggests that regions with better socioeconomic conditions, such as higher human development, require fewer community conservation efforts as their populations exert less pressure on the ecosystem. Therefore, to increase the conservation success of the studied biosphere reserves we should conceive them as integral socioecological systems embedded into socioeconomic contexts. To prevent forest loss and its negative effects on biodiversity, in general (*SI Appendix*, Fig. S2), and on disturbance-sensitive guilds, in particular, we need to increase sustainable nonfarm occupation and planning population density around reserves. In Mexico, some programs promote employment in nonagricultural sectors in protected areas encouraged by both governmental and nongovernmental institutions (e.g., the conservation program for sustainable development and the program for temporal employment of the National Commission on Protected Areas, CONANP in Spanish). Furthermore, tourist activities in protected areas represent economic alternatives for the population that in other studies have shown to have positive effects on the livelihoods of local communities (73) and on reducing forest loss (74). Therefore, this research suggests that supporting and reinforcing this type of program and economic activities are needed to mitigate anthropogenic impacts on biosphere reserves (a list of alternatives is available in *SI Appendix*, Table S14).

Of course, all these strategies may be insufficient to preserve biodiversity if we do not avoid the impact of relatively "silent" but chronic threats such as the illegal extraction of flora and fauna. Thus, enforcing the boundaries of the reserve and its core zone is paramount. Considering that some of the documented changes in forest cover most likely stem from unpermitted activities (especially those that occurred in the core area), there is certainly an undeniable need to strengthen law enforcement efforts. Mexican institutions carry on patrolling activities in some protected areas, nonetheless (*SI Appendix*, Fig. S5), vigilance and administrative support are considered poor by the group of experts (*SI Appendix*, Fig. S6). Yet, this variable was not identified as a major underlying driver in our study (*SI Appendix*, Tables S11 and S12 and Fig. S7). In Mexico, reserve vigilance is carried out not only by rangers but also by local communities. Officially, there is one ranger per 261 km^2 of reserve (75). However, when considering local people who develop vigilance activities (76) this ratio decreases to one ranger per 65 km^2, which is comparable to the numbers found in European or US reserves (*SI Appendix*, Table S15). Nonetheless, this scenario is still far from the optimum suggested by the IUCN (one ranger per 5 km^2, see ref. (77)). Thus, involving local communities in vigilance activities could potentially reduce threats to biodiversity (e.g., poaching) and increase nonfarm occupation, thereby positively impacting conservation efforts.

Given that our study relies on expert knowledge, it is important to acknowledge the inherent limitations associated with this approach, including potential issues such as expert availability, bias, and uncertainties (78). However, the knowledge generated by our study serves as a valuable baseline that can aid in decision-making processes. Promoting and supporting the establishment of systematic long-term biodiversity monitoring programs that rely on empirical data, such as permanent plots, camera traps, and bird count points, is strongly recommended. Such programs would greatly enhance our understanding of biodiversity dynamics, identify cascading effects that threaten biodiversity (79), and improve the effectiveness of conservation efforts. A recent review by the International Panel for Biodiversity and Ecosystem Services highlights that engaging communities, particularly Indigenous people, in protected area management boosts reserves' effectiveness and fosters a mutually beneficial relationship between ecological and social aspects (80). Our finding that nonfarm occupation around biosphere reserves can decrease human threats to these areas is key for policymakers to consider in enhancing conservation efforts within the reserves of the Mesoamerican Biodiversity Hotspot.

Materials and Methods

Study System. We selected 14 Mexican biosphere reserves in the biodiverse Mesoamerican region (*SI Appendix*, Fig. S8 and Table S1). The reserves encompass various vegetation types, including tropical rainforest, tropical dry forest, temperate forest, cloud forest, and mangrove. They represent a range of human disturbance levels, with forest cover remaining at 44 to 98% and with different levels of human influence (i.e., human population and road extension, see *SI Appendix*, Table S16 and *S2 Appendix*). Vigilance efforts in the reserves involve federal institutions (CONANP and PROFEPA), nongovernmental organizations, and local community authorities (*SI Appendix, Fig.* S9).

Assessing Biodiversity Changes.

Biodiversity data. In the absence of long-term empirical data for multiple taxa, we employed an expert knowledge-based approach to gathering valuable information for urgent conservation decisions (28, 78). This approach, increasingly used in ecology and conservation, has proven effective in identifying biodiversity threats (81), studying forest succession dynamics (82), identifying knowledge gaps (83), and estimating biodiversity trends (13). We collected data on biodiversity changes in the studied reserves over the past three decades (sensu ref. (13)) by conducting electronic surveys using Google Forms (*SI Appendix*,*S1 Appendix*). These surveys focused on assessing the richness and abundance of 31 biological groups (hereafter guilds, which are groups of organisms with taxonomic or functional similarities). We followed a purposive sampling design where the focus was researchers and members of CONANP with extensive experience working with reserves biodiversity documentation and monitoring. The first and corresponding authors of this study began by collecting scientific articles that reported information on the richness and abundance of terrestrial vertebrates and plants in any of the studied reserves. Then, scientists with the most experience documenting the biodiversity of specific biological groups (e.g., mammologists, botanists, herpetologists, entomologists, ecologists, among others) were identified and invited to join the study. Also, the head director of each biosphere reserve was invited. Additionally, the collaborators suggested other researchers with extensive experience in the biodiversity of some of the reserves studied. Our research team is a diverse group, including experts from different academic backgrounds, genders, and areas of expertise. A total of 64 experts from various institutions, regions, and countries, with an average of 21 y of experience working in the reserves, participated in the surveys (*SI Appendix*, Fig. S10).

Each expert provided information on the level and direction of change (positive/negative) in richness and abundance for each guild. We categorized the changes as follows: no change (less than 5% change), small change (5 to 25% change), high change (25 to 50% change), and strong change (>50% change). Numeric values ranging from 0 to 3 were assigned to these categories, with positive values indicating an increase in abundance and richness and negative values indicating a decrease. Experts also provided a level of certainty for their answers, categorized as "high" if based on direct evidence, "good" if based on literature knowledge, or "speculation" if suspected without direct evidence. To ensure data certainty, we followed the criteria of Laurance et al. (13) and included data from 10 biosphere reserves with surveys conducted by at least three different experts. Data where researchers declared speculation about a particular change were excluded (*SI Appendix*, Fig. S11). All responses that met the above criteria were equally weighted in this study. Similarly to another study (13), we classified the more representative guilds ($n > 18$ surveys) into two groups: disturbance-sensitive (including large-sized animals and/or those at high trophic levels, and shade-tolerant plants) and disturbance-tolerant (including small-sized and habitat generalist animals, and light-demanding plants; Table 1).

Biodiversity changes. To identify temporal changes in the richness and abundance of general biodiversity (all guilds), we utilized bootstrap resampling with 10,000 iterations. Bootstrap estimation allowed us to determine mean values and 95% CIs that approximate population parameters (84). We tested the null hypothesis of no significant changes by examining whether the 95% CIs overlapped zero, using bootstrapping P-values estimator. The same procedure was applied to assess changes in disturbance-sensitive and disturbance-tolerant guilds. Additionally, we examined significant changes in the abundance and richness of each guild. The *boot* R package (85) was used for these analyses.

Testing the Causal Model of Biodiversity Changes.

Underlying drivers. Previous studies have highlighted the significance of various drivers, including human population growth and density (19, 86), market access (57), nonfarm occupation (21), vigilance (87), and governmental subsidies (88), in contributing to forest loss. To understand the underlying drivers of change, we focused on three categories: demographic, political/institutional, and economic factors. Data on these indicators were collected from reliable sources such as the National Institute of Statistics and Geography (INEGI) and the Mexican Commission on Protected Areas (CONANP) for the study period of 1990 to 2022. Demographic factors considered included population growth rate (1990 to 2020), population density (1990), and density of rural settlements (2000). Political/institutional factors encompassed governmental subsidies for agriculture (2013 to 2018) and a vigilance/administrative support index (VASI, year 2022) for protected areas. VASI measures the level of administrative support (personnel, budget, and infrastructure), ranging from 0 to 100, the highest support value (89). Economic factors considered were distance to cities (settlements with ≥15,000 people in

1990), the unemployment rate in 1990, and nonfarm occupation (proportion of the population engaged in industrial, professional, or services activities in 1990). Except for VASI, all variables were aggregated at the municipality level by averaging values for municipalities with at least 10% of their territory within the reserves (*SI Appendix, S1 Appendix*).

Proximate drivers. We examined two significant drivers of forest loss, road, and agriculture expansion, which have been previously identified in studies (17, 18). We assessed the change in road density between 2008 and 2019. To this end, we obtained data on the road network from the national road network for these 2 y and conducted kernel density analysis with a 5 km search radius and 100 m cell size. We calculated the average road density within each reserve and determined the difference between 2008 and 2019 to obtain a single value per reserve. To measure agriculture expansion, we calculated the annual agriculture cover rate change (r) from 1990 to 2019 using the formula:

$$r = \frac{A_{2019} - A_{1990}}{A_0} * \frac{1}{t_1 - t_0}, \qquad [\mathbf{1}]$$

where A_{2019} and A_{1990} are the areas covered by agriculture and pasture inside a reserve in 2019(t_1) and 1990(t_0), respectively, and A_0 is the area available in 1990 for agriculture expansion (i.e., area covered by forest). The agricultural area for each year was obtained from the supervised classification of Landsat images described below.

Forest spatial changes. To characterize forest and anthropic cover inside the studied reserves, we gathered Landsat images around the years 1990 and 2019. We performed a supervised classification of these images to identify the following land cover classes for each year: tropical rainforest, tropical dry forest, cloud forest, temperate forest, mangrove, shrubland, cropland, pasture, urban zones (cities and roads), and water bodies (*SI Appendix, S1 Appendix*). We merged these classes to create three major land-cover categories: forest (all-natural vegetation composed of trees and shrubs), anthropic areas (agriculture lands, pasturelands, and urban zones), and water bodies. We estimated the land-cover classification accuracy using a confusion matrix and land-cover truth points derived from ancillary data (*SI Appendix,* Table S18). We estimated that overall accuracy was 92.2% (±0.04 SD) for 1990 and 91.63% (±0.04) for 2019, which suggests that our forest spatial changes estimations are reasonably reliable.

Within each reserve, we calculated five metrics related to forest spatial patterns. We quantified the area of forest loss by assessing the land that was originally forested in 1990 but had transitioned to a different land cover class by 2019 (F_{2019}-F_{1990}). Then, we calculated the forest loss rate using formula 1 where Ao = F1990. Additionally, we assessed the impact of landscape attributes on plant and animal abundance and richness by measuring metrics such as the number of patches, mean patch size, mean interpatch isolation distance, and edge density for both 1990 and 2019. The relative change in each metric (RC) was calculated using a specific equation.

$$\mathrm{RC}_i = \frac{M_{2019} - M_{1990}}{M_{1990}}, \qquad [\mathbf{2}]$$

where M_{2019} and M_{1990} correspond to the value of metric i for the years 2019 and 1990, respectively.

Biodiversity indicators. We assessed the impact of underlying and proximate factors on general biodiversity and on guilds with varying sensitivity to disturbance. We estimated the mean abundance and species richness changes reported by experts for each guild in each reserve. Principal component analyses were conducted to synthesize this information. The scores of the first principal component represented general changes in abundance and richness, while scores of the first and second principal components indicated changes in disturbance-sensitive and disturbance-tolerant guilds, respectively (*SI Appendix*, Fig. S12). The scores were rescaled to a range of 0 to 1, with positive values indicating positive changes in diversity (abundance and richness).

Statistical analyses. We employed a multimodel inference approach (90) to select the most relevant variables and simplify the relationships (paths) in our framework (Fig. 1). Linear models were performed for each pathway using the *glmulti* package in R (86), and the model with the lowest Akaike Information Criterion corrected for small samples (AICc) was chosen. To identify important predictors of underlying and proximate drivers, linear models were used with each proximate driver as a response variable and all underlying indicators as predictors. Based on model results, we selected nonfarm occupation as the underlying driver for agriculture expansion and population density and nonfarm occupation as underlying factors for road density change (*SI Appendix*, Fig. S13). Forest loss rate and interpatch isolation were found to better predict biodiversity trends, so they were included in the structural equation model (SEM). Since the reserves are composed of two zones, we tested whether biodiversity changes were more related to forest spatial changes assessed in the core area, buffer area, or the whole reserve through linear models. Forest loss was significantly associated with the changes in disturbance-sensitive guilds at all the zones. However, we selected the model that included data from the whole reserve because it accounted for the lowest AIC (*SI Appendix*, Table S13). We also selected the interpatch isolation distance calculated at the whole reserve because only this was significantly associated with the changes in the disturbance-tolerant guild. The *picewiseSEM* package in R (91) was used for SEM analysis, examining the cascading effects of socioeconomic drivers on biodiversity changes. Separate SEM models were built for general biodiversity and disturbance-sensitive and disturbance-tolerant guilds. The overall fit of the models and missing paths were evaluated using Shipley's test of d-separation, which considers Fisher's C statistic and AIC. The data used in all these analyzes is available in (92).

Data, Materials, and Software Availability. Data on biodiversity changes, proximate drivers, underlying drivers, and forest spatial changes, for each studied biosphere reserve, as well as the code for structural equation models, can be consulted at https://doi.org/10.6084/m9.figshare.24083247 (92).

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