



Animal soundscapes reveal key markers of Amazon forest degradation from fire and logging

Danielle I. Rappaport^{a,1} , Anshuman Swain^b , William F. Fagan^b, Ralph Dubayah^a, and Douglas C. Morton^{a,c}

Edited by Rodolfo Dirzo, Stanford University, Stanford, CA; received February 11, 2021; accepted February 24, 2022

Safeguarding tropical forest biodiversity requires solutions for monitoring ecosystem structure over time. In the Amazon, logging and fire reduce forest carbon stocks and alter habitat, but the long-term consequences for wildlife remain unclear, especially for lesser-known taxa. Here, we combined multiday acoustic surveys, airborne lidar, and satellite time series covering logged and burned forests ($n = 39$) in the southern Brazilian Amazon to identify acoustic markers of forest degradation. Our findings contradict expectations from the Acoustic Niche Hypothesis that animal communities in more degraded habitats occupy fewer “acoustic niches” defined by time and frequency. Instead, we found that aboveground biomass was not a consistent proxy for acoustic biodiversity due to the divergent patterns of “acoustic space occupancy” between logged and burned forests. Ecosystem soundscapes highlighted a stark, and sustained reorganization in acoustic community assembly after multiple fires; animal communication networks were quieter, more homogenous, and less acoustically integrated in forests burned multiple times than in logged or once-burned forests. These findings demonstrate strong biodiversity co-benefits from protecting burned Amazon forests from recurrent fire. By contrast, soundscape changes after logging were subtle and more consistent with acoustic community recovery than reassembly. In both logged and burned forests, insects were the dominant acoustic markers of degradation, particularly during midday and nighttime hours, which are not typically sampled by traditional biodiversity field surveys. The acoustic fingerprints of degradation history were conserved across replicate recording locations, indicating that soundscapes may offer a robust, taxonomically inclusive solution for digitally tracking changes in acoustic community composition over time.

bioacoustics | ecosystem services | land use | habitat loss | forest disturbance

Biological diversity is disappearing rapidly in response to human activity, especially in tropical forests, which are home to well over half of Earth’s terrestrial species (1). Global concern over greenhouse gas emissions from tropical forests (2) has led to international efforts to Reduce Emissions from Deforestation and Forest Degradation (REDD+) (3). Retention of diverse ecosystems supports climate change mitigation and adaptation (4); yet, carbon-focused conservation may not result in a commensurate win for tropical forest biodiversity (5). Longstanding data gaps on species distributions and uncertainty regarding the direct and indirect impacts of human activity on biodiversity complicate efforts to quantify the interplay between carbon and biodiversity (6, 7).

Across the tropics, the Brazilian Amazon has the highest rates of deforestation (8), and forest degradation from fire and logging may double biodiversity loss from deforestation alone (9). However, the long-term impacts of human activity on Amazon biodiversity remain highly uncertain due, in part, to the spatial heterogeneity among degraded forests from differences in the timing, frequency, extent, and severity of disturbances (10). Time-varying heterogeneity in the biodiversity of degraded forests may also explain some of the apparent contradictions in previous studies of degradation impacts on birds, the most well-studied Amazonian taxa. Many nectarivorous birds, for example, increase in abundance immediately after logging but ultimately decline. Yet, many insectivorous birds show immediate sensitivity to changes in habitat from logging but continue to decline in abundance over time (11). Time dependence also complicates efforts to measure the effects of degradation on insects, a problem confounded by limited research (12).

Addressing the tropical biodiversity extinction crisis, therefore, requires an efficient, distributed, long-term monitoring system to assess ecosystem structure (13). Traditional, ground-based biodiversity inventories are logistically prohibitive to conduct at scale, and limited taxonomic expertise perpetuates large data discrepancies for lesser-known taxa, such as insects, which constitute the bulk of tropical biodiversity (7). Advances in the emerging discipline of acoustic remote sensing, or ecoacoustics, may permit large-scale biodiversity monitoring for multiple taxa, including unidentifiable

Significance

Fire and logging reduce the carbon stored in Amazon forests, but the long-term impact of forest degradation on animal communities remains unclear. We recorded thousands of hours of ecosystem sounds to investigate the acoustic fingerprint of the animal community in degraded Amazon forests following fire and logging. The emergent 24-h patterns of acoustic activity differed between logged and burned forests, and we observed large and sustained shifts in acoustic community assembly after multiple fires. Soundscape differences among degraded forests were clearest during insect-dominated hours rarely sampled in field studies of biodiversity. These findings demonstrate that acoustic monitoring holds promise for routine biodiversity assessments, even by non-experts, to capture a holistic measure of sound-producing animals and track ecosystem changes over time.

Author contributions: D.I.R., W.F.F., R.D., and D.C.M. designed research; D.I.R., A.S., W.F.F., and D.C.M. performed research; D.I.R. and A.S. contributed new reagents/analytic tools; D.I.R. and A.S. analyzed data; and D.I.R. and D.C.M. wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

Copyright © 2022 the Author(s). Published by PNAS. This open access article is distributed under Creative Commons Attribution-NonCommercial-NoDerivatives License 4.0 (CC BY-NC-ND).

¹To whom correspondence may be addressed. Email: danielle.rappaport@gmail.com.

This article contains supporting information online at <http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2102878119/-DCSupplemental>.

Published April 26, 2022.

species, based on the aggregate sound signature of the animal community, or soundscape (14–16). Since multiple sites can be recorded simultaneously over time, sound surveys reduce the effort and cost associated with routine monitoring and facilitate standardized assessments of community variation and ecosystem recovery. Most previous efforts to utilize acoustic data for biodiversity monitoring have focused on detecting known vocalizations associated with individual species (17, 18), but there is increasing interest in evaluating the entire collection of signals in a given soundscape to derive measures of ecosystem intactness that include all sound-generating taxa without definitive species identification (15, 16, 19, 20).

The Acoustic Niche Hypothesis (ANH) (21) is a core premise of ecoacoustics and the prevailing organizing principle for assessing diversity (16), community similarity (22), and human impacts (23, 24) using soundscape data. The ANH posits that more intact habitats support more biodiverse communities that occupy more “acoustic niches.” Greater niche partitioning of available acoustic space, defined by frequency and time of day, is posited to minimize communication interference among coexisting species. The ANH implies a positive linear relationship between habitat intactness (i.e., biomass) and acoustic niche infilling or acoustic space occupancy (ASO) by the “animal orchestra.” The corollary is that more degraded habitats support less acoustic infilling due to vacant acoustic niches from local species extirpations (25). Ecoacoustic approaches have great potential to extend monitoring capabilities in the hyperdiverse tropics, where competition for acoustic space is strongest (16, 26). Still, large uncertainties remain as to whether soundscape infilling can be used as a robust proxy for ecosystem intactness to monitor landscapes altered by human activity (27).

Here, we test the ANH across logged and burned Amazon forests to identify acoustic markers of forest degradation (Fig. 1). We collected coincident high-density airborne lidar data and multiday acoustic recordings (214 24-h surveys) during September and October 2016 in 39 forests with different times since logging (4 to 23 y) and histories of fire activity (1 to 5 fires), stratified based on a 33-y time series of annual Landsat imagery (10). We used space-for-time substitution and two complementary analytic approaches to characterize threshold effects and time dependence for changes in the structure of animal soundscapes along gradients of degradation history (see *Materials and Methods*). First, we calculated ASO for each site at hourly and 1-min time steps to test the ANH and to quantify the magnitude, persistence, and variability in the infilling of acoustic space following forest degradation. Second, we developed a network-based approach to capture additional complexity from the soundscape data to track the composition and co-occurrences of “acoustic pseudotaxa” (defined as the community components that occupy the same acoustic niche) along degradation and recovery pathways. Our findings demonstrate that soundscapes encode digital markers of the history of degradation from human activity, revealing distinct patterns of community change following logging and fire. This study paves the way for more widespread use of ecoacoustics to benchmark and monitor changes in acoustic community composition in human-altered tropical forest landscapes, especially in remote regions with many unknown species.

Results

Soundscape data from degraded Amazon forests did not support the ANH (Fig. 2). Instead, acoustic analyses revealed contrasting impacts of fire and logging on acoustic community structure.

After fire, daily ASO increased linearly with estimated aboveground biomass, whereas daily ASO in logged forests did not increase with biomass (Fig. 2). Importantly, ASO–degradation relationships varied with time of day (Fig. 2 and *SI Appendix, Fig. S1*), highlighting the value of full-day measurements from autonomous recording devices for detailed investigations of the ANH and the dominant indicators of degradation.

Insects were the most obvious markers of changing acoustic community composition in burned forests. ASO during insect-dominated periods of the day (e.g., midmorning, noon, nighttime) strongly differentiated burned forests as a function of both biomass (max $|r| = 0.9$ at 2200 to 2300 hours) and fire frequency (max $|r| = 0.82$ at 2000 to 2100 hours), and these time periods governed the overall daily trend (Fig. 2). Notably, ASO relationships with biomass and fire frequency were weakest during the 0500 to 0600 dawn chorus typical of bird surveys ($P > 0.05$; Fig. 2). In logged forests, the only time interval that exhibited a moderately strong relationship with logging age (max $|r| = 0.61$ at 2200 to 2300) showed an unexpected decline in ASO with increasing time since logging. ASO and biomass in logged forests were not correlated for any time period. Relationships between ASO and degradation history were consistent when aggregating acoustic niches at both hourly and minute time scales (*SI Appendix, Fig. S2*).

The 24-h profile of ASO and peaks of acoustic activity varied markedly among burned forests as a function of fire frequency and aboveground biomass and less so among logged forests, despite a large range (50%) in aboveground biomass (Fig. 3 and *SI Appendix, Fig. S3*). The timing and magnitude of the dominant acoustic activity peaks were similar among logged forests (Fig. 3), which varied broadly in terms of time since logging (4 to 23 y) and potential impacts of logging infrastructure (e.g., skid trails, tree-fall gaps) (Fig. 1). Animal orchestras in both logged and once-burned forests exhibited greater daily variability and overall ASO than recurrently burned forests (Fig. 3 and *SI Appendix, Fig. S3*). Acoustic communities in recurrently burned forests occupied the smallest amount of frequency space during all time periods except dusk, which was the most heavily occupied time window for all degradation classes (1700 to 1800). Dawn hours had the lowest ASO across all 24-h soundscapes except in the most heavily degraded forests, burned three or more times.

We identified a breakpoint in acoustic community composition between forests burned once and forests burned two or more times. This threshold effect from recurrent fire activity manifested as a sustained reduction in ASO from late morning through mid-afternoon (1000 to 1500; Fig. 3 and *SI Appendix, Fig. S3*). Differences across levels of initial fire severity were also most evident during this time interval, reflecting localized impacts of burn intensity on acoustic communities, even at short length scales (300 m) within the same fire event (Fig. 4). In contrast to the nonlinear shifts observed midday, ASO declined linearly with increasing fire frequency after dusk (Fig. 3).

Network analyses confirmed that differences in ASO, the frequency-agnostic measure of soundscape intactness, reflected frequency-specific differences in the composition of animal communities following logging and fire. The majority of frequencies outside the midrange (~ 3.7 to 5.2 kHz) were more prevalent in logged and once-burned forests than in forests burned multiple times. Evidence for this comes from the frequency-specific measure, partner diversity (PD), which is the *Shannon diversity* of hours in which a given frequency band is detected; see *Materials and Methods* (Fig. 3 and *SI Appendix, Fig. S3*). We found strong suppression of PD for most spectra in burned forests after two or more fires. Importantly, the



Fig. 1. Acoustic recording sites in logged and burned forests ($n = 39$) were distributed across 9,400 km² in northern Mato Grosso, Brazil (Upper Left). Colored boxes identify subsets of the study domain to illustrate how the triplicate sampling scheme was designed to capture the heterogeneity in habitat structure and acoustic community composition in logged (yellow) and burned (black) forests. False-color composites of Landsat imagery (2014, 543-RGB) in each panel show deforested areas in magenta and gradients of forest cover in shades of green.

frequency bands that best differentiated burned habitat condition (3.5 kHz, 6.7 to 7.4 kHz) were not the same frequencies that best differentiated logged habitat condition (4.2 kHz; Fig. 3 and *SI Appendix*, Fig. S3). For most frequency bands, the greatest daily prevalence (PD) was observed in logged forests after 4 y of regeneration, followed by a sharp but short-term dip in PD between 4 and 10 y (Fig. 3 and *SI Appendix*, Fig. S3). Still, the relative dynamic range of network attributes was much more limited among logged classes than among burned classes.

Overall, fire resulted in more empty acoustic niches across the 24-h soundscape than logging, and recurrent burns led to a major restructuring of the acoustic community. Matrix subtraction provided complementary insight into the recovery of soundscape structure following logging and the reorganization of soundscape structure following multiple burns. After logging, several acoustic pseudotaxa appeared and disappeared with time since logging (e.g., 4.2 kHz), but most time-frequency niches that went silent between 4 and 10 y after logging were reoccupied between 10 and 23 y of recovery (Figs. 3 and 4). By contrast, the transition pathways after fire indicated a possible divergence following initial and repeated burns (Fig. 4). There were large pseudotaxa losses when comparing a forest burned once with a forest burned a second time. By contrast, comparing a twice-burned forest with a forest burned five times

revealed large gains in pseudotaxa. Importantly, the colonizing assemblages of pseudotaxa gained between the second and fifth fires appear to be fundamentally distinct from the assemblages of pseudotaxa initially lost between the first and second fires (Fig. 4). In all transitions, losses and gains were clustered in time-frequency space. For example, a large cluster of losses during the transition from one to five fires was detected midday (1000 to 1500; Fig. 4), the same time period shown in Fig. 2 that clearly differentiated forests by fire frequency.

Animal communication networks also became more acoustically homogenous with increasing fire recurrence. Alatalo interaction evenness (AIE), a measure of the homogeneity of signal interactions across time-frequency space, increased linearly with increasing fire frequency (Fig. 5). The variance among replicates within each burn class declined linearly with increasing fire frequency. The evenness of the communication network further explained variation in successional recovery after fire: AIE was consistently lower in younger once-burned stands than older once-burned stands, reflecting an increased dominance of fewer sets of sounds.

The clustering of sounds provides further insight into the component processes that drive system-level patterns such as ASO and evenness. These local-scale metrics (e.g., clustering coefficient [CC]) measure the transitivity of co-occurrences of acoustic

Degradation History ● Burned ● Logged

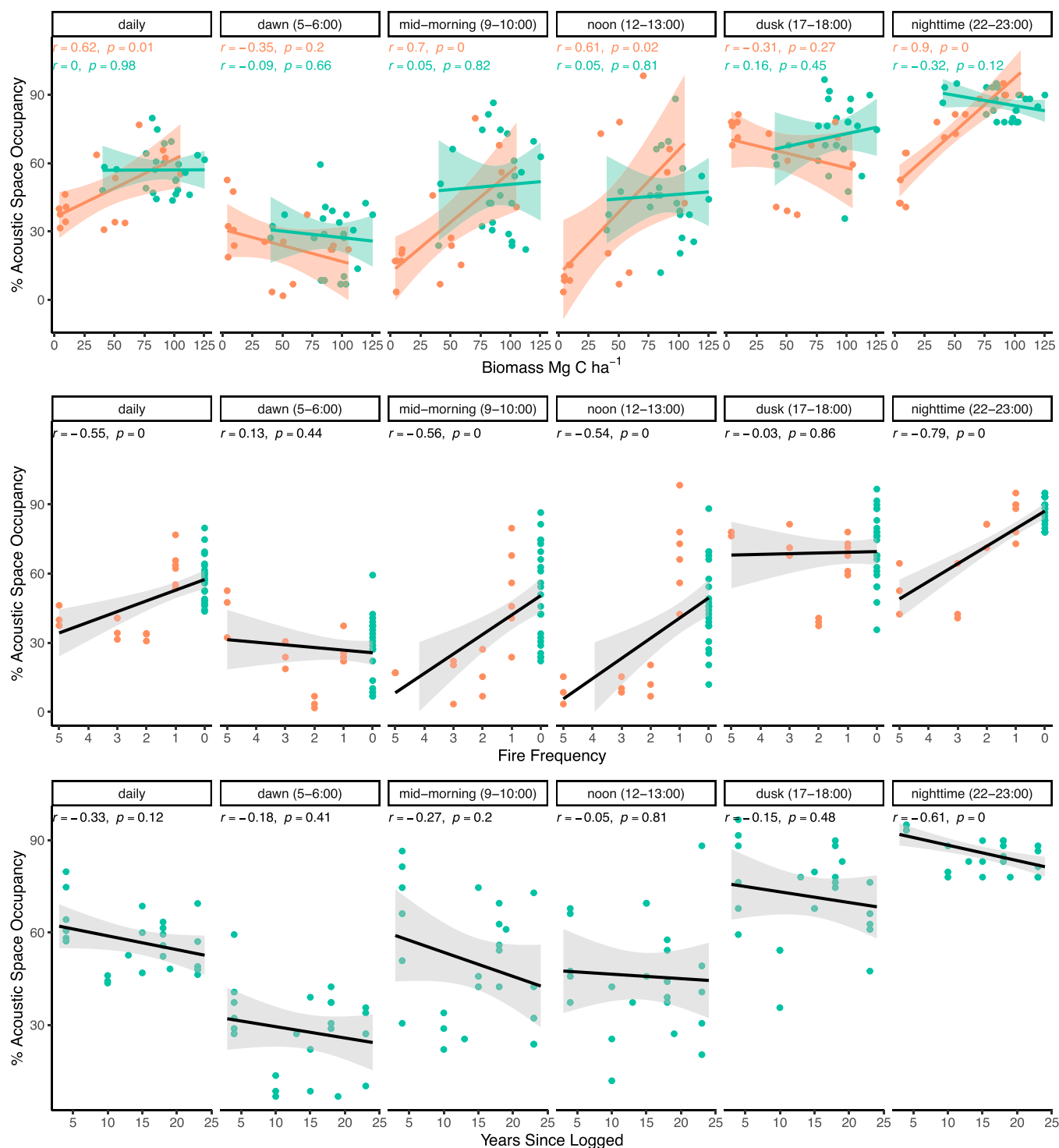


Fig. 2. Patterns of soundscape infilling did not conform to expectations from the ANH that animal communities in more-intact habitats occupy more of the 24-h soundscape, with intactness measured as either aboveground biomass (*Top*), fire frequency (*Middle*), or years since logging (*Bottom*). Individual panels summarize the ASO of the animal community, which responds differently to logged and burned forests. ASO is aggregated over specific time intervals of known biological activity for birds and insects to pinpoint likely taxonomic contributions to daily trends. *SI Appendix, Fig. S1* provides the full 24-h profiles for logged and burned forests, and *SI Appendix, Fig. S2* compares ASO relationships aggregated at 1-min and hourly resolutions.

pseudotaxa over frequency or time. The large drop in the CC of frequency bands between one and two fires indicated a disintegration of time-synchronized groups of spectrally similar sounds (Fig. 5). The subsequent increase in the clustering tendency of acoustic pseudotaxa between two and five fires was of a

fundamentally different character, as new acoustic pseudotaxa appeared at frequencies that had limited overlap with the acoustic pseudotaxa lost between one and two fires (Figs. 4 and 5).

By contrast, animal communication networks after logging suggested community-level recovery rather than the reorganization

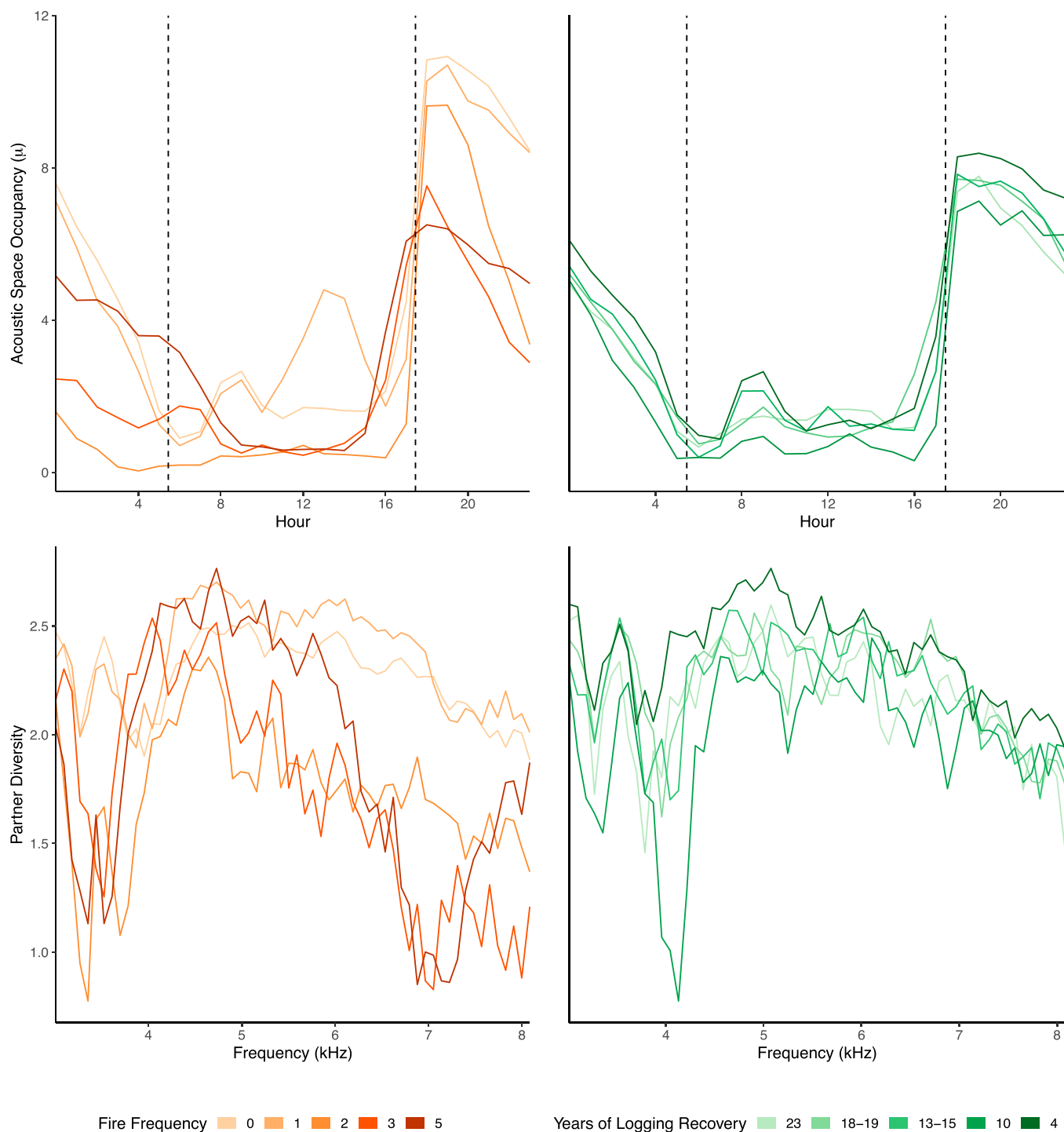


Fig. 3. Soundscape data sampled across gradients in fire frequency (orange) and time since logging (green) reveal distinct ecosystem breakpoints as a function of recurrent burning, compared to the more subtle soundscape differences observed among logged forests. (*Top*) Mean daily profiles of ASO, a frequency-agnostic measure of the proportion of potential “acoustic niches” occupied per time step. (*Bottom*) PD, a network-based metric that disaggregates the ASO profiles into a frequency-specific assessment of the prevalence of acoustic pseudotaxa during the 24-h cycle, where a lower PD indicates lower daily occurrence of a given sound frequency band. Colored lines represent the average response per degradation stratum. Results for each recording site are shown in [SI Appendix, Fig. S3](#) (ASO and PD of sound frequency bands) and [SI Appendix, Fig. S4](#) (PD of sound hours). Dashed vertical lines indicate sunrise and sunset.

observed due to fires. We observed a short-term decline in AIE and the CC of sound hours and sound frequency bands between 4 and 10 y after logging (Fig. 5). However, this effect appeared transient, with soundscapes of logged forests far less variable than fire-affected soundscapes, based on the similarity in ASO and network patterns and the transition matrices of losses and gains of acoustic pseudotaxa (Figs. 3–5).

Discussion

Acoustic soundscapes capture the full 24-h profile of animal activity in species-rich tropical forest ecosystems to provide a holistic digital assessment of acoustic community changes and reassembly following forest degradation. Results from this study expand upon previous field studies restricted to specific taxa

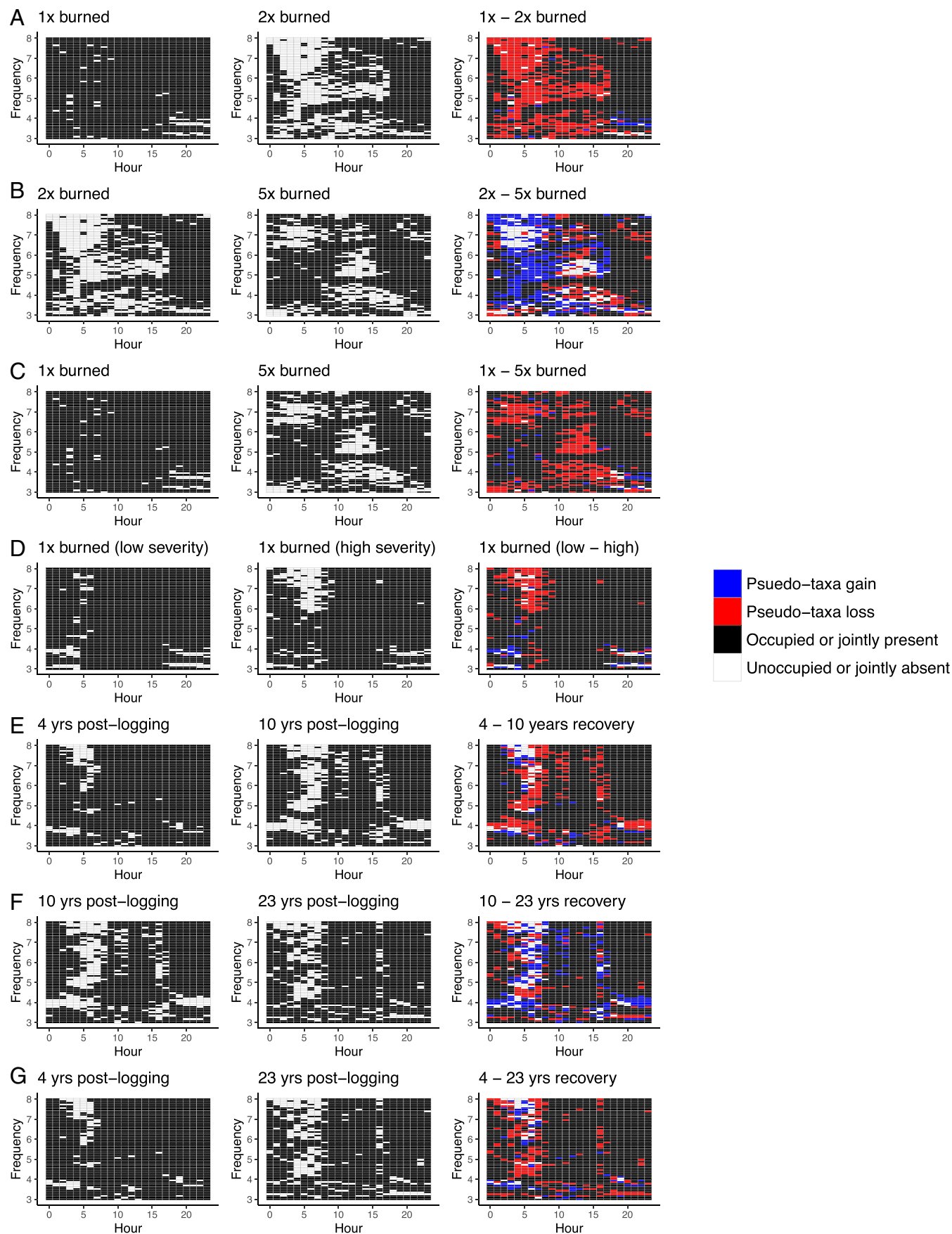


Fig. 4. Soundscape transition matrices identify coordinated losses (red) and gains (blue) of acoustic pseudotaxa (*Right*) based on the subtraction of paired matrices of ASO (*Left* and *Center*), stratified by degradation history. (A–C) Gradients of fire frequency, (D) gradients of burn intensity from daytime and nighttime variation in relative humidity, and (E–G) gradients of recovery after logging.

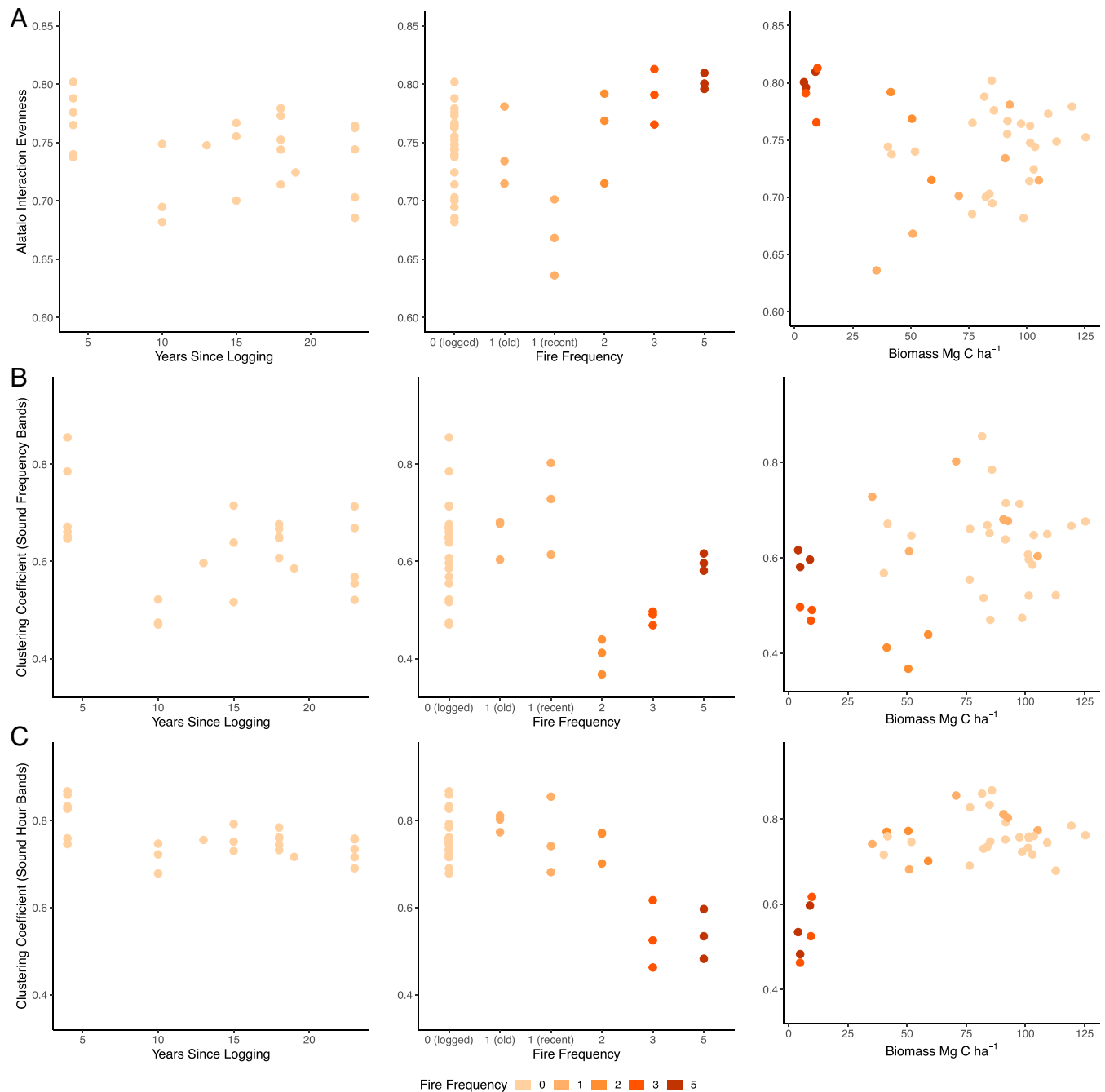


Fig. 5. Forest degradation alters animal communication networks in frontier Amazon forests, as measured by (A) AIE and the CC of (B) sound frequency and (C) sound hour bands. AIE quantifies the homogenization and dominance of signals across the animal communication network, defined by time and frequency. A higher value indicates more homogenous signal activity during the course of a day. The CC corresponds to the tendency for acoustic pseudotaxa to form coordinated clusters of synchronous activity over (B) frequency space and (C) temporal space. A higher value indicates greater local connectivity among pseudotaxa. Stratification by logging history (Left), fire history (Center), and aboveground biomass (Right) reveals distinct successional pathways following logging and fire.

over limited survey periods and narrow habitat ranges (28–30). Soundscape data highlighted distinct trajectories of acoustic community assembly after logging and fire, which did not correlate with aboveground biomass recovery. Differences in acoustic community composition between burned and logged forests underscore the need to track long-term changes in tropical forest biodiversity to complement carbon-centric conservation strategies such as REDD+. In particular, we found major restructuring of the acoustic community after two or more fires. Soundscape markers of forest degradation were strongest and most consistent during midday and midnight hours typically

dominated by insect choruses, time periods rarely sampled in field-based inventories of birds, the most commonly studied taxa (7). By revealing the hidden structure of acoustic assemblages, the network-based methods in this study offer a window into the nature of animal communities in frontier Amazon forests. Network analyses of ecoacoustic remote sensing data represent a scalable approach to benchmark and track changes in ecosystem structure over space and time.

Patterns of ASO following logging and fire did not vary predictably with aboveground biomass, a common metric of tropical forest intactness (31) and part of the theoretical basis for the

ANH. Contrary to expectation, we found that animal communities in less-intact forests did not contain more soundscape gaps (i.e., empty acoustic niches). One possible explanation is that the long-term evolutionary mechanisms that favor acoustic niche partitioning may lose relevance during transient periods as animal communities respond to or reorganize following disturbances (32). Further work that directly compares acoustic community structure before and after forest degradation may help to resolve this incongruity. Surveys in forests without a history of logging or fire may reveal additional insights about the ANH and baseline patterns of ASO, although intact forests are rare in older frontier Amazon landscapes, given the cumulative impact of decades of human activity. Longer-term surveys of ASO may also help interrogate the ANH across seasonal time scales, such as during the rainy season when there is greater acoustic sensitivity to amphibians. Independent of the lack of support for the ANH, the consistent acoustic fingerprints that we identified among replicate sites and surveys suggest that the application of network theory to soundscape data may help to better differentiate among animal community assemblages following forest degradation than measures of habitat structure alone. These results corroborate previous reports based on acoustic studies of birds that soundscapes function as memory banks of Amazon forest modification (33). This study goes further to demonstrate that soundscapes may be far more valuable when collected as 24-h records that capture all acoustically active taxa, beyond those that are readily identifiable, and when analyzed as system-level interaction networks.

Insects (e.g., orthopterans, hemipterans), not birds, were the strongest acoustic markers of threshold changes in degraded forest communities, highlighting the value of nighttime surveys of insect choruses for a more complete picture of the animal community in human-modified forests. By contrast, soundscape measures from bird-dominated dawn and dusk intervals did not differentiate degraded frontier forests, possibly because bird choruses decline rapidly in response to even moderate perturbations to forest cover (23). In Borneo, degraded forest soundscapes were also found to be noisier and more homogeneous at night, which was attributed to an influx of generalist insect species following logging (22). The major contribution of insects to the soundscape record in this study, and their sensitivity to microhabitat changes following modification of forest structure, may further explain the observed differences across degraded Amazon forests.

The mechanisms for partitioning communication space to reduce interspecific competition and maximize signal transmission vary among the major sound producers in diverse terrestrial systems. For example, co-occurring assemblages of cricket species avoid masking by finely partitioning spectral space into nearly pure-tone frequency channels (34). By contrast, tropical cicadas emit broadband signals that occupy more frequencies (i.e., a larger “niche breadth”) such that neighboring species stratify acoustic space vertically—from the ground to canopy top—to avoid signal overlap. Consequently, cicadas have evolved to occupy extremely narrow thermal niches that make them immediately responsive to changes in forest structure from human disturbance. Importantly, the timing of the noisy cicada chorus, which is governed in part by temperature, affects the periods of acoustic activity by other species (35). This interplay among forest structure (36), microclimate (37), and animal habitat may contribute to the observed restructuring of the entire 24-h animal communication network in burned forests, given that fire has more substantial and long-lasting impacts on forest structure than selective logging in this region (10).

We found that animal communication networks in burned Amazon forests became quieter, less connected, and more homogenous after degradation from multiple fire events. The application of network theory to high-throughput acoustic surveys revealed a coordinated loss and gain of acoustic pseudotaxa suggestive of distinct trajectories of biotic reorganization following one to five burns. Acoustic evidence for successional divergence following repeated burning is consistent with experimental manipulation (38) and traditional species inventories (39). Because Amazonian forests are not adapted to fire, species that do survive initial or repeated burning can influence recovery pathways. For example, bird assemblages in Amazon forests burned multiple times are almost completely distinct from nearby unburned forests (40). In this study, the linear change in AIE after each recurrent fire event indicated increasing biotic homogenization, as reflected by the shifting dominance of fewer sets of sounds in the 24-h soundscape. The change in the CC following repeated fire indicated that the assemblage of acoustic pseudotaxa lost between one and two fires was distinct from the colonizing assemblage between two and five fires. The CC may be a particularly useful marker of forest degradation because it is sensitive to biological mechanisms that occupy conspicuous swaths of acoustic space (e.g., cricket choruses, cicada tymbal vibrations).

After selective logging, acoustic communication networks indicate a pattern of acoustic community recovery, rather than the reassembly observed following fire. Logging altered the grouping tendency of acoustic pseudotaxa and the PD per sound frequency band, but only in the short term. Smaller effect sizes in both ASO and network metrics after logging than after fire are consistent with the selective nature of logging in Amazon forests. Previous research suggests that the effect of logging on tropical forest biota is governed less by time since recovery and more by logging intensity (41), which may be less variable in the Amazon than other tropical forests. Overall, evidence for acoustic community recovery in this study is consistent with the retention of guild structure following selective logging based on species-level responses from field studies (28).

The introduction of network tools to interpret soundscape data opens avenues for monitoring biological communities at an intermediate level of complexity. This middle ground draws upon clusters of sound production to identify patterns of interaction and connectivity within the acoustic communication network that cannot be ascertained from simpler soundscape measures such as ASO or highly aggregated indices of diversity (19). These network measures of the acoustic community assemblage may enable long-term monitoring and change detection efforts, while circumventing the burden of individual species identification (42, 43). Importantly, acoustic communication networks also provide clues to help target specific time and frequency ranges in subsequent investigations of individual species. Traditional species presence/absence measurements or machine learning approaches to parse vocalizations (18) can use the same set of soundscape recordings, underscoring the flexibility of acoustic measurements.

Ecoacoustic surveys have the potential to accelerate our understanding of animal community dynamics, and the ecological resilience of Amazon forests, in response to a range of disturbance types and frequency regimes. In the Amazon, longstanding interest in island biogeography has spurred studies of forest fragmentation (44) and edge effects (45). Yet, the diversity of disturbance types across the Amazon region is large and not easily replicated by experimental manipulation studies (44, 46), given the observed differences in habitat structure (10) and acoustic activity within forests based on the specific timing, frequency,

and severity of forest degradation from logging and fire. Ecoacoustic surveys complement traditional taxa-constrained field approaches with full-day measurements of all sound-producing taxa, providing an inclusive, objective, and scalable approach to monitor the acoustic community across disturbance types since monitoring can be implemented by experts and nonexperts alike, and measurements can be collected simultaneously across large spatial extents. The cumulative impact of human activity along the arc of deforestation gives rise to broad gradients of forest condition from cycles of logging, fire, and land abandonment, in addition to differences in fragment size or pressure from hunting, grazing, or harvesting. Ecoacoustic surveys offer a pathway to rapidly assess acoustic community composition in these dynamic, human-modified landscapes.

Long-term monitoring of the acoustic community may also reveal important time lags between disturbance and recovery for coevolved animal and floristic communities, as well as ecological thresholds from novel disturbance types or extreme events, such as drought. Despite broad recognition of the role of the animal community for mediating Amazon vegetation succession through seed dispersal (47) and pollination (44), the time scales and dependencies of vegetation and animal community recovery following forest disturbance remain uncertain. Soundscape data from ecoacoustic monitoring have the potential to define important time lags in animal community recovery that may delay or interrupt these critical mechanisms, potentially triggering persistent shifts in ecosystem composition and function. In grassland ecosystems where fires are a natural feature on the landscape, increasing fire frequency has been shown to result in long-term animal community stability despite temporally unstable plant communities (48). By contrast, frequent fires are a novel disturbance regime as a result of recent human occupation in Amazon forests, which are not evolutionarily adapted to fire, even low-intensity surface fires that primarily consume litter and downed woody debris (49–52). Our findings demonstrate that acoustic surveys, in tandem with data on habitat structure and land-use dynamics, can advance our understanding of the time scales for recovery of ecological structure in burned forests and the conditions under which burned forests may shift into persistent alternative ecosystem states. New extremes in fire activity may also alter the magnitude of impacts to vegetation and animal communities, even in fire-adapted ecosystems such as the neighboring Pantanal biome, given the unprecedented size and severity of recent burns. The ability to rapidly deploy networks of ecoacoustic monitoring devices opens the possibility for greater understanding of tipping points and the component processes of acoustic community composition following disturbance based on the coevolution of habitat use and habitat structure.

We anticipate several future avenues for building upon this work to bolster capabilities for rapid and continuous monitoring of ecosystem degradation in the species-rich tropics. Longer-term observations are needed to further constrain the time scales for recovery and confirm the results from space-for-time sampling. Importantly, when collected over longer time frames, acoustic data provide an opportunity to work with seasonal and annual datasets to account for variation from phenology. For example, future work could evaluate associations between habitat condition and animal communication networks outside of the breeding bird period frequently targeted in such studies. Studies testing the ANH during the wet season may allow greater insight into changes in anuran assemblages. Linking ecoacoustic observations with traditional species-level measurements, which could be ascertained through reanalysis

of the same set of acoustic surveys (18), is an important next step for enabling biological attribution from changes in animal communication networks. Further elucidation of the links among soundscape structure, species composition, and habitat structure is needed to better understand the breakpoints associated with recurrent fire events and to target evidence for local species extirpations of seed dispersers and pollinators that could alter the time scales and trajectories of forest succession. The lack of an intact reference soundscape is a limitation of this investigation but a constraint that is, unfortunately, common across tropical frontier regions, where intact refugia are scarce in human-dominated landscapes. Amazon forests without a history of recent logging, fire, hunting, or fragmentation are, therefore, a priority for future ecoacoustic studies. Finally, we demonstrate that animal communication networks are a promising synthetic analytic framework for characterizing differences in biotic assembly based on the coordinated behavior of sound-producing species. Further development of these network approaches to analyze soundscape data may provide additional insights about the complex structure and dynamics of acoustic communities over time.

Acoustic measurements strongly differentiate between burned and logged Amazon forests and provide clear evidence for breakpoints in acoustic community structure following recurrent burning. Divergent patterns of acoustic activity were most pronounced during midday and nighttime hours, underscoring the unique insights from multiday recordings and the contributions from lesser-known taxa, such as insects. Ecoacoustic surveys are inclusive, capturing all sound-producing taxa, and they represent objective long-term records of ecosystem structure that support a range of analytic approaches from community network analyses to individual species detection. Given observed differences in acoustic communities within and between logged and burned forests, acoustic monitoring is an important complement to satellite and airborne remote sensing measures of forest structure to track ecosystem changes from human activity over time at the tropical forest frontier. Large and persistent changes in acoustic community composition following recurrent fires highlight the potential benefits of policies and management to limit further fire activity, particularly in frontier forest regions where recurrent burning is most concentrated. Given the potential biodiversity benefits of protecting burned Amazon forests from additional fires, the coordinated use of ecoacoustic and satellite fire monitoring data may improve biodiversity retention in frontier forests by supporting more robust biodiversity safeguards for REDD+ and related tropical forest conservation efforts.

Materials and Methods

Remote Sensing Data. We selected 39 degraded Amazon forest study sites using a 33-y timeseries of annual Landsat imagery (1984 to 2017) to track the cumulative history of understory fires and selective logging in the municipalities of Nova Ubiratã and Feliz Natal in the Brazilian state of Mato Grosso (Fig. 1 and *SI Appendix, Table S1*) (10). Acoustic communities in selectively logged sites ($n = 24$) were sampled between 4 and 23 y postdisturbance, and burned sites ($n = 15$) were sampled between 1 ($n = 3$) and 17 ($n = 3$) y postdisturbance. Recurrently burned sites had a history of two ($n = 3$), three ($n = 3$), or five ($n = 3$) fires prior to airborne lidar and acoustic survey acquisitions. Sites were selected to represent the broad continuum of habitat succession following degradation, reflecting both the time-integrated effects (i.e., frequency, recovery) and the spatial heterogeneity of damages (i.e., fire severity, logging infrastructure). High-density airborne lidar data were acquired between 2013 and 2016 (≥ 14 returns per m^2) (data available from <https://www.paisagenslidar.cnptia.embrapa.br/webgis/>), and a regional model calibrated with forest inventory data in frontier

forests was used to convert top-of-canopy-height estimates to aboveground biomass (36) for each study site. See Rappaport et al. (10) for a detailed explanation of the lidar processing and analysis workflows.

Acoustic Surveys and Data Processing. Circular forest sites (50-m radius) were located at least 300 m from other recording sites or the forest edge and embedded in forest patches (≥ 300 -m radius) with uniform degradation history (SI Appendix, Table S1). Most degradation strata contained three spatially proximate sites to capture the characteristic heterogeneity in forest structure at short length scales from logging infrastructure and differences in fire severity within a single burn scar (10). Passive ARBIMON sound recorders (Automated Remote Biodiversity Monitoring Network) (17) were installed at breast height (1.37 m) at the center of each site and programmed to record 1 min of sound (0 to 22 kHz) every 5 min at a sampling rate of 44.1 kHz over 2 to 8 d during September and October 2016, coincident with the local bird breeding season. In total, 214 full-day records were collected.

Based on a data record of 30,816 1-min recordings, each acoustic sample was transformed into a spectrogram using the ARBIMON analysis platform (<https://arbimon.rfcx.org/>), which graphically decomposed all detected sounds into the spectra of composite frequencies that vary in time and signal strength (sound amplitude). Spectrograms were analyzed in the packages tuneR (53) and seewave (54) using R Version 4.0.3 to catalog all spectral peaks detected by the autonomous sound recorders during every 1-min sample and replicate 24-h survey. Detected peaks were aggregated into daily three-dimensional (3D) sound-scape matrices, which discretized signal detections across "acoustic niche" space defined by time of day (x axis) and sound frequency (y axis). A frequency bin of 86 Hz was selected for acoustic niche size to retain sensitivity to organisms with narrow acoustic niche breadths, including crickets (16, 34). This has the consequence that broadband sound producers may map to multiple acoustic niches. Signal peaks were aggregated at two different time steps—at native 1-min resolution and at 1-h resolution—generating two sets of 3D soundscapes (SI Appendix, Fig. S2). Presence/absence was calculated for each "niche," stratified by time of day and frequency, based on an amplitude filtering threshold of 0.2 to account for signal interference from rain. Amplitude values were normalized by the maximum amplitude values in each soundscape to standardize the amplitude range from 0 to 1 before applying the threshold. The resulting soundscape matrices provided taxonomically synoptic fingerprints of acoustic community composition at each site and time step. From the 3D matrices, ASO was calculated for every unit of time as the percentage of spectral space occupied by detected animal signals (16). Analyses were constrained to frequencies between 3 and 8 kHz, the zone with the greatest spectral overlap among tropical bird, insect, and amphibian species (16) and the spectral range with the lowest likelihood for detection bias from acoustic attenuation due to vegetation scattering in Amazon forests (20).

A correlation analysis was used to evaluate ASO and habitat relationships at the scale of the day and ecologically important time intervals for both temporal aggregation scales (by minute and hour) (SI Appendix, Fig. S2).

Network Analyses. ASO matrices were used to construct weighted bipartite networks with sound frequency bins and sound hour bins as the two classes of nodes. Links between the two classes of nodes depicted occupancy of a given "acoustic niche" (presence of a sound frequency bin during a noted sound hour bin). Links were weighted according to the average number of observations for the link per day. Two levels of network metrics were constructed for each of the 39 sites in the dataset: the global-level analyses summarized the overall time-frequency topology of acoustic communication networks at a given site (AIE; refs. 55–57), and the local-level analyses (node/class) unmixed ASO into the constituent elements that drive overall differences in network structure and connectivity [CC (58) and PD (59)]. The network analyses were performed with the aid of the following packages in R: "igraph" (60), "vegan" (61), and "bipartite" (59).

AIE measures homogeneity in interactions across the network. Greater AIE means that sound hour-sound frequency linkages are more equally distributed

across the day, whereas smaller AIE means that certain sound hours or certain sound frequency bins are more heavily connected than others. Here, we focus on the frequency bins as total n entries, with p_k as proportions of interactions of bin k , and calculate the metric as

$$AIE = \frac{(\sum_n p_k^2)^{-1} - 1}{\prod_n p_k - 1}$$

CC measures transitivity in co-occurrences/connection among the nodes of the same class. It can be calculated for the whole network, the class level, and the node level. Here, we evaluated the CC separately for sound frequency bins and sound hour bins by averaging the CCs of all nodes in a given class (i.e., rows and columns separately). Clustering here refers to the degree to which adjacent nodes in a graph tend to cluster together. In other words, if a frequency bin is present in two or more time bins, how many other frequency bins also share the same structure? Calculations for CC are based on the idea of triplets (58), which consist of three nodes that are joined via either two (open triplet) or three (closed triplet) undirected ties, and indicate the degree of local connectivity in the network. The CC is defined as

$$CC = \frac{\text{number of closed triplets}}{\text{total number of triplets}}$$

PD is the Shannon diversity of the number of interactions for a given node:

$$PD_k = - \sum_m p_i \ln(p_i)$$

where PD_k is the PD of node k of a given class, which has m weighted connections from the other class of nodes, each of which has a proportion of interaction p_i for a node i from the other bipartite node class. This value of PD can be calculated as prescribed for a node and then averaged for a given class, weighted by their marginal totals. PD can also be calculated for the entire network by weighted average of all the nodes' PD values. PD of sound hours is consistent with ASO (SI Appendix, Fig. S4).

To determine the frequency bins with maximum disparity of PD among burned and logged strata, generalized linear models were constructed for PD as a function of fire frequency and years since logging at each frequency band. Then, to evaluate effect size, standardized mean difference was calculated (Cohen's D) using the R package "emmeans" for each frequency band to assess pairwise differences between levels for the two models, and the sum of all the pairwise effect sizes was assessed to estimate the frequency bin of maximum change in each case.

Data Availability. Soundscape matrices data have been deposited in Mendeley Data (<https://dx.doi.org/10.17632/yvysykrfdj.1>) (62).

ACKNOWLEDGMENTS. We gratefully acknowledge the support from the NASA Earth and Space Science Fellowship program and NASA's Biological Diversity and Ecological Forecasting Program to D.I.R. and NASA's Carbon Monitoring System to D.C.M. We also recognize support from the National Science Foundation through the Doctoral Dissertation Research Improvement Grant to D.I.R. and through award DGE-1632976 that supported A.S. Lidar data were acquired by Sustainable Landscapes Brazil with support from the US State Department, US Agency for International Development, and USDA Forest Service. Marcos Longo, Maiza Dos-Santos, and Hyeungu Choi provided assistance with lidar data processing, and Eveline Salvático provided field support for soundscape surveys in this study. We would also like to acknowledge Michael Keller and Matthew Hansen for their feedback on the study design and analysis.

Author affiliations: ^aDepartment of Geographical Sciences, University of Maryland, College Park, MD 20742; ^bDepartment of Biological Sciences, University of Maryland, College Park, MD 20742; and ^cBiospheric Sciences Laboratory, NASA Goddard Space Flight Center, Greenbelt, MD 20771

1. T. A. Gardner et al., Prospects for tropical forest biodiversity in a human-modified world. *Ecol. Lett.* **12**, 561–582 (2009).
2. G. R. Van der Werf et al., CO₂ emissions from forest loss. *Nat. Geosci.* **2**, 737–738 (2009).
3. United Nations Framework Convention on Climate Change, 2021 REDD+ Platform. <https://redd.unfccc.int/>. Accessed 30 January 2021.
4. N. Seddon, B. Turner, P. Berry, A. Chausson, C. A. J. Girardin, Grounding nature-based climate solutions in sound biodiversity science. *Nat. Clim. Chang.* **9**, 84–87 (2019).
5. J. Ferreira et al., Carbon-focused conservation may fail to protect the most biodiverse tropical forests. *Nat. Clim. Chang.* **8**, 744–749 (2018).
6. C. Meyer, H. Kreft, R. Guralnick, W. Jetz, Global priorities for an effective information basis of biodiversity distributions. *Nat. Commun.* **6**, 8221 (2015).

7. J. Troudet, P. Grandcolas, A. Blin, R. Vignes-Lebbe, F. Legendre, Taxonomic bias in biodiversity data and societal preferences. *Sci. Rep.* **7**, 9132 (2017).
8. P. G. Curtis, C. M. Slay, N. L. Harris, A. Tyukavina, M. C. Hansen, Classifying drivers of global forest loss. *Science* **361**, 1108–1111 (2018).
9. J. Barlow *et al.*, Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature* **535**, 144–147 (2016).
10. D. I. Rappaport *et al.*, Quantifying long-term changes in carbon stocks and forest structure from Amazon forest degradation. *Environ. Res. Lett.* **13**, 065013 (2018).
11. Z. Burivalova *et al.*, Avian responses to selective logging shaped by species traits and logging practices. *Proc. Biol. Sci.* **282**, 20150164 (2015).
12. F. França *et al.*, Do space-for-time assessments underestimate the impacts of logging on tropical biodiversity? An Amazonian case study using dung beetles. *J. Appl. Ecol.* **53**, 1098–1105 (2016).
13. M. Dornelas *et al.*, Towards a macroscope: Leveraging technology to transform the breadth, scale and resolution of macroecological data. *Glob. Ecol. Biogeogr.* **28**, 1937–1948 (2019).
14. R. Gibb, E. Browning, P. Glover-Kapfer, K. E. Jones, Emerging opportunities and challenges for passive acoustics in ecological assessment and monitoring. *Methods Ecol. Evol.* **10**, 169–185 (2018).
15. S. S. Sethi *et al.*, Characterizing soundscapes across diverse ecosystems using a universal acoustic feature set. *Proc. Natl. Acad. Sci. U.S.A.* **117**, 17049–17055 (2020).
16. T. M. Aide, A. Hernández-Serna, M. Campos-Cerqueira, O. Acevedo-Charry, J. L. Deichmann, Species richness (of insects) drives the use of acoustic space in the tropics. *Remote Sens.* **9**, 1096 (2017).
17. T. M. Aide *et al.*, Real-time bioacoustics monitoring and automated species identification. *PeerJ* **1**, e103 (2013).
18. J. LeBien *et al.*, A pipeline for identification of bird and frog species in tropical soundscape recordings using a convolutional neural network. *Ecol. Inform.* **59**, 101113 (2020).
19. J. Sueur, A. Farina, A. Gasc, N. Pieretti, S. Pavoine, Acoustic indices for biodiversity assessment and landscape investigation. *Acta Acust. United Acust.* **100**, 772–781 (2014).
20. D. I. Rappaport, J. A. Royle, D. C. Morton, Acoustic space occupancy: Combining ecoacoustics and lidar to model biodiversity variation and detection bias across heterogeneous landscapes. *Ecol. Indic.* **113**, 106172 (2020).
21. B. Krause, Bioacoustics, habitat ambience in ecological balance. *Whole Earth Rev.* **57**, 14–18 (1987).
22. Z. Burivalova *et al.*, Using soundscapes to investigate homogenization of tropical forest diversity in selectively logged forests. *J. Appl. Ecol.* **56**, 2493–2504 (2019).
23. Z. Burivalova *et al.*, Using soundscapes to detect variable degrees of human influence on tropical forests in Papua New Guinea. *Conserv. Biol.* **32**, 205–215 (2018).
24. J. L. Deichmann, A. Hernández-Serna, J. A. Delgado, C. M. Campos-Cerqueira, T. M. Aide, Soundscape analysis and acoustic monitoring document impacts of natural gas exploration on biodiversity in a tropical forest. *Ecol. Indic.* **74**, 39–48 (2017).
25. S. L. Dumyahn, B. C. Pijanowski, Soundscape conservation. *Landsc. Ecol.* **26**, 1327–1344 (2011).
26. R. Planqué, H. Slabbekoorn, Spectral overlap in songs and temporal avoidance in a Peruvian bird assemblage. *Ethology* **114**, 262–271 (2008).
27. A. Eldridge *et al.*, Sounding out ecoacoustic metrics: Avian species richness is predicted by acoustic indices in temperate but not tropical habitats. *Ecol. Indic.* **95**, 939–952 (2018).
28. J. Barlow, C. A. Peres, L. M. P. Henriques, P. C. Stouffer, J. M. Wunderle, The responses of understorey birds to forest fragmentation, logging and wildfires: An Amazonian synthesis. *Biol. Conserv.* **128**, 182–192 (2006).
29. R. B. de Andrade *et al.*, Tropical forest fires and biodiversity: Dung beetle community and biomass responses in a northern Brazilian Amazon forest. *J. Insect Conserv.* **18**, 1097–1104 (2014).
30. N. G. Moura *et al.*, Idiosyncratic responses of Amazonian birds to primary forest disturbance. *Oecologia* **180**, 903–916 (2016).
31. S. Frokling *et al.*, Forest disturbance and recovery: A general review in the context of spaceborne remote sensing of impacts on aboveground biomass and canopy structure. *J. Geophys. Res.* **114**, G00E02 (2009).
32. L. A. Rabin, C. M. Greene, Changes to acoustic communication systems in human-altered environments. *J. Comp. Psychol.* **116**, 137–141 (2002).
33. U. de Camargo, T. Roslin, O. Ovaskainen, Spatio-temporal scaling of biodiversity in acoustic tropical bird communities. *Ecography* **42**, 1936–1947 (2019).
34. A. K. Schmidt, H. Römer, K. Riede, Spectral niche segregation and community organization in a tropical cricket assemblage. *Behav. Ecol.* **24**, 470–480 (2012).
35. C. Q. Stanley, M. H. Walter, M. X. Venkatraman, G. S. Wilkinson, Insect noise avoidance in the dawn chorus of Neotropical birds. *Anim. Behav.* **112**, 255–265 (2016).
36. M. Longo *et al.*, Aboveground biomass variability across intact and degraded forests in the Brazilian Amazon. *Global Biogeochem. Cycles* **30**, 1639–1660 (2016).
37. M. M. Mollinari, C. A. Peres, D. P. Edwards, Rapid recovery of thermal environment after selective logging in the Amazon. *Agric. For. Meteorol.* **278**, 107637 (2019).
38. J. K. Balch, T. J. Massad, P. M. Brando, D. C. Nepstad, L. M. Curran, Effects of high-frequency understorey fires on woody plant regeneration in southeastern Amazonian forests. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **368**, 20120157 (2013).
39. R. R. Solar *et al.*, How pervasive is biotic homogenization in human-modified tropical forest landscapes? *Ecol. Lett.* **18**, 1108–1118 (2015).
40. J. M. Silveira *et al.*, A multi-taxa assessment of biodiversity change after single and recurrent wildfires in a Brazilian Amazon forest. *Biotropica* **48**, 170–180 (2016).
41. Z. Burivalova, Ç. H. Sekercioglu, L. P. Koh, Thresholds of logging intensity to maintain tropical forest biodiversity. *Curr. Biol.* **24**, 1893–1898 (2014).
42. C. Gray *et al.*, FORUM: Ecological networks: The missing links in biomonitoring science. *J. Appl. Ecol.* **51**, 1444–1449 (2014).
43. H. Hillebrand *et al.*, Biodiversity change is uncoupled from species richness trends: Consequences for conservation and monitoring. *J. Appl. Ecol.* **55**, 169–184 (2018).
44. W. F. Laurance *et al.*, An Amazonian rainforest and its fragments as a laboratory of global change. *Biol. Rev. Camb. Philos. Soc.* **93**, 223–247 (2018).
45. M. Pfeifer *et al.*, Creation of forest edges has a global impact on forest vertebrates. *Nature* **551**, 187–191 (2017).
46. P. M. Brando *et al.*, Abrupt increases in Amazonian tree mortality due to drought-fire interactions. *Proc. Natl. Acad. Sci. U.S.A.* **111**, 6347–6352 (2014).
47. C. A. Peres, T. Emilio, J. Schietti, S. J. Desmoulière, T. Levi, Dispersal limitation induces long-term biomass collapse in overhunted Amazonian forests. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 892–897 (2016).
48. S. L. Collins, Disturbance frequency and community stability in native tallgrass prairie. *Am. Nat.* **155**, 311–325 (2000).
49. P. M. Fearnside, "Fire in the tropical rain forest of the Amazon basin" in *Fire in the Tropical Biota*, J. Goldammer, Ed. (Springer, 1990), pp. 106–116.
50. M. A. Cochrane, M. D. Schulze, Fire as a recurrent event in tropical forests of the eastern Amazon: Effects on forest structure, biomass, and species composition¹. *Biotropica* **31**, 2–16 (1999).
51. J. K. Balch *et al.*, The susceptibility of southeastern Amazon forests to fire: Insights from a large-scale burn experiment. *Bioscience* **65**, 893–905 (2015).
52. A. C. Staver *et al.*, Thinner bark increases sensitivity of wetter Amazonian tropical forests to fire. *Ecol. Lett.* **23**, 99–106 (2020).
53. U. Ligges, *et al.*, tuneR-analysis of music (R Foundation, 2016).
54. J. Sueur, T. Aubin, C. Simonis, Seewave, a free modular tool for sound analysis and synthesis. *Bioacoustics* **18**, 213–226 (2008).
55. R. V. Alatalo, Problems in the measurement of evenness in ecology. *Oikos* **37**, 199–204 (1981).
56. C. B. Muller, I. C. T. Adriaanse, R. Belshaw, H. C. J. Godfray, The structure of an aphid-parasitoid community. *J. Anim. Ecol.* **68**, 346–370 (1999).
57. G. Stirling, B. Wilsey, Empirical relationships between species richness, evenness, and proportional diversity. *Am. Nat.* **158**, 286–299 (2001).
58. D. J. Watts, S. H. Strogatz, Collective dynamics of 'small-world' networks. *Nature* **393**, 440–442 (1998).
59. C. Dormann, How to be a specialist? Quantifying specialisation in pollination networks. *Network Biol.* **1**, 1–20 (2011).
60. G. Csardi, T. Nepusz, The igraph software package for complex network research. *InterJournal Complex Syst.* **1695**, 1–9 (2006).
61. J. Oksanen *et al.*, Community ecology package (R Package Version 2, R Core Team Vienna, Austria, 2013).
62. D. Rappaport, Amazon forest soundscapes affected by fire and logging. Mendeley Data. <https://data.mendeley.com/datasets/yjvysykrfdj/1>. Deposited 7 April 2022.