



An intermediate level of disturbance with customary agricultural practices increases species diversity in Maya community forests in Belize

Sean S. Downey ^{1,2,3✉}, Matthew Walker³, Jacob Moschler⁴, Filiberto Penados⁵, William Peterman⁶, Juan Pop⁷, Rongjun Qin^{3,8,9}, Shane A. Scaggs¹ & Shuang Song ⁸

Across the planet, Indigenous societies control, use, and manage large tracts of tropical forest that are crucial for combating climate change. Here we investigate whether customary Indigenous agricultural practices can increase forest species diversity using swidden (aka, slash-and-burn) agriculture. We examine the community lands surrounding two Q'eqchi' Maya villages in southern Belize using high-resolution multispectral imagery that we collected with drones, ground truth data related to land use and history, and a plant and tree biodiversity survey. We use computational methods including simulation and Bayesian modeling to analyze the relationship between spectral diversity, forest diversity, and landscape disturbance. Our key result, replicated in both villages, is that the highest level of spectral diversity (a proxy for forest diversity) is associated with an intermediate level of forest disturbance. In conclusion, we suggest that concepts from complex adaptive systems can provide an important conceptual framework for understanding how ecosystem enhancement can emerge from customary Indigenous land use practices.

¹ Anthropology Department, The Ohio State University, Columbus, USA. ² Sustainability Institute, The Ohio State University, Columbus, USA. ³ Translational Data Analytics Institute, The Ohio State University, Columbus, USA. ⁴ Moschler Robotics, Hyattsville, Maryland, USA. ⁵ Galen University, Cayo, Belize. ⁶ School of Environment and Natural Resources, The Ohio State University, Columbus, USA. ⁷ Crique Sarco Village, Toledo District, Belize. ⁸ Department of Civil, Environmental and Geodetic Engineering, The Ohio State University, Columbus, USA. ⁹ Department of Electrical and Computer Engineering, The Ohio State University, Columbus, USA. ✉email: downey.205@osu.edu

A 2021 report by the Forest Carbon Partnership Facility (REDD+) highlights the importance of recognizing Indigenous People's land rights and institutions for meeting global conservation goals and supporting local livelihoods^{1–3}. Land controlled by forest-based communities contains up to 17% of all carbon found in tropical and subtropical forests⁴, and the communities make crucial contributions to reducing deforestation rates⁵, global carbon emissions^{6,7}, and nitrogen fixation⁸. The importance of recognizing Indigenous land tenure is clear⁹; however, much less is understood about how land use decisions that are made by Indigenous households¹⁰ affect biodiversity patterns at regional and landscape spatial scales, particularly when the development of secondary forests follow multiple pathways that are contingent upon complex interactions among successional dynamics, landscape-level variables, and socio-economic factors, all of which interact at local, landscape, and regional scales¹¹.

The complexity of this system, its overall unpredictability, the importance of customary cultural practices, and the lack of models and information linking household-level land use decisions to large-scale sustainable patterns make it difficult for Indigenous peoples to convince policymakers to support practices and institutions that may seem distantly related to conservation, but which may be critical to Indigenous cultures and livelihoods. A better scientific understanding of how Indigenous practices relate to large-scale ecological dynamics will also help national and global climate change initiatives to more effectively support Indigenous peoples in sustaining their contributions to combating climate change. Further, systematic investigation of the mechanics and dynamics of Indigenous land use and local ecological processes can support Indigenous peoples' efforts by helping them present the strongest possible argument in dialog with policymakers.

Our approach for studying Indigenous swidden landscapes expands on a model proposed by R. Bliège Bird that demonstrates how anthropogenic intermediate-scale disturbances are an emergent property of human-environment interactions, and that they can shape environments through space and time and thereby pattern the “sustainability of subsistence”¹². Here, we extend this model to test the hypothesis that intermediate-scale swidden disturbances can increase tropical canopy tree diversity that is inferred from spectral analysis in the community forests in two Maya villages in southern Belize.

Debates about customary ecosystem management center on whether environmental conservation must be an intended outcome of the actions of Indigenous communities (e.g., ref. 13), whether it can be an unconscious by-product of human action and the result of trial-and-error coevolution (e.g., ref. 14); or, alternatively if both processes are required¹⁵. Studies in Mesoamerican agroecology have shown that both ancient and modern Maya communities enhanced biodiversity, soil fertility, and ecosystem health in tropical forests by coupling land use and management strategies, detailed ecological knowledge, and human labor, with ecosystem processes such as seed dispersal, soil fertility recovery, and forest succession dynamics^{16–19}. In some cases, the overt goals of these activities are not only to provide for immediate consumption, but to enhance the ecosystem with species that are useful to humans, to improve soil fertility, and over time to create a forest that has been fundamentally shaped by human activity²⁰. A prototypical example of intentional forest modification is the Yukatek Maya Pet Kot—a managed tree garden—that becomes an ecological niche in an otherwise harsh environment that is used to cultivate culturally and economically important species²¹. Another example is a sophisticated agroforestry strategy of intercropping and field rotation that permits shorter fallow periods and increased productivity that has been

labeled “high-performance milpa”²². Studies of the long-term effects of Maya forest management have also detected links between ancient “forest gardens” and modern species composition in and around archeological sites using pollen cores²³ and in forest inventory surveys²⁴. A study of contemporary swidden cultivation in the Selva Lacandon examined animal and plant diversity and found that intermediate-sized swidden disturbances increase overall diversity, and that bats played a key role in forest succession in different forest patches such as cornfields, fallow swidden fields, cacao plantations, and primary rainforest plots²⁵. Thus, there is evidence that the Maya use customary environmental knowledge and practices in order to manage forest ecosystems intentionally and that these practices conserve and enhance soil fertility and species composition in local ecosystems.

However, there is also evidence from Indigenous subsistence systems around the world that suggests intentionality may not be necessary to improve long-term forest outcomes²⁶, providing an alternative theory based on principles from complex adaptive systems for explaining sustainable customary ecosystem management^{27,28}. For example, coordinating planting schedules among Balinese farmers can optimize rice harvests in a complex of irrigation canals and rice terraces without top-down management of cropping patterns²⁹, and controlled burning by Aboriginal Martu increases the population density of sand lizards and kangaroos in fire mosaics in Australia^{12,30,31}. Other examples of emergent ecosystem enhancement include the population level of key species such as Baird's tapir in Honduras³², Baka hunter-gatherer yam gardens in the Congo Basin³³, and clam gardens in the Pacific Northwest³⁴. In our own work, we conducted public goods experiments in the same two Q'eqchi Maya villages in Belize that are sites in the current study, and we found that framing the experiments using social norms related to cooperation and sanctioning improved outcomes for the simulated community forests even when participants were not allowed to communicate³⁵. One way this can occur is a process of “emergent sustainability” where sustainable outcomes emerge out of the interactions among the low-level household, social, cultural, and ecological system properties and dynamics²⁸. Following Bliège Bird¹², we suggest intentionality and emergence are complementary explanatory models and that characteristics of complex adaptive systems²⁷ may help explain how customary swidden practices can affect the trajectories of large-scale tropical forest ecosystems and provide functional and efficient pathways to sustainable forest outcomes.

A key question for theories of swidden agroecology is to explain how reliable and sustainable harvests are affected by the regrowth trajectories of secondary forests, which are very difficult to predict due to the complex and non-linear interactions between forest succession dynamics, landscape-scale properties, and social processes¹¹. In some cases, even nearby swidden fields with the same fallow age, soil type, and climate conditions recover along different successional pathways and result in different species compositions, structures, and functions^{36,37}. This complexity may be one reason that despite the substantial body of evidence for effective Indigenous management of tropical forests, swidden remains widely thought to have negative impacts that lead to environmental degradation and deforestation³⁸. So, on the one hand, ethnographic and ethnohistorical research suggests that swidden societies possess significant cultural knowledge about the dynamics of tropical forest succession³⁹ and that patterns of swidden clearings reflect natural forest succession dynamics that optimize or enhance ecosystem services^{40–42}; while on the other hand, human activity has been shown to reduce functional redundancy and diversity across human land use gradients^{43,44}. Nevertheless, a 2022 remote sensing analysis found less permanent forest loss in southern Belize where the most

concentrated practices of swidden occur than in other parts of the country⁴⁵.

A complex adaptive system model for intermediate-level swidden disturbance. Clearly, many important questions remain regarding the socioecological dynamics of swidden systems, including how ecosystem variables are affected both positively and negatively by human activity, the socioecological mechanisms driving these effects, and understanding the spatial scales at which these effects operate and can be detected. Our study deepens our understanding of the landscape-scale effects of customary Maya swidden practices by analyzing whether intermediate levels of swidden disturbance increase the spectral diversity of canopy tree species in community forests at large spatial scales. The intermediate disturbance hypothesis (IDH) proposes that the diversity of competing species should be greatest when the frequency or intensity of disturbances are neither too large nor too small⁴⁶ (see Supplementary Note 6 “Intermediate disturbance model”). Thus, one mechanism for ecosystem enhancement is when the spatial and temporal pattern of swidden disturbances are intermediate in size and frequency, leading to the creation of diverse niches for rare species and a temporary release from interspecific competition²⁵. The IDH is highly debated in community ecology⁴⁷, but we suggest that it is a plausible pattern to emerge in tropical forests from the household-level decisions and activities related to swidden agriculture⁴⁸. To investigate this, we draw on concepts from complex adaptive systems to hypothesize that increased spectral diversity at intermediate levels of disturbance may be an emergent property of the interaction between Maya land use decisions and tropical forest ecosystem dynamics^{27,49}. We use the term “spectral diversity” to refer to a way of quantifying multispectral information with high spatial resolution to differentiate forest species or groups of species based on how their visible traits correspond to the reflectance values in each pixel⁵⁰. Higher levels of spectral diversity correspond with higher levels of functional diversity⁵¹, and increased species diversity is widely understood to contribute positively to ecosystem functioning, productivity, stability, invasibility, and nutrient dynamics⁵². A non-linear response of a dependent variable such as the convex curve that characterizes the intermediate disturbance hypothesis is a key characteristic of a complex adaptive system. In this case, there are two stable attractors: a deforested state with high levels of disturbance (low diversity), a forested state with low levels of natural disturbance (higher diversity), and an unstable enhanced intermediate disturbance state (highest diversity), which is documented in our study. Because the enhanced diversity state is unstable, it requires human intervention to maintain: energy and coordination of labor to create disturbances, and social norms to prevent over-exploitation³⁵.

Following Bliege Bird, we propose a model that can explain how enhanced spectral diversity can emerge from household-level decision-making in Maya communities: swidden mosaics are centered around the village and adjacent roads because it diminishes the energetic costs of additional travel time to swidden fields^{12,53}, but after multiple cultivation cycles, community forests evolve into spatially complex mosaics with emergent properties⁵⁴. In our model, most of the decisions related to swidden cultivation are made within households and they are governed by social norms and customary practices. Key decisions include the size and location of swidden clearings, the timing and frequency at which new fields are cleared from mature forest, and when fallow fields are replanted. The effects of these decisions aggregate across all households to determine the intensity of disturbance across the community’s forest. The degree and

characteristics of swidden disturbance will interact with ecosystem dynamics such as soil fertility recovery, seed dispersal, and forest regeneration to determine the characteristics and composition of the emergent forest mosaic. Under this model, the intermediate disturbance hypothesis predicts that spectral diversity will peak at intermediate levels of swidden disturbance¹¹.

Study area

The approximately 18,000-acre study area in the Toledo District, Belize, encompasses the community forests of two Maya villages, each of which includes a large swidden mosaic, adjoining areas consisting of undisturbed forest, and a mix of land types including undisturbed lowland tropical forest, rivers, secondary forest, and riparian areas. Crique Sarco was settled in 1910 and Graham Creek in 1998, and both are linked to a market town by trails and a dirt road⁵⁵. The lead author has been working in these villages since 2005. In 2018 we conducted fieldwork including a drone scan, land use mapping, and a comprehensive household survey in both study villages. The household survey indicated that subsistence-oriented swidden was ranked as the first or second most important livelihood support in 75% of the households in Crique Sarco (76 out of 83 households surveyed) and 93% in Graham Creek (14 out of 15 households surveyed). In addition to customarily using swidden to cultivate maize, ground foods (yam, potato), onions and spices, some households use lands for commercial purposes such as cacao, pineapple, or cattle pasture^{56,57}.

In most Maya communities in southern Belize, swidden is the most common type of land use^{10,56}. Swidden is known in Q’eqchi’ Mayan as k’atk’al (a first corn crop planted in April/May), saqiway (a second crop planted in December), or in much of Central America by the Spanish-introduced term milpa. Decisions regarding the size, location, frequency, and use of fields for subsistence and cash crops are normally made at the household level^{10,58}. Historically and into the present, groups of men and women worked together on labor-intensive tasks such as forest clearing and planting, and the customary rituals and practices that sustained many Maya communities constitute an important form of Indigenous cultural identity, and help to resist colonization and globalization during the modern period^{10,55,59}. The swidden agricultural cycle involves choosing a forest location for cultivation, cutting, drying and burning large trees and above-ground biomass, and planting and harvesting important crops, primarily maize but also yucca, sweet potato, yam, chili pepper, and other crops⁵⁶. This swidden sequence may be repeated for two or more years before the location is allowed to return to a forested state, while a new location is used. Customarily, households retain exclusive usage rights to previously cleared locations. These land use decisions are typically made in the context of household demand and growing family size that may increase the need for cultivable land and cash income, social factors such as the availability of labor, the desirability of the intended land use, and environmental factors such as land availability and suitability for cultivation⁵⁸.

Approach

We use methods from remote sensing, ecoinformatics, and landscape ecology to examine how the size and distribution of swidden disturbance relate to the spectral diversity of the forest canopy using reflectance values from visible and invisible regions of the light spectrum (see “Methods”). Previous studies investigating ecosystem enhancement typically focus on focal areas or focal species^{31,33,49} or a small number of forest inventory transects^{40,60}, however, forest inventory studies that adequately sample across the entire swidden disturbance gradient are rare⁴⁸.

Our study documents spectral diversity of the forest canopy and levels of landscape disturbance in the primary swidden use areas for both villages in the study area using drones and a multi-spectral sensor. We quantify the intensity of landscape disturbance that results from the timing, location, and intensity of swidden activities by calculating edge density from a classified land use history map that models the complete swidden disturbance gradient spanning forest successional stages, primary and secondary forests, active cornfields, and pastures. We operationalize forest species diversity using the concept of “spectral species”, which results from k-means clustering of raw multi-spectral reflectance values (see “Methods” and ref. 50). We then sample the landscape, and model the relationship between the two landscape statistics to assess whether an intermediate level of landscape diversity is related to a higher level of spectral species diversity.

During April 2018 (the dry season), we used long range drones flying at 1500 feet and fitted with a 5-band multispectral sensor to scan approximately 18,000 acres surrounding both villages. During the scanning, we worked with local mapping teams with extensive knowledge of community forests and land use history to survey as much of this area as possible and collect ground-truthing data about land use history, fallow age, and canopy tree species diversity using forest inventory plots. Our analysis involves classifying reflectance values in the remotely sensed multispectral images using the community mapping team’s land

use history data, identifying and validating spectral signatures in the remote sensing data that can be used to infer canopy tree species diversity⁵⁰, quantifying disturbance using landscape fragmentation statistics, sampling sub-regions of the landscape using a hexagonal grid, and modeling the relationship between spectral diversity and landscape disturbance (see “Methods”).

Results

To present our results, we address three questions: (1) How does spectral diversity associate with the land use classification that results from historical land use patterns in the study villages? (2) How does landscape fragmentation vary among land classes and across swidden mosaics? And (3) Is spectral diversity greatest at intermediate levels of swidden disturbance?

How does spectral diversity associate with land use classes? The spectral variation hypothesis states that spectral variance in remote sensing images correlates with habitat heterogeneity and species diversity^{61,62}. The land use class of each pixel is determined using field observations of land class and fallow age assigned by the community mapping team and a semi-automated land use classification algorithm (see Fig. 1a, and Supplementary Note 2 “Land use classification”). Our process for inferring species diversity uses principal component analysis and k-means clustering to assign a spectral species to each raster pixel⁵⁰. Patches are defined as a set of contiguous pixels sharing a land use

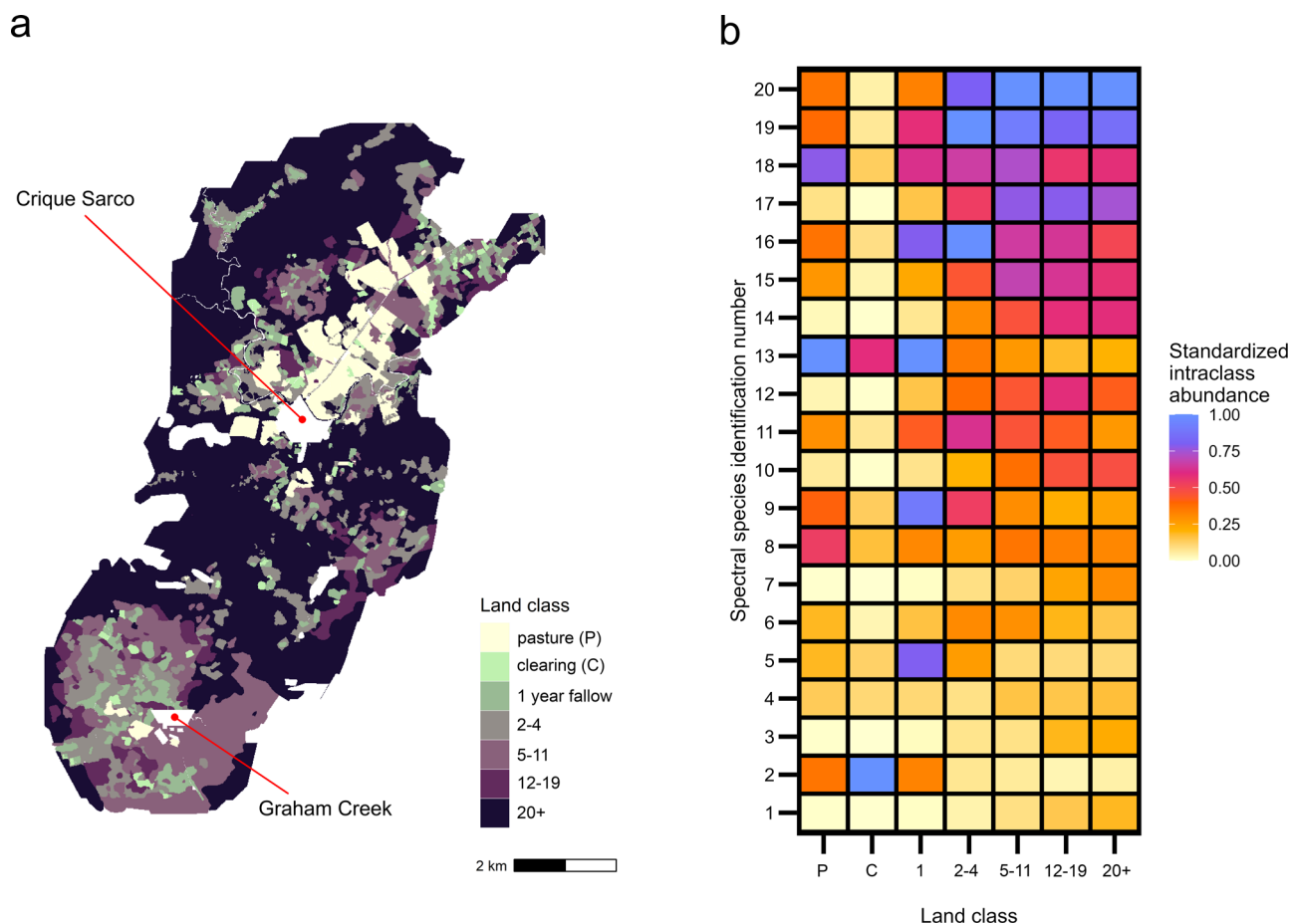


Fig. 1 Land use classification map and spectral species composition. **a** Land use map generated from drone imagery and GPS data that shows the locations of the village centers in 2018 in relation to the classified landscape. Spatially masked areas are shown in white. **b** Spectral species composition for each land class where each pixel has been assigned a spectral species identification number. To illustrate differences in species composition between land use classes which vary in area, relative spectral species abundance is calculated by dividing each species abundance by the maximum species abundance within each class. Thus, the most abundant spectral species within each class will have a standardized intraclass abundance of 1.

class and based on these assignments, we calculate the spectral alpha diversity as the Shannon’s diversity of spectral species for all pixels that share a land use class. Class-level statistics are aggregated summaries of all patches belonging to each class. Effective spectral species diversity (H) is low in early fallow classes such as 1 y ($H = 13.5$), 2–4 y (15.3), 5–11 y (15.7), higher in 12–19 y (16.1) and 20+ forest (16.5), and lower in pastures (12.8) and recently disturbed areas such as 2018 clearings (7.35).

Asymptotic species accumulation curves suggest adequate sampling and show that, overall, older land classes exhibit a more diverse composition of spectral species (See Supplementary Fig. S13). We found that the variation in spectral species composition is a function of land use class and that the distribution of spectral species within each class constitutes distinctive spectral signatures (Fig. 1b). The median patch area is 0.76 ha, so arbitrary spatial sampling units greater than this size will tend to represent differences in diversity, nestedness of patches, and spectral beta diversity (see Supplementary Note 5 “Landscape sampling framework” and Supplementary Figs. S17 and S18).

How does landscape fragmentation vary among land classes and across swidden mosaics? Forest fragmentation occurs when a large contiguous area of forest is subdivided into smaller, geometrically complex and sometimes isolated patches due to human processes such as land clearing and natural processes such as tree falls and succession⁶³. The IDH proposes that the diversity of plant and tree species will be highest when the spatial and temporal intensity of forest fragmentation is at intermediate levels. Table 1 reports the relationship between each land class and a set of fragmentation statistics that minimally covary and which encompass different dimensions of fragmentation^{64,65}. Two key variables are patch area, which measures patch size in hectares, and edge density which measures the total length of edges between adjacent patches of different classes in meters, divided by the total landscape area in square meters. Fragmentation tends to be lower in areas that had been cleared for cultivation in 2018, and increases with the age of the class (1 y, 2–4 y); however, in older classes (5–11 y, 12–19 y), edge density decreases as ecosystems transition away from cleared states, and individual patches begin to merge. Mean patch area and variation is high in the

20+ y forest class due to natural disturbance processes and it may also be an edge effect of landscape sampling. Overall, edge density decreases with distance from village (Fig. 2), though significant variability remains at all distances due to the greater variety of land uses near residential areas, the presence of pastures, and natural disturbances in mature forest. Planting high productivity grasses and fencing also homogenizes the landscape and introduces new pressures on ecosystem structure and function due to the intentional exclusion of native species^{66,67}. The conversion of community forests to cattle pasture is relatively recent in the study area (post 2000), but cattle ranching is now important for some Maya households’ livelihoods, even though it was not a customary practice in the past. When conversion to pasture does occur, it is common to leave palms and other tree species standing for shade and for use as building material (as noted elsewhere in Latin America, see ref. 68). Overall, this practice increases landscape heterogeneity, causing the pasture class to have a higher level of fragmentation than the least fragmented land class, 2018 clearings.

Is spectral diversity greatest at intermediate levels of swidden disturbance? We analyze the relationship between spectral species diversity and forest disturbance using multilevel Bayesian modeling. Spectral species diversity within each hexagon was modeled as a non-linear quadratic relationship with edge density. The social and ecological dynamics of forest conversion to pasture differ significantly from customary swidden practices, so we include a term to explain the variance that results from the presence of cattle pastures (see “Methods”, Supplementary Note 7 “Full model introduction”, and Supplementary Note 11. Summary of model reported in main paper). The relationship between edge density and spectral species diversity was notably non-linear for both villages, and the convex shape of this relationship is consistent with the predictions of the IDH (Fig. 3a; Supplementary Table S8). The strength of this effect is greater in Crique Sarco, likely because the swidden mosaic in Graham Creek has fewer samples with high edge density.

To understand and visualize the spatial effect of disturbance on effective spectral species diversity, we made spatial predictions using an intrinsic autoregressive model for areal data (ICAR) at three different levels of edge density (Fig. 3b, c). Notably,

Table 1 Fragmentation metrics for each land use class.

Class metric	Pasture	2018 Clearing	1 y	2–4 y	5–11 y	12–19 y	20+ y
AI ^a	98.57	96.77	97.34	97.59	98.72	98.44	99.36
Area (Mean)	7.72	1.27	2.09	3.49	7.90	5.93	32.53
Area (SD)	17.41	1.32	3.62	10.38	36.52	7.97	311.96
ED ^b	12.20	6.72	19.29	42.06	23.75	13.80	39.49
NND ^c (Mean)	143.77	204.47	104.08	61.11	92.21	147.64	54.22
NND (SD)	364.76	235.79	136.77	97.54	130.91	244.08	71.70
Frac ^d (Mean)	1.12	1.09	1.10	1.13	1.11	1.10	1.13
Frac (SD)	0.07	0.06	0.05	0.08	0.07	0.05	0.08
LPI ^e	1.75	0.12	0.41	1.91	5.61	0.64	49.48
PD ^f	0.88	1.15	2.52	3.70	1.71	1.01	1.66
PLAND ^g	6.76	1.46	5.28	12.91	13.49	6.01	54.09
Shape ^h (Mean)	1.78	1.55	1.62	1.93	1.77	1.65	1.82
Shape (SD)	0.73	0.45	0.48	0.86	0.72	0.40	1.09

^aAggregation Index: 0–100, increases when a class has more like adjacencies.

^bEdge density: 0 if the class has a single patch, increases as landscapes become more fragmented.

^cNearest neighbor Distance: edge-to-edge Euclidean distance between patches in class.

^dFractal dimensions: equal to 1 when a patch is square, increases as shape becomes more irregular.

^eLargest patch Index: percentage of the landscape covered by the largest patch in each class.

^fPatch density: patches per 100 hectares.

^gPercentage of landscape: the percentage of the entire landscape covered by all patches in class.

^hShape Index: ratio of the perimeter of a patch and a maximally compact perimeter of equal area (a circle). AI, ED, LPI, PD, PLAND do not include standard deviations because they are aggregated for each class at the landscape level.

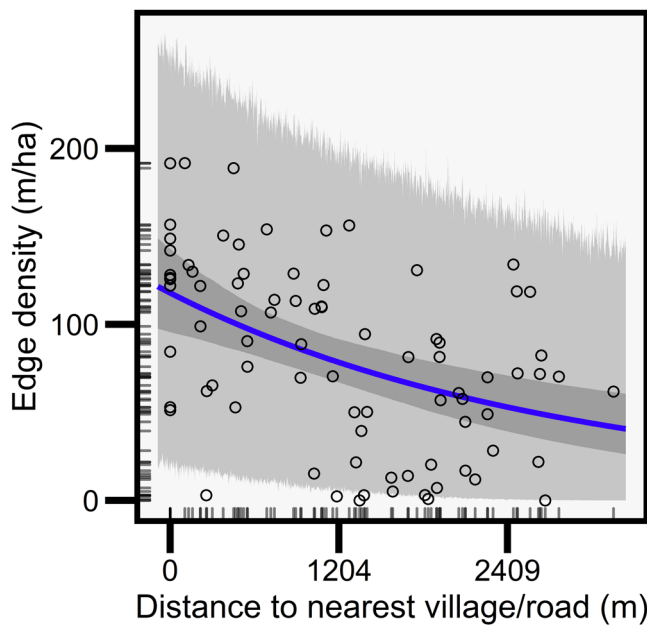


Fig. 2 Disturbance decreases with distance from village or road. Edge density decreases as a function of distance from the village center or road using a contiguous sampling grid (hollow points, axis ticks). Blue line shows fitted trendline. Dark shaded regions indicate 89% fitted credibility intervals and light shaded regions indicate 89% predicted credibility intervals.

predictions using the mean observed edge density produce the highest overall mean effective spectral species diversity and lowest standard deviation, which is consistent with the IDH.

Discussion

As stewards of a significant proportion of the planet's remaining tropical forests, Indigenous communities are increasingly drawn into discussions about how to enact policies designed to combat climate change. Key questions in Indigenous management of tropical forests ask, how do land use decisions that customarily occur at the household level and community governance interact with complex ecosystem processes at local, landscape, and regional scales? And, under what conditions do household decisions affect landscape processes and patterns that support or enhance tropical ecosystems and global climate change initiatives? The Maya people in Belize are an example of an Indigenous society that is at the nexus of the global Indigenous rights movement and biodiversity conservation efforts. In 2010, the Government of Belize joined REDD+, the United Nations program to reduce emissions from deforestation and forest degradation in developing countries⁶⁹. After a decades-long legal battle with the Government of Belize, courts upheld customary land rights for the Indigenous Maya of southern Belize and emphasized the need for free and informed prior consent when accessing Maya community lands^{70,71}. However, coming amid a protracted battle and sometimes contentious relationship with the Maya communities over customary land tenure⁷², the arrival of REDD+ in Belize now requires Maya leaders and communities to actively engage in negotiating customary land use practices, new forms of community governance, global conservation organizations, and climate change policy and planning regulations.

Unlike large-scale industrialized societies where top-down institutions are conceived to manage and protect natural resources, democratically elected Maya village leaders have a less direct role in actively protecting community forests. Rather, in many contemporary Maya communities, land use decisions

predominantly occur at the household level¹⁰. Families navigate a myriad of social and economic challenges⁷³, encompassing interpersonal dynamics, various political levels (local to international), and institutional influences, both governmental and non-governmental. Additionally, they respond to global market fluctuations, especially in lumber and fuel, fulfill religious and ceremonial obligations, and address the fundamental needs of feeding and educating their families. Many if not most of the ecological dynamics in tropical forests are also complex and operate across spatial and temporal scales, making the management of tropical forests both a theoretical and practical challenge⁷⁴. Swidden agriculture remains a critical livelihood strategy in many Maya households, so understanding how customary Indigenous cultural practices affect these land use decisions and tropical ecosystem dynamics, including evidence for emergent sustainability²⁸, has both theoretical and practical importance.

We propose that concepts from complex adaptive systems about the emergence of system-level properties from lower-level dynamics²⁷, and from landscape ecology regarding non-linear landscape dynamics and spatial heterogeneity⁷⁵ provide new insights into the resilience of swidden agriculture, and ways it can support sustainability⁷⁶. There is no doubt that there is a vast repository of customary ecological knowledge that Maya farmers draw upon, and social skill is required to manage the cultural norms of labor reciprocity as well as requisite ritual obligations and taboos. Yet, complex adaptive systems research shows that non-deterministic system-level properties can also emerge spontaneously from lower-level decisions in complex socioecological systems²⁹. Often, these lower-level dynamics involve simple decision rules that occur at lever points, which are places in a complex system where a small change can cause large positive changes in the system overall^{77,78}. These ideas help explain how a small number of decisions that Maya households make related to the placement and timing of swidden fields can affect landscape-scale biodiversity.

Landscape ecology suggests that ecosystem disturbances, such as those made by swidden farmers clearing fields for cultivation, can create emergent spatial patterns through non-linear feedback between ecosystem processes such as nutrient cycling, seed dispersal, biomass accumulation, and biodiversity⁷⁹. The essential tools of swidden agriculture are little more than an axe, machete, and a source of fire; from the perspective of landscape ecology, there are three primary decisions that will have a disproportionate impact on the development of swidden mosaics: (1) where to place a field; (2) whether to replant an existing field or move to a new location; and (3) the size of the area to clear and cultivate. These decisions will have a significant effect on the spatial structure of the swidden mosaics that develop over time and, therefore, they constitute an important lever point that may lead to the emergence of intermediate-scale landscape mosaics that support household livelihoods by maintaining or even enhancing key ecosystem structures and functions like seed dispersal, robust seed banks, and diverse forest canopies. We do not suggest that the emergent properties of swidden agriculture are solely responsible for sustainable forest outcomes; rather, customary ecological knowledge, cultural practices, community governance and social norms all inform Maya households as they make land use decisions that become indirect drivers of change that can increase ecosystem resilience and sustainability by maintaining community forests in an emergent intermediate state of disturbance⁸⁰. The relative efficiency of these decision rules affords Maya swidden agriculture flexibility, adaptability, and resilience in the context of the complex social, economic, political, and environmental dynamics of contemporary village life.

Our study demonstrates that Indigenous communities, supported by customary practices and cultural norms, can maintain

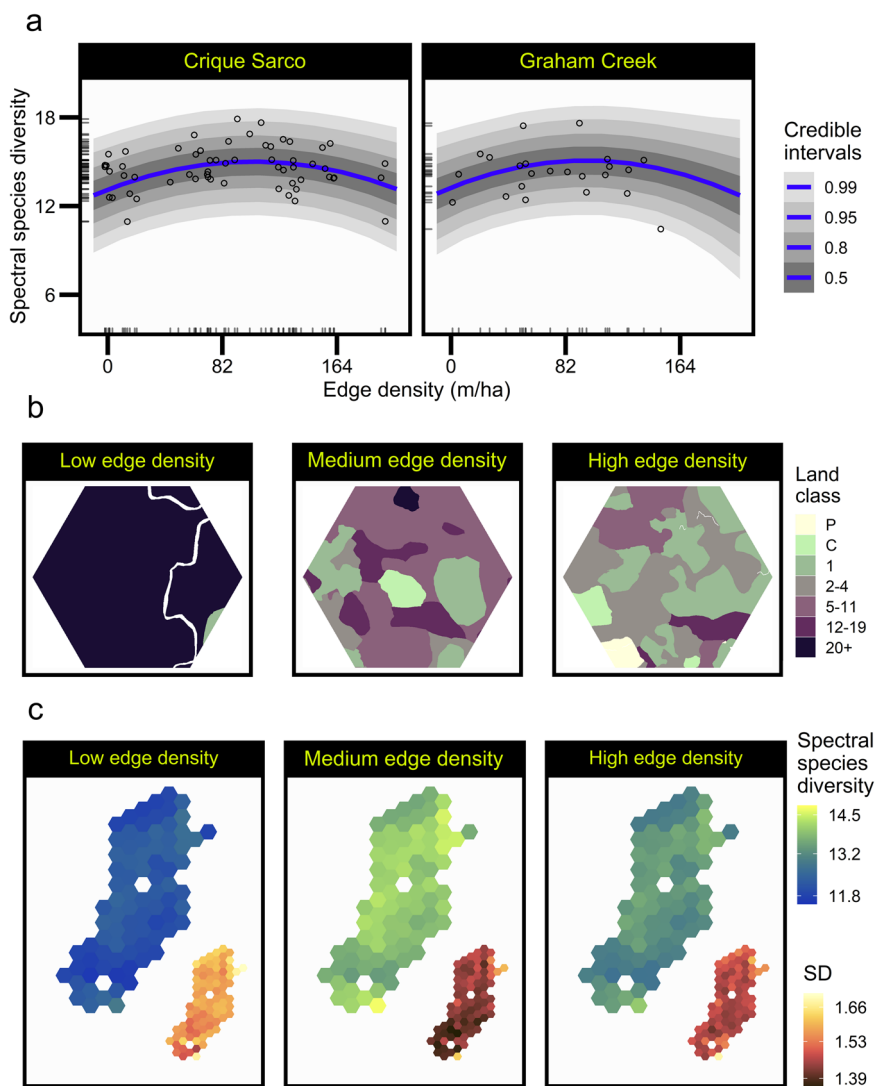


Fig. 3 The relationship between swidden disturbance and spectral diversity. **a** Each point represents one hexagonal sampling unit (see Supplementary Note 5 “Landscape sampling framework”). Measured values (points, ticks) and posterior predictions indicate a convex relationship between edge density and effective spectral species diversity, suggesting that the highest level is at intermediate levels of disturbance in both villages. **b** Examples of low (minimum $ed = 0$), medium (mean $ed = 82$), and high (maximum $ed = 164$) edge density hexagons. Low and high edge density hexagons are defined as one standard deviation below and above the mean (medium), respectively. **c** Hexagonal grids show model predictions of effective spectral species diversity. Each hexagon sampling unit shows the predicted mean when there is zero pasture and average levels of 20+ forest. Small hexagonal maps show the standard deviation around the predicted mean values.

swidden mosaics in a quasi-equilibrium intermediate disturbance state that supports or even enhances underlying ecological dynamics. For example, a higher density of diverse land classes can provide more primary habitats and smaller “stepping-stone” habitats that facilitate the movement of seed dispersers across fragmented landscapes^{25,81}. We also found that high levels of spectral beta diversity are associated with intermediate levels of swidden disturbance, and under these conditions, there are more spatially heterogeneous combinations of patches from different land classes that may provide niches for rare species that contribute to the overall richness of the ecological community. The presence of mature forests in swidden mosaics also serves as seed banks that can support the regrowth of recently cleared swidden fields²⁵, as well as diverse floral habitats with stark habitat edges that could support greater faunal diversity and encourage seed transportation, dispersal, and plant regrowth. Finally, swidden mosaics may also increase socioecological resilience by providing opportunities for innovation: economically valuable species such

as palms⁸² are often left standing to provide building material and habitat for game animals that support hunting.

It is important to recognize the advantages and disadvantages of a remote sensing approach to inferring biodiversity in landscape ecology. Undoubtedly, forest inventory studies provide the most accurate estimates of biodiversity. For example, one exhaustive study analyzed inventory data from 2504 one-hectare plots in Ghana and found statistical support for the hypothesis that disturbance explains variation in diversity in dry tropical forests⁴⁸. However, biodiversity inventories can be time-consuming and expensive, limiting the information about community composition over wide areas and across landscapes. Remote sensing is suitable for collecting data across large areas and remote sensing methods are readily adaptable to other study areas, which facilitates replication of study results. Spectral species classifications using remotely sensed data have been shown to correlate with ground-truthed biodiversity data from forest inventories, leading to the proposition that spectral species can be

used as an index for quantifying biodiversity at large spatial scales⁸³. While our primary analysis focused on remote sensing data from our drone scanning, we also conducted a limited forest inventory survey in five plots across a gradient of swidden fallows. We then analyzed the correlation of these manual counts with spectral species variation estimated from corresponding regions in the drone scan (Spearman's $Rho = 0.77$, $p = 0.072$; see Supplementary Note 4 "Forest inventory survey and spectral species validation"). Clearly, spectral species diversity primarily captures information about treetop floral diversity; it does not estimate sub-canopy or faunal diversity and spectral signatures may be driven in part by seasonality and plant physiology. The correlation between spectral diversity and the diversity in the 10% tallest trees in the manual inventory was slightly stronger (See Supplementary Table S6). Overall, these results confirm that there are distinct communities of spectral species associated with the land classes that result from customary Maya swidden practices (Fig. 1b). The benefit of the remote sensing approach is that species diversity can be analyzed across entire landscape mosaics and at multiple spatial scales, which is critical for understanding landscape ecological patterns generally⁸⁴, and for analyzing the trajectories of multiple successional pathways in secondary forests¹¹, all of which are necessary to understand the socio-ecological dynamics of Indigenous swidden cultivation.

Overall, our modeling results suggest that the spectral diversity of the swidden mosaics surrounding the study villages peaks at intermediate levels of landscape fragmentation. Both villages have mixed economies that blend subsistence cultivation and market engagement, collective land rights, and customary institutions that allocate most land use decision-making to households, rather than specialized natural resource managers. Our statistical models control for variation that might result from differences in practices and norms between villages, and they show that an intermediate level of landscape fragmentation is associated with an increase in forest diversity inferred from spectral analysis. The extent of landscape fragmentation observed in swidden mosaics can be efficiently controlled by farmers meeting their subsistence and economic needs using a flexible decision model that can adjust the location and size of new fields, the frequency that fields are re-cultivated or fallowed, and the size of fields to be cleared. These are relatively low-cost decisions, but they interact in important ways with ecosystem processes to enhance canopy tree diversity at intermediate scales of disturbance. We highlight that this need not be a conscious process of long-term ecosystem management: farmers do not need to intentionally position their fields to control landscape-scale edge density because they hope to reap the benefits of enhanced biodiversity years in the future; rather, the increased levels of spectral diversity are an emergent property of the swidden disturbances that result from interaction between household-level land use decisions and the spatio-temporal dynamics of tropical forests.

Lastly, our findings have implications for theory in ecology. The IDH has empirical support in a range of natural ecosystems⁸⁵, and a recent meta-analysis of evidence for the IDH⁸⁶ found key differences in empirical support between aquatic and terrestrial environments. While the theoretical basis of the IDH has been critiqued^{47,87}, Huston cautions that lack of empirical support in any particular case study may be due to failing to account for differences in productivity⁸⁵. Productivity is important because species with low growth rates can be driven to extinction under intermediate or high levels of disturbance (so high biodiversity only occurs when disturbance is low), and species with high growth rates quickly return, resulting in competitive exclusion (so high biodiversity only occurs when disturbance is high). Further, Huston suggests that studies that do not control for individual species growth rates may fail to identify

an IDH pattern because species with low and high growth rates can cancel each other out. Thus, for understanding swidden systems, it is particularly important that tropical forests tend to have low net primary productivity, where the highest levels of diversity will occur under relatively low levels of productivity⁸⁵. Our approach uses remote sensing data from a single year to infer tree diversity from spectral diversity. It does not distinguish between the different rates at which individual plants or trees grow, so all inferred spectral species are assumed to grow at the same rate. Therefore, following Huston's logic, it would be considered a conservative test of the IDH hypothesis because it would be more likely to find a negative result (or less likely to find a positive result). The detection of IDH can also be an issue of scale: if the spatial scale of study plots does not align with the study system, then IDH may not be detectable. Our analysis of remote sensing data is ideally suited for analyzing scale-dependent processes such as swidden agriculture (see Supplementary Note 5 "Landscape sampling framework"), and our modeling analysis finds significant support for the IDH in Maya swidden mosaics. Given this, it is notable that a recent survey of the IDH literature categorizes studies by terrestrial, freshwater, and marine ecosystems, but it does not distinguish studies where anthropogenic landscapes may have been present⁸⁶. A brief literature review using the same publication date criteria (1978–2017) found additional studies with quantitative evidence supporting the IDH in human-dominated ecosystems^{31,88–90} and even more since 2017^{91–107}. This growing body of knowledge supports claims that the IDH is a characteristic property of certain types of human-dominated ecosystems¹², and it also highlights the theoretical importance of analyzing anthropogenic disturbances for understanding ecosystem structure and function.

Conclusion

Indigenous People worldwide are at the nexus of two significant socio-environmental issues: increasing legal recognition of their customary land rights and global conservation efforts to combat climate change. While it is impossible to estimate accurately the number of people practicing swidden, recent studies suggest between 280 and 1000 Mha of land show signs of swidden globally¹⁰⁸. The longoverdue legal recognition of customary lands and appreciation for Indigenous contributions to global conservation highlight the importance of Indigenous communities in combating global climate change. Swidden agriculture is a critical source of subsistence for many Indigenous communities in tropical parts of the world and it is also one of the oldest forms of agriculture. At the same time, it is widely identified as one of the drivers of deforestation. We suggest that one reason that Indigenous swidden systems have long been considered a source of deforestation is the lack of adequate models for sustainable swidden cultivation. Our analysis provides a better understanding of how swidden agricultural practices can create gradients in tropical forest canopies and landscape-scale fragmentation mosaics that maximize diversity at intermediate levels of disturbance. Critically, this pattern of ecosystem enhancement does not result from top-down land use planning or intentional conservation efforts on behalf of the communities. Rather, increased spectral diversity is an emergent property that results from interaction among customary Maya land use decisions made at the household level and tropical ecosystem dynamics.

Methods

We used field-based data collection methods, drone-based remote sensing, and Bayesian statistics to analyze, model, and validate the relationship between landscape fragmentation and spectral

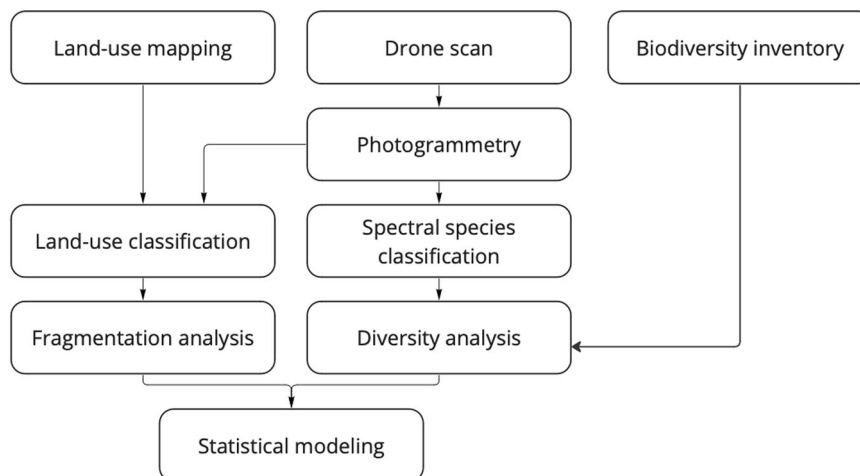


Fig. 4 Overview of methodology. The study involved field-based data collection with a community-based mapping team, remote sensing with long-range drones, a computational pipelines for photogrammetry landscape analyses and data validation, and multi-level Bayesian modelling.

species diversity. Drone scanning and land use mapping were conducted in the Toledo District, Belize, in April–May 2018. The biodiversity inventory study used to validate the spectral species diversity proxy was conducted the following year in May 2019. Figure 4 (and Supplementary Fig. S1) provides a high-level overview of the data collection and analysis workflow. In this section, we provide an overview of our methods. Additional details are provided in Supplementary Information.

Ethical considerations. Permission to conduct the research was obtained from the leaders in both study villages according to customary cultural practices. Scientific research permits were obtained from the Belize Department of Civil Aviation for drone research flight permits, and from the Belize Institute for Social and Cultural Research for ethnographic fieldwork and land use mapping. The research project was reviewed and approved by the Ohio State University Institutional Review Board.

Drone-based remote sensing. We chose to use drones to collect remote sensing data to achieve decimeter-level resolution at the large spatial scales that are necessary to image Maya community forests, and to accurately assess landscape fragmentation and canopy tree diversity (Supplementary Table S1). In addition, when compared to the costs of scanning with light aircraft, drones address the following requirements: (1) The need for low-cost data collection; (2) The need for minimal impact on the people living in the study villages; and (3) Safety of flight personnel and people living in the study villages. Scans were conducted over a period of two weeks, between April 16 and 27, 2018. Flight planning was adjusted daily to account for changing wind velocity and dynamic constraints such as clouds, smoke, and frequent interference or masking of the link between the drone and ground control stations (Supplementary Fig. S2). Flights were conducted during daylight hours between 8 AM and 5 PM when weather and technical considerations permitted. The remoteness of the study area, fieldwork conditions, and extreme tropical climate at times created an “uncontrolled field environment” (James et al., 2019)¹⁰⁹ that requires deviation from ideal data collection standards such as scanning only when the sun is at or near its apogee. We used a MicaSense RedEdge 3 sensor to collect five reflectance bands (red, green, blue, Red Edge, and near-infrared). The remote sensing dataset consists of 52,798 5-band georeferenced images and 630 ground truth points.

Radiometric processing. The images were processed and stitched with the photogrammetry software program Pix4D¹¹⁰, and a bespoke workflow (See Supplementary Note 1 “Drone data collection and photogrammetry”, Supplementary Fig. S3, left). Radiometric image correction was evaluated with information from a calibration panel and a down-welling light sensor that was mounted on the top of the drone during flights to collect irradiance levels (Supplementary Tables S3 and S4). Radiometric processing resulted in a single 5-band raster image (Supplementary Table S2).

Land use classification. To produce a classification map, we used GPS training points collected by a community mapping team with extensive knowledge of each community’s forests and land use history (Supplementary Fig. S4). For each point, the surveyor answered a number of land use questions (Supplementary Fig. S5), including the following one which was used to generate the land use classification: “If this is a huamil, what year was this LAST cleared (e.g., 2013)?” (Huamil is a Spanish word used locally to refer to a fallow agricultural field). Their estimates were made based on either specific knowledge of the year a field or plot was worked, or an estimate based on customary ecological knowledge of soil characteristics, species composition, and/or species height. These points were manually digitized into polygons and pixels were sampled from them for use in training and testing a classification model (Supplementary Figs. S6 and S7). Land use and spectral species classification maps were produced using semi-automated classification workflow¹¹¹ (Supplementary Fig. 3, right). We used confusion matrices to assess the performance of the classification algorithm and to determine the temporal resolution of the final land use classification map (Supplementary Figs. S8–S10).

Spectral diversity analysis. We used a remote sensing approach to infer forest species diversity and landscape disturbance from images collected by drones. Remote sensing is increasingly used to monitor biodiversity, biological organization, and ecosystem functioning across a range of temporal and spatial scales because it is important to have precise, accurate, efficient, and inexpensive information about ecosystems worldwide^{112,113}. The primary reason for this approach is that testing the IDH requires that the extent of the study area matches the swidden use area and that our methods of analysis can quantify landscape characteristics at this scale of analysis. This would have been difficult to achieve using traditional sampling methods¹¹⁴. Our approach is based on

two key principals: first, the spectral variation hypothesis, which states that greater pixel heterogeneity reflects higher niche heterogeneity, allowing more organisms to coexist¹¹⁵; and second, the concept of optical types, which hypothesizes that functional types can be distinguished largely on the basis of optical properties detectable by remote sensing¹¹⁶. We used a two-stage process (See Supplementary Note 3 “Spectral species classification”, Supplementary Fig. S11, Supplementary Table S5) that first reduces the dimensionality of the spectral variance using principal components analysis, and then uses k-means analysis to cluster pixels and assign them to putative spectral species⁸³. This approach has been applied at scales of analysis ranging from localized areas¹¹⁷ to regions as large as Europe¹¹⁵.

We used *biodivMapR* to perform the spectral species analysis⁵⁰. A key parameter is the number of clusters k , which defines the total number of spectral species. In almost all cases, k will be less than the total number of actual species in the forest, which is usually an unknown parameter. Thus, the inferred spectral species abundance and diversity estimates reflect the number of discernible spectral clusters rather than the actual number of species in the forest. The authors of the software note that k may also vary depending on the level of heterogeneity of the landscape. Recent studies use a range of k values including $k = 10$,¹¹⁸ $k = 40$,⁸³ and $k = 200$.¹¹⁵ We follow guidelines provided by the software authors and evaluated k at three levels ($k = 20$, $k = 35$, and $k = 50$), and correlate spectral diversity with measured diversity from a forest inventory ground-truth survey (described below). We found that $k = 20$ has the highest correlation with both the total diversity of the forest inventory plots and with the tallest 10 percent of tree species that are the most likely to be visible in the drone imagery (Supplementary Figs. S12 and S13, Supplementary Table S7). This finding is also consistent with the software authors’ recommendation to define $k = 20$ for estimating spectral diversity using Shannon entropy⁵⁰.

The use of remote sensing for biodiversity monitoring is growing rapidly, but the question remains about the relationship between spectral diversity and species diversity. For example, does each spectral species represent a single plant species or, as suggested by the optical types hypothesis, a group of plants with common physiological, structural and/or phenological responses to environmental resources and conditions? Is spectral variation caused by species diversity, or by seasonality and physiological status¹¹⁹? The answers to these questions depend in part on the resolution of the sensor (pixel grain size), the ability of the sensor bands to measure different characteristics of the flora, and the timing of sampling in relation to seasonality and climatic conditions^{115,120,121}. While some studies have had limited success correlating spectral diversity to plant diversity^{122,123}, others have found that spectral diversity correlates with functional diversity, phylogenetic distance, and above-ground productivity⁵¹. One recent study that found a strong relationship between functional occupation patterns and spectral patterns is particularly relevant to ours because it also uses drone-based remote sensing and a Micasense RedEdge 3 sensor, the same model we used¹¹⁷. Nevertheless, we acknowledge that spectral diversity analysis is an emerging approach to studying biodiversity, yet we suggest that the approach is sufficiently mature to allow the tentative conclusions presented here.

Spectral diversity validation. In order to validate the spectral diversity analysis, we worked with Indigenous collaborators trained in local species identification to conduct a vascular plant diversity survey. We used modified gentry plots designed for rapid ecological assessments¹²⁴ (Supplementary Fig. S14). In 2019, the season following the drone scan, we established five

sampling plots in four of the land use classes across the disturbance gradient: 20+ y (two plots), 12–19 y, 5–11 y, and 2–4 y (Supplementary Fig. S15). Within each plot, five 2×50 m fixed width transects were established parallel to each other at 20-m intervals and all vascular plants and trees greater than 2.5 cm diameter at breast height were measured and identified using a taxonomic, parataxonomic, or Indigenous classification system (see Supplementary Note 4 “Forest inventory survey and spectral species validation”). Across all five plots, we counted 1847 vascular plants from 139 different species. We then calculated several diversity statistics for each land use class (Supplementary Table S6).

We analyzed the correlation between diversity estimates from the validation dataset and the spectral species diversity estimated from corresponding regions in the drone scan. First, we simulated a land use class that modeled the diversity of cornfields using published ethnographic information⁵⁶. Second, we subsetted the data to account for the perspective of the sensor, which is most likely to model the diversity of the tallest trees that form the forest canopy and the grasses, palms, and bushes that characterize earlier successional stages. The subset contains only the vascular plants in the 90% percentile or above in height within each plot. Third, we investigated whether the correlations were sensitive to the number of spectral species defined in the spectral diversity analysis, so we performed the correlations with three different values of k (Supplementary Table S7). Overall, we find a positive correlation between spectral species diversity and measured vascular plant diversity ($\rho = 0.77$, $p < 0.1$), and with the tallest 10 percent of vascular plant species ($\rho = 0.83$, $p < 0.05$). Positive correlations are insensitive to the value of k .

Landscape sampling. To sample the landscape we overlaid a hexagonal grid onto the landscape (Supplementary Fig. S16). The effects of swidden disturbances on tropical forests are scale-dependent, because of environmental limits such as the maximum distances seeds can disperse in fragmented environments^{25,81}, and human factors such as the travel costs that limit the distance that farmers are willing to walk to a field¹⁰. Therefore, there will likely be an optimal spatial scale at which the intermediate levels of disturbance can be detected in swidden systems, and scales of analysis that are too large or too small may fail to detect the pattern of interest. We used a hexagonal grid and performed a sensitivity analysis across a range of spatial scales to identify the best level to sample the landscape (Supplementary Figs. S17 and S18). We determined that 70.15 ha is an asymptotic value that captures landscape beta diversity and also provides a sufficient number of sampling units for statistical analysis. To sample the landscape we overlaid the sampling grid onto the spectral species raster and the classified land use raster, and within each hexagonal sampling unit we calculated spectral species diversity, landscape fragmentation statistics, and key covariates, including the proportion of pasture, the proportion of 20+ forest, and the distance from the nearest village or road. All fragmentation and diversity statistics and landscape sampling were conducted with *landscapemetrics*⁶⁵.

Intermediate disturbance model. We developed an intermediate disturbance model and simulated the effect of a range of disturbance levels on a hypothetical landscape (Supplementary Fig. S19). We then fit a generalized linear model with a second-order polynomial family to the simulated data and used the resulting coefficient estimates as reference values when interpreting the posterior predictions from the statistical analysis of sampled data (Supplementary Fig. S20).

Statistical modeling. We used Bayesian multilevel modeling to estimate the effect that landscape disturbances have on effective spectral species diversity. Modeling was conducted with brms¹²⁵. We defined the effective number of spectral species as exponentiated Shannon diversity^{126,127} and modeled landscape fragmentation as a function of edge density (ED), the proportion of pasture within each hexagon (PPAST), the proportion of 20+-year-old forest within each hexagon (PPF), and the village with which each hexagon is associated (Supplementary Fig. S21). We modeled spectral species diversity within each hexagon as a non-linear quadratic relationship with edge density and we used informed priors that constrained the shape of the polynomial distribution to ecologically plausible values (Supplementary Equation S1). We included an intrinsic conditional autoregression (ICAR) term (ϕ) to accommodate spatial trends in disturbance history and spectral species diversity. Supplementary Information contains summaries of the statistical models following the Bayesian analysis reporting guidelines¹²⁸, including the full model specification (Supplementary Note 7 “Full model introduction”), prior predictive simulations and an evaluation of a range of broad and weakly informed priors demonstrating the insensitivity of our results (Supplementary Note 8 “Polynomial simulations and prior selection”, Supplementary Figs. S22–S26), details of the ICAR term (Supplementary Note 9 “Spatial autocorrelation”, Supplementary Fig. S27, Supplementary Table S8, Supplementary Equation S2), model convergence diagnostics (Supplementary Note 10 “MCMC resolution and convergence”, Supplementary Figs. S28–S33), and a summary of the model reported in the main paper (Supplementary Note 11 “Summary of model reported in main paper”, Supplementary Table S9, Supplementary Fig. S34).

Data availability

The data used to replicate the methods and findings from this paper are available at <https://github.com/downey205/MayaSwiddenIDH-CEE>.

Code availability

The code used to replicate the methods and findings from this paper is available at <https://github.com/downey205/MayaSwiddenIDH-CEE>.

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Author contributions

S.S.D. conceived and planned the research, led the project and the writing, and secured funding; S.S.D. and J.M. planned the drone data collection; J.M. built the drones, developed the flight plans, and piloted drones; S.S.D., J.P. and S.A.S. designed the land use mapping data collection and biodiversity inventory; S.S.D., J.M., J.P. and S.A.S. collected land use mapping data collection and biodiversity inventory; R.Q. and S.S. designed and performed the photogrammetry and landscape classification; S.S.D., S.A.S., and M.W. designed the spectral species analysis; M.W. performed the spectral species analysis; S.S.D., W.P., S.A.S. and M.W. designed the statistical analysis; S.A.S. and M.W. performed the data analysis; S.S.D., M.W., J.M., F.P., W.P., R.Q., S.A.S. and S.S. wrote the paper; all authors approved the manuscript.

Competing interests

The authors declare no competing interests.

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Correspondence and requests for materials should be addressed to Sean S. Downey.

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