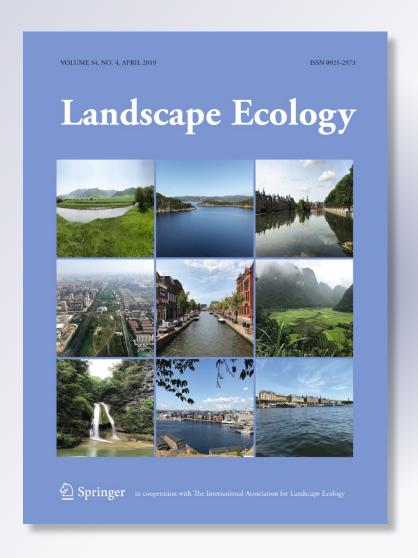
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RESEARCH ARTICLE



Using soundscapes to assess biodiversity in Neotropical oil palm landscapes

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Abstract

Context Expanding oil palm plantations have caused widespread deforestation and biodiversity loss in Southeast Asia, stigmatizing the industry around the world regardless of regional context. In Latin America, oil palm plantations are primarily replacing other agroindustrial land uses with uncertain implications for local biodiversity.

Objectives Our aim was to create empirical baseline data to help guide development of future plantations into areas where biodiversity impacts are minimized. We used soundscapes to assess fauna in oil palm landscapes of Colombia, the world's 4th largest palm oil producer.

Methods Soundscapes capture daily patterns of acoustic activity that can be used to measure differences between biotic communities between habitats.

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Using remnant forest fragments as reference sites, we sampled land use classes that are commonly replaced by commercial oil palm including cattle pastures, rice fields, and banana plantations.

Results Soundscape analysis showed that even highly degraded forests have a unique soundscape compared to production systems. Similarities were found among closed canopy production sites (oil palm, banana) and open production habitat (pastures, rice), suggesting the importance of habitat structure for acoustic communities. Oil palm also showed notable overlap with pastures, but had soundscapes that were more similar to forest than the other production types.

Conclusions Future oil palm development in Latin America can replace cattle pastures and other commodity plantation agriculture with minimal impacts on acoustic communities. New supply chain governance approaches such as the zero-deforestation agreements being implemented in the Colombian oil palm and cattle sectors may help guide the industry toward more sustainable development by continuing to target previously cleared lands.

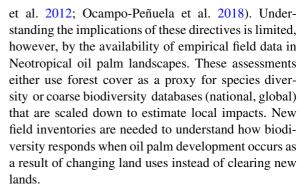
Keywords Bioacoustics · Biodiversity conservation · Commodity crops · Forest patch · Indicator species · Latin America · Riparian forest · Sustainability



Introduction

The global expansion of oil palm monocultures (Elaeis guineensis) to meet increased vegetable oil demand is transforming landscapes and livelihoods across the tropics. Though an important economic engine in rural areas, the industry is controversial due to the environmental impacts it has caused. Specifically, oil palm agriculture has been directly responsible for widespread deforestation and habitat loss in Southeast Asia, with corresponding impacts on biodiversity and ecosystem functioning (Koh and Wilcove 2008; Savilaakso et al. 2014; Barnes et al. 2014). Most attention has focused on the oil palm landscapes of Malaysia and Indonesia, where commercial plantations have often been established on primary or logged forest frontiers (Gaveau et al. 2016); therefore, most of our knowledge of how oil palm development impacts biodiversity comes from comparisons between plantations and forest (Foster et al. 2011; Dislich et al. 2017). Minimal consideration has been given to oil palm replacing non-rainforest habitats or other productive land uses, especially outside of Asia (Pardo et al. 2015).

This research gap is particularly wide for Latin America, where nearly 80% of oil palm expansion has replaced non-forested areas, typically cattle pastures and other commodity crops such as banana plantations (Furumo and Aide 2017). In Colombia, the largest palm oil producer in the region and 4th largest worldwide, the legacy of export-oriented plantation agriculture (Richardson 1995) and pervasive cattle ranching (Etter et al. 2008) has resulted in highly heterogeneous and ecologically degraded oil palm landscapes unlike those of Asia. With projections of continued oil palm expansion in the region, there is a strong need for field-based evidence to inform development policies that can direct oil palm production to areas where impacts on biodiversity are minimized (Gilroy et al. 2014). Thus far, these efforts have focused on spatial expansion scenarios at the territory or regional level to direct future plantation development (Garcia-Ulloa et al. 2012; Castiblanco et al. 2013; de Carvalho et al. 2015; Ocampo-Peñuela et al. 2018). In general, these studies have prioritized nonor previously degraded achieve "biodiversity neutral" expansion, especially given the abundance of these previously cleared lands adjacent to current areas of production (Garcia-Ulloa



The implications for biodiversity when converting different land uses to oil palm are largely unknown. Meta-analyses of the impacts of forest conversion to different land uses suggest that non-timber plantation monocultures like oil palm are more impactful to biodiversity than timber plantations or selectivelylogged forests (Chaudhary et al. 2016) but are less determinantal to species than open-canopy agricultural (Gibson et al. 2011). Could oil palm provide a better habitat or matrix for forest species movement than pastures and other crops, due to its long productive lifespan and closed canopy structure (Alexander von Humboldt Institute 2000)? Though structurally simplified compared to forests, mature, closed canopy oil palm plantations form microhabitats in the understory (leaf litter) and trunks (epiphytes) that can influence local biodiversity (Koh 2008; Azhar et al. 2011). These microhabitats are essentially absent in cattle pastures. Perhaps more important for animal communities may be the relatively long life cycle of oil palm plantations compared to other perennial (e.g. banana) and seasonal (e.g. rice) crops in these landscapes, providing a habitat that remains relatively undisturbed for at least 20-25 years, until replanting. Furthermore, harvesting is done manually, usually twice a month with periods of relative inactivity in between. Finally, chemical pesticide use is lower on oil palm plantations compared to both banana and rice, which require high inputs to prevent crop loss (Barraza et al. 2011; personal observation).

To understand the distribution of biodiversity in highly modified and degraded Neotropical oil palm landscapes, we used bioacoustic monitoring—an emerging tool of landscape ecology. Sound recorded in the environment is composed of three sources—geophony (e.g. stream, wind), biophony (e.g. bird song), and anthrophony (e.g. machinery)—which together make up the *soundscape* (Pijanowski et al.



2011). Soundscapes allow researchers to visualize patterns of acoustic activity in a habitat throughout a defined period of time (e.g. day, month, year) to monitor temporal differences in acoustic communities that can be attributed to heterogeneity in the environment. In essence, soundscapes provide a measure of how biogeophysical and anthropogenic factors influence the presence and behavior of vocalizing species. Soundscape analysis has provided a useful tool to study biodiversity along gradients of human disturbance (Tucker et al. 2014; Bobryk et al. 2016; Burivalova et al. 2017; Deichmann et al. 2017), though researchers have not tapped this potential to understand the impacts of different land use activities at larger spatial scales (i.e. regional, national) beyond the forest setting.

Here, we compare the acoustic communities of different land covers commonly replaced by expanding oil palm plantations in the Neotropics. Specifically, we analyze the soundscapes of six habitats forest patches, riparian forest, oil palm plantations, banana plantations, rice fields, and cattle pastures that define oil palm landscapes in northern Colombia. We predict that the closed canopy structure and permanence of oil palm crops will result in soundscapes that have more similarity to forest patch reference sites than do other production habitats. We also use species indicator analysis to evaluate which regions of the soundscape (time and frequency) are most important in defining each habitat, and we examine the original recordings to determine the source of this acoustic activity. We discuss the implications of our findings in the context of regional land use change dynamics and conservation initiatives.

Materials and methods

Study site

The majority of oil palm production in Colombia is concentrated in three primary production zones known as the North, Central, and East zones (Fig. 1b). The North production zone is situated in the oldest and most densely populated agro-industrial region of Colombia (Ospina and Ochoa 1998), between two important natural, protected areas: (1) the Sierra Nevada de Santa Marta, and (2) the Ciénega Grande

de Santa Marta (Fig. 1c, d). The United Fruit Company began operations in the region over 100 years ago growing banana, and planted the first oil palms in 1945 (Ospina and Ochoa 1998). Other crops such as cotton and rice have also had an important tradition in the region, as well as extensive cattle ranching. Booms in oil palm planting occurred some years later, replacing banana and other crops in the 60s and again in the early 80s (Ospina and Ochoa 1998). In the last decade production has nearly doubled, and today about 125,000 hectares of oil palm are planted in the North zone (Fedepalma 2017).

Due to the long history of production in the region, the North zone is also the most transformed of Colombia's oil palm production zones. Very little lowland forest cover remains, and rarely are these remnants found in patches larger than a few hectares. Most forest fragments are in some stage of regeneration, or found in thin strips along waterways or on poor soils (high salinity, flooded areas). Colombian law stipulates a 30-m natural vegetation buffer along major waterways (Decree 2811, 1974), but this is rarely enforced. Population pressure on the land has resulted in degradation of the remaining forests, with local residents commonly extracting wood for fence building and firewood, as well as using these habitats for hunting and fishing. The resulting landscape is markedly anthropogenic, and this is reflected in the heterogeneity of land covers in oil palm landscapes. In this study, we sampled biodiversity on oil palm plantations and surrounding land covers in the Magdalena and Cesar departments of northern Colombia (Fig. 1). This region features tropical dry forest and xeric shrubland biomes. Field sampling was conducted from October to December 2016, during the transition between the wet and dry season in the region. All oil palm plantations included in the sample were in production and had a fully formed canopy (> 8 years old).

Acoustic data collection

We used the Automated Remote Biodiversity Monitoring Network (ARBIMON) platform for analysis of acoustic data, and portable sound recorders programmed with the ARBIMON Touch application for data collection (https://arbimon.sieve-analytics.com/). At each site, we programmed recording devices to record 1 minute of audio every 10 min throughout the



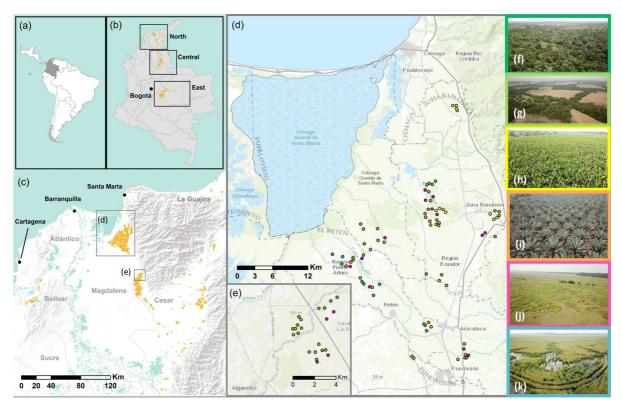
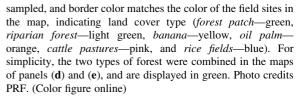


Fig. 1 Map of study region in Colombia (**a**) featuring the three primary oil palm production zones: North, Central, and East zones (**b**). Oil palm plantations are indicated by orange polygons (from Furumo and Aide 2017). Study was conducted in the North production zone (**c**) with field sites situated in the boxes around the *Zona Bananera* (**d**) and *Ariguani* (**e**) regions (basemap from ESRI). **d**, **e** Expanded to show field sites in greater detail (n = 102 total). **f-k** The land cover classes

24-h cycle, resulting in 144 samples per day. We installed recorders at a height of 1-2 m on plantation vegetation, small bushes (pastures and rice), or trees (forest). We separated recorders by at least 300 m in the field to ensure independent samples; we also tried to maintain a minimum of 300 m from habitat edges to avoid edge effects or fauna associated with other habitats. This was not always possible, due to the limited size of forest fragments. We selected the largest remnants of forest available in these landscapes as control sites. Recorders were active in the field for 4-7 days or until battery depletion, producing an average of 675 one-minute recordings at each site. Recorders used a sampling rate of 44.1 kHz/16 bit and detected sounds emitted between 0 and 22 kHz, corresponding with the frequency ranges of most birds, amphibians, insects, and mammals (excluding bats).



Soundscapes

Soundscapes (i.e. a three-dimensional representation of the soundscape used for analysis) are essentially a spectrogram, or visualization of the patterns of acoustic activity (call frequencies) displayed throughout the course of a day (24 h). We followed the approach of Campos-Cerqueira and Aide (2017) to generate soundscapes using ARBIMON; we aggregated recordings by hour of day (24 h) for each site, using a frequency bin size of 172 Hz, but we used an amplitude-filtering threshold of 0.007 rather than 0.01. Campos-Cerqueira and Aide (2017) sampled one habitat type (i.e. forest), while our study included multiple habitat types with differing acoustic environments. Due to this variation, we experimented with several different amplitude thresholds (i.e. 0.004,



0.007, and 0.01) and found that 0.007 was the most balanced and consistent across habitat types. For instance, a threshold of 0.01 filtered out many insect signals present at higher frequencies, while 0.004 included too much background noise. The amplitude threshold is relative and as long as the same value is used for this parameter at each site they are comparable. This process yields a three-dimensional display of acoustic activity, with time (hours) on the x-axis, acoustic frequency (Hz) on the y-axis, and proportion of recordings with a peak of activity > 0.007 amplitude on the z-axis (Fig. 2). We normalized the data based on the number of recordings collected for each hour to control for differences between sites. Each

soundscape contained 3072 time—frequency bins (24 h * 128 frequency bins), and each bin is a variable for comparing different regions of the soundscape among sites. We generated a soundscape for each of our 102 field sites (forest patches n = 14, riparian forest n = 10, oil palm n = 44, banana n = 11, pasture n = 17, rice n = 6; Fig. 2).

NMDS ordination

We plotted the sites (n = 102) in ordination space based on the 3072 time-frequency bins associated with each soundscape, to evaluate the effect of habitat type (Fig. 3). We used the *metaMDS* function from the

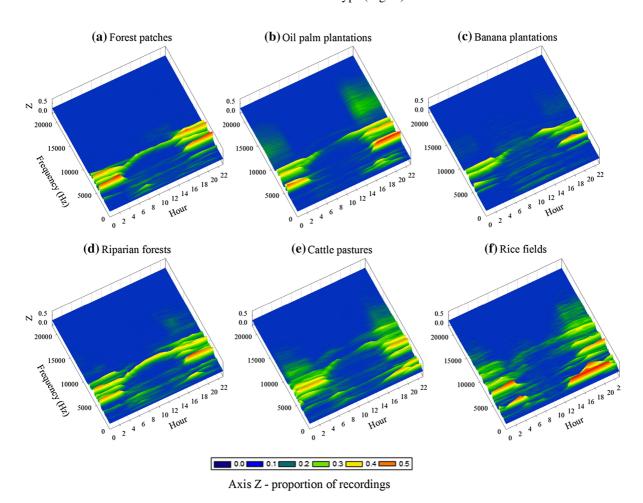
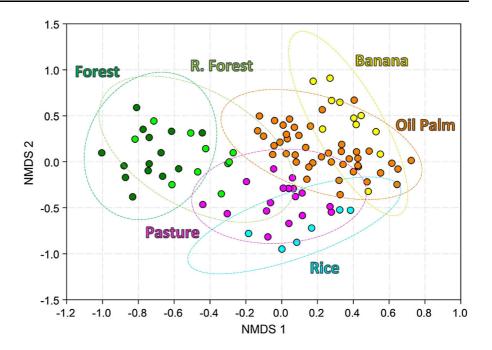


Fig. 2 Global soundscapes based on all recordings from all replicates of each habitat type (forest patches n = 14 [8967 recordings]; oil palm n = 44 [29,566 recordings]; banana n = 11 [8399 recordings], riparian forest n = 10 [6592 recordings]; cattle pastures n = 17 [11,633 recordings]; rice fields n = 6 [3630 recordings]). Time (h) displayed on x-axis; frequency

(Hz) displayed on y-axis, proportion of recordings with peaks above amplitude threshold displayed on z-axis. General frequency ranges of different taxa: Low (< 4 kHz)—anthropogenic, anurans; primates; Medium (4-6 kHz)—birds, insects; primates; High (> 6 kHz)—insects



Fig. 3 NMDS ordination of 102 soundscapes from oil palm landscapes of northern Colombia. Group centroids are shown with 95% confidence interval ellipses. Forest patch (dark green) n = 14; riparian forest (light green) n = 10; oil palm (orange) n = 44; banana (yellow) n = 11; cattle pastures (pink) n = 17; rice fields (light blue) n = 6. Average dissimilarity between forest (patch and riparian) and production habitats: forest versus oil palm/pasture = 78%; forest versus banana/rice = 84%. (Color figure online)



vegan package in R (R v1.0.136, 2013), which performs a non-metric multidimensional scaling (NMDS) based on Bray–Curtis dissimilarity indices. NMDS facilitates visualization and interpretation of complex ecological information by collapsing data from multiple dimensions into few; the test uses rank orders (instead of absolute abundances) of distances, or pair-wise dissimilarity, to find a solution configuration of points that minimizes stress (see Supporting Information). We performed ANOVA with the NMDS scores to determine which land covers had statistically similar soundscapes when plotted in ordination space. In addition to data visualization with NMDS, we used the original dissimilarity indices to calculate the average dissimilarity between land cover classes.

Indicator bins

To identify which time-frequency bins were most important in classifying soundscapes into their respective habitat types, we used tools from the Vegan package in R to conduct an indicator species analysis. We first used Bray-Curtis distances between sound-scapes to perform a hierarchical clustering of our sites based on average distances (Oksanen 2014). Then we conducted an indicator species analysis to summarize community composition of each cluster using the function *indval* from the *labdsv* package in R. The

function indval combines relative frequency and relative average abundance of species in each cluster to find species assemblages that characterize groups of sites (Oksanen 2014). The indicator index is maximized when "all individuals of a species are found in a single group of sites and when the species occurs in all sites of that group" (Dufrene and Legendre 1997). When working with soundscapes, the "species" are equivalent to the time-frequency bins; however, just because two sites have bins in common with acoustic activity does not necessarily mean that these vocalizations are from the same biological source. We selected the significant indicator bins (p </= 0.001) and used ARBIMON to visualize these regions of the soundscape and determine the taxa responsible for the corresponding acoustic activity in each bin.

Results

Soundscapes

We sampled a total of 102 sites representing the six major habitat types in the region: oil palm plantations (n = 44), cattle pastures (n = 17), forest patches (n = 14), riparian forest (n = 10), banana plantations (n = 11), and rice fields (n = 6). For each habitat type, we created a global soundscape for all sites (n) sampled



(Fig. 2). Despite the often degraded state of forest fragments in oil palm landscapes of northern Colombia, we use the forest patch class as our reference habitat type due to a lack of remaining lowland contiguous forest. When considering the forest patch as a control group, a pattern emerges when comparing soundscapes along a disturbance gradient from natural sites (forest) to production sites (agriculture). The forest patch soundscape features a characteristic "arc" of insect activity during the daytime hours, as well as a more conspicuous morning chorus of bird activity from 0500 to 0800 h (Fig. 2a). This general arc structure of the soundscape is conserved in the riparian forest sites, and to a lesser extent in the oil palm and banana sites. This signal becomes more degraded in pasture and rice sites as the soundscapes become more saturated with insect and anuran activity (Fig. 2e, f). This pattern also reflects habitat structure, from closed canopy (forest, oil palm, banana) to open habitats (pasture, rice).

NMDS ordination

The differences observed in soundscapes are given new perspective in the NMDS ordination (Fig. 3; stress = 0.21). The 102 soundscapes form groups according to land cover classes that reflect habitat type. We first note the separation of "natural" sites (forest patches and riparian forest) from "production" sites (oil palm, banana, cattle pastures, rice) along the x-axis of the ordination (NMDS 1). Along the y-axis (NMDS 2), the production sites separate into regions of ordination space that represent closed habitat (oil palm, banana) and open habitat (pasture, rice), with banana and rice on the fringes of these regions, respectively. There is considerable overlap between sites of oil palm and cattle pastures along this axis; however, the majority of oil palm sites are plotted between -0.25 and 0.5 on NMDS 2, showing the closest similarity with forest sites along this axis. Using only forest patch sites as a reference class (dark green, Fig. 3), ANOVA shows no significant differences between oil palm and forest along NMDS 2 (p = 0.62) whereas strong statistical differences were found between forest and other production types along this axis (p = < 0.0001). Although production sites showed large overall dissimilarity with forest sites, oil palm and pastures had soundscapes more similar to forest sites than banana and rice (78% and 84% average dissimilarity, respectively).

Indicator bins

The cluster analysis yielded four clusters to conduct the indicator species analysis (see Supporting Information). The indicator species analysis identified 410 significant time-frequency bins in total: open habitat (195), oil palm (97), forest (88), and banana (30). We plotted these indicator bins in a soundscape to better visualize the signature regions for each habitat type (Fig. 4). We also determined the source of sound responsible for acoustic activity in these bins from the original recordings. Of the 410 total indicator bins, we identified 31 unique sources of sounds, or acoustic morphospecies (morphos), present in the time-frequency bins. Most morphos were attributed to insect taxa (65%), but we also identified several species of bird, amphibian, and a mammal species present (Table 1). Several insect morphos were found in the indicator bins of more than one habitat (see Supporting Information).

The characteristic arc structure of soundscapes from forest sites was also evident from the indicator bins, and attributed to three morphos, m8-10. Two of these (m8-9) were found in the indicator bins located between 5160 and 6078 Hz, with the three lowest frequency bins in this range containing only morpho m8 (Fig. 4a). The forest cluster (Table S1) featured five birds as indicator species (Leptotila verreauxi, Hypnelus ruficollis, Thamnophilus doliatus, Campylorhynchus griseus, Ortalis garrula) and the only mammal (Alouatta seniculus). The open habitat sites have the only other frequency bin driven by bird activity (Furnarius leucopus), an ovenbird species common in open areas, as well as the only indicator bins containing anuran species (Boana xerophyla, Leptodactylus fragilis, Leptodactylus fuscus). All indicator bins for the oil palm group were associated with insect activity. In banana sites, we identified two morphospecies of insects, and the only group with an anthropogenic morpho—16 indicator bins ranging from 688 to 14,792 Hz around midday, representing the sound produced by sprinkler irrigation, a mainstay of banana plantations.



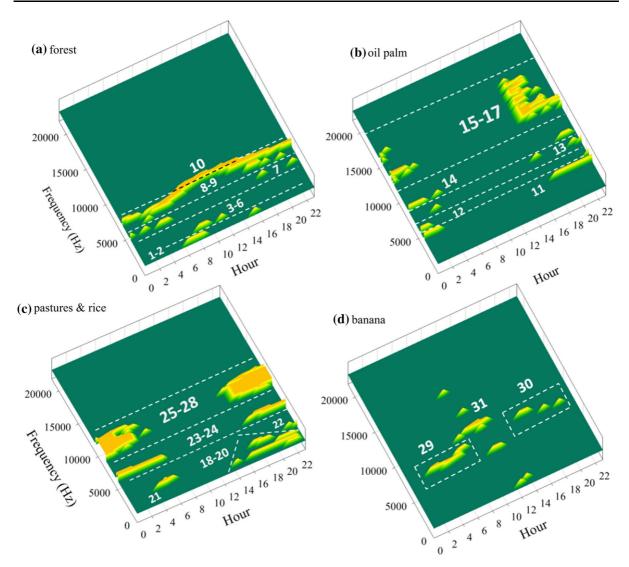


Fig. 4 Soundscapes of indicator bins for four groups returned from cluster analysis: **a** natural (forest patches and riparian forest), **b** oil palm, **c** open habitat (rice and pasture), and **d** banana. Soundscapes were plotted with presence/absence of indicator bins. For illustration, the presence of a bin is indicated

by a 3-D tri-colored green, yellow, and orange peak. The numbered boxes and bands represent the morphospecies associated with individual or groups of indicator bins (from column "Morpho" in Table 1). (Color figure online)

Discussion

A central challenge for the global palm oil industry moving forward will be balancing environmental and socio-economic priorities while increasing production to meet consumer demand that is more concerned with sustainability (Eakin et al. 2017; Rueda et al. 2017). The highly transformed production landscapes of Latin America—defined by ample, low-density cattle ranchlands—may present an opportunity to develop

the oil palm sector while minimizing the impact on biodiversity (Gilroy et al. 2014; Ocampo-Peñuela et al. 2018). However, a lack of field data in these landscapes still hampers the effort to identify areas where oil palm should be directed on a local scale. In particular, the ecological implications of oil palm supplanting other commodities have so far been unexplored in the region, despite this representing a common pathway for oil palm development (Furumo and Aide 2017). We build on previous work in



Table 1 Biotic and anthropogenic sources of indicator bins identified to taxa or species level where possible

Morpho (m)	Class	Frequency bin range	Taxa	Species
1	Forest	516–688	Mammal	Alouatta seniculus
2		516–688	Bird	Leptotila verreauxi
3		1548-1892	Bird	Hypnelus ruficolis
4		1548-1892	Bird	Thamnophilus doliatus
5		1548-1892	Bird	Campylorhynchus griseu
6		1548-1892	Bird	Ortalis garrula
7		3956-4128	Insect	
8		5160-6708	Insect	
9		5676–6708	Insect	
10		6536–7224	Insect	
11	Oil palm	3956-4128	Insect	
12		4816-4988	Insect	
13		6536-7052	Insect	
14		7912-8084	Insect	
15		11,696–17,200	Insect	
16		11,696–17,200	Insect	
17		11,696–17,200	Insect	
18	Open (pasture/rice)	688-1548	Anuran	Boana xerophyla
19		1032-1548	Anuran	Leptodactylus fragilis
20		2236-2408	Anuran	Leptodactylus fuscus
21		2408-2580	Bird	Furnarius leucopus
22		2580–2752	Insect	
23		5332-11,180	Insect	
24		5332-11,180	Insect	
25		8428-8772	Insect	
26		8428-11,008	Insect	
27		8944-11,008	Insect	
28		8944-11,008	Insect	
29	Banana	6536–7568	Insect	
30		7740–8428	Insect	
31		688-14,792	Anthrophony	Irrigation sprinkler

Column "Class" is based on the four clusters identified by cluster analysis. Column "Frequency bin range" indicates the minimum and maximum frequency of the indicator bins in which a morphospecies was found (based on 172 Hz frequency intervals of bins). Note that some indicator bins contain multiple morphospecies. Morphos 23 and 24 are likely two different vocalizations of the same species

Colombia by using soundscapes to show that oil palm plantations have acoustic communities that are more similar to remnant forest fragments than are other productive land uses—i.e. cattle pasture, banana, rice. Our results provide evidence that these non-forest, production land uses can be converted to oil palm plantations with minimal impacts on forest species. Furthermore, our study demonstrates the potential of

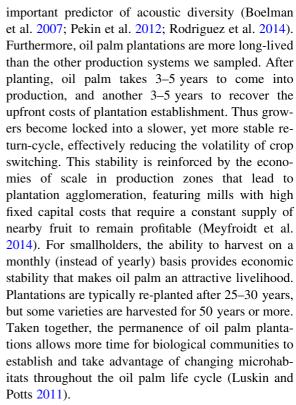
acoustic ecology as a novel and informative approach to rapidly evaluate the effects of landscape-level changes on biodiversity.

Soundscape analysis is effective in differentiating land uses. Even though the forest "reference" sites in our study were highly degraded, these soundscapes were significantly different from the soundscapes of the production sites when plotted in ordination space.



The increased diversity of forest sites is also supported by indicator species analysis which shows that nearly all bird morphos and the only mammal morpho, a howler monkey, were found in forest sites. Three of these birds (C. griseus, H. ruficollis, O. garrula) have relatively small ranges limited to dry forests and shrublands of northern South America, while L. verreauxi and T. doliatus have non-specific ranges that extend throughout the Americas. However, all species are common in secondary or degraded forests, as well as habitat edges, suggesting that these are more generalist species in these oil palm landscapes. Nonetheless, soundscape analysis suggests that small forest fragments may have understated conservation value in highly modified landscapes when contiguous forest is absent. Studies in oil palm landscapes of Asia conclude that only large forest fragments can approach the conservation value of contiguous forests (700 ha; Edwards et al. 2010) or contribute to adjacent plantation diversity through spillover (200 ha; Lucey et al. 2014). The forest patches we sampled ranged between 2 and 275 hectares; withholding the two largest patches (275 and 162 ha), the average patch size was only 30 hectares. Yet these forest patches show more separation from oil palm and other production sites in ordination space than similar comparisons of species assemblages in Asia sampled using traditional field surveys (Edwards et al. 2010). If the lack of regional, lowland contiguous forest raises the conservation stakes of remaining patches, this may be exacerbated in the North zone of Colombia where these small forest remnants provide the only habitat connectivity between protected areas (Fig. 1c). Protection of these remaining habitat patches should therefore be prioritized by oil palm growers at both the plantation and landscape level.

Soundscapes from oil palm plantations and pastures were most similar to forest soundscapes, and NMDS ordination suggests that the acoustic communities in oil palm have the most in common with forest communities (Fig. 3). Similarities between oil palm and forest soundscapes are undoubtedly attributed to the vertical structure of oil palm plantations, which form a 10–15 m closed canopy that increases availability of understory microhabitats, and more closely resemble forest structure than the other production systems sampled (Danielsen et al. 2009; Correa et al. 2015). Vertical vegetation structure and thereby complexity of habitat has been shown to be an



While indicator species analysis allowed us to derive a degree of species-level information from acoustic communities in soundscapes—i.e. which species contributed most to defining the soundscape of each habitat—we acknowledge the need to include parameters such as species richness and composition to understand detailed species-level responses to land use changes. This is especially true for bird and mammal taxa since soundscapes tend to be dominated by insect activity (Aide et al. 2017). Oil palm habitat shares elements of both open and closed canopy systems, reflected in the considerable overlap with pasture sites in ordination space. On a species-level, our soundscape results are in line with a study conducted in the East zone of the Colombian oil palm sector that compared different taxa among oil palm plantations, cattle pastures, and forest fragments, and found that oil palm had similar or higher species richness than pastures across most taxa, but lower species richness than forests (Gilroy et al. 2014). It was evident from the soundscapes that anurans are present in oil palm plantations (peaks < 4 kHz between 1500 and 2200 h; Fig. 2b), but only anurans from the open habitat sites registered as indicator species. This is likely due to their higher abundance in



open habitat at the time of sampling, as rice fields and pastures become flooded during the rainy season and support dense populations of both anurans and water birds. While oil palm will never be a replacement for forest, soundscape analysis suggests it may provide a better matrix for forest species movement through the landscape than other production systems. Future studies could link species-level acoustic data with landscape variables (e.g. composition, configuration) to better understand how species use different habitats and navigate human-modified landscapes (Knowlton et al. 2017).

Future oil palm plantations will likely be developed near the infrastructure of existing production nuclei to access extension services and minimize distances for transporting fruit (Meyfroidt et al. 2014). In Colombia, there are ample previously cleared lands surrounding existing plantations and these areas show little overlap with endangered species (Garcia-Ulloa et al. 2012; Ocampo-Peñuela et al. 2018). We echo other researchers in prioritizing the development of these lands for future plantations, and we present field evidence that oil palm can be pursued here with neutral effects on the acoustically active fauna. Policies supporting plantation development onto previously cleared lands, however, must still address the risk of indirect land use changes such as the displacement of ranching or other agricultural activities to forest frontiers (Lambin and Meyfroidt 2011). This risk may be lower in Colombia where the average stocking rate is low (0.6 heads of cattle per hectare), and pasturelands are estimated to already occupy some 40 million hectares, or 35% of the national territory (Tapasco et al. 2015). Indeed, many pastures are often found in a state of abandonment, and oil palm expansion onto these degraded lands may preclude indirect land use changes elsewhere (Hennenberg et al. 2009). In November 2017, a zero-deforestation agreement was signed among stakeholders in the Colombian palm oil supply chain, including over 20 mills, national/international processors and traders, civil society groups, and the national government (TFA2020 2017). Organized under the Tropical Forest Alliance 2020 initiative, a parallel effort is also being developed for the national beef and dairy sectors. If these programs are successful, pastures and other degraded land uses will continue to be important sources of future oil palm expansion, and the coordinated intervention across cattle and oil palm sectors may help mitigate indirect land use change effects. Such public—private partnerships are gaining recognition for bringing a variety of stakeholders together to govern along regional or jurisdictional boundaries and broadening the scope of commitments set forth by certification programs like the Roundtable on Sustainable Palm Oil (RSPO), with potential to deliver greater benefits for biodiversity in production land-scapes (Fishman et al. 2017; Lambin et al. 2018).

Conclusion

If cattle pastures continue to be the primary source of new oil palm plantations in Latin America, soundscape analysis suggests that there will be neutral or even slightly positive outcomes for biodiversity. While this study focuses on the response of acoustic communities to oil palm expansion in Colombia, future studies will benefit from compiling species lists to understand the species-specific responses to these land use changes, and considering the effects of the larger landscape context on plantation biodiversity. In addition to the availability of previously cleared lands for oil palm development in the region, new publicprivate governance mechanisms are building on existing market-based tools to prevent deforestation in the palm oil supply chain, yet most standards still inadequately address biodiversity. For instance, land cover (i.e. forest) is still often used as a blanket proxy for conservation value in certification programs (Yu Ting et al. 2016), but this approach will have limited application in the non-forested or highly modified oil palm production landscapes of Latin America. Fieldbased monitoring therefore remains critical to evaluate the effectiveness of these conservation initiatives in situ, and acoustic tools offer a systematic and standardized solution (Deichmann et al. 2018). Our study demonstrates the value of low-cost, automated recorders for rapidly generating data at large spatial scales that can be used to extract different tiers of ecological information (i.e. community, species). Another advantage is that recordings provide a permanent record that can be referenced for future studies and as a potential solution to long-term biodiversity monitoring and management plans required by RSPO certification.

While this study assessed the biodiversity of common land use alternatives to oil palm in northern



Colombia, other major oilseed alternatives are not grown in this region, so what do these results mean for the global debate on palm oil? Based on the differences in soundscapes we observed between open and closed-canopy production systems, it is doubtful that the open crop structure and short harvest cycle of other major oilseeds grown in the tropics (i.e. soybean) could support more biodiversity than oil palm plantations (Meijaard et al. 2018). Oil palm is also over four times more productive than alternative oilseeds, reducing the land area needed to meet demand for vegetable oil. Efforts of banning palm oil would therefore be better directed toward improving and increasing the adoption of current initiatives for more sustainable production.

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