

REVIEW

Detecting ecological thresholds for biodiversity in tropical forests: Knowledge gaps and future directions

Yara Shennan-Farpón^{1,2}  | Piero Visconti³  | Ken Norris⁴ 

¹ZSL Institute of Zoology, Regent's Park Outer Circle, London, UK

²Department of Anthropology, University College London, London, UK

³International Institute for Applied Systems Analysis, Laxenburg, Austria

⁴Natural History Museum, London, UK

Correspondence

Yara Shennan-Farpón, ZSL Institute of Zoology, Regent's Park Outer Circle, London NW1 4RY, UK
Email: yara.shennan-farpon.17@ucl.ac.uk

Funding information

Natural Environment Research Council, Grant/Award Number: NE/L002485/1

Associate Editor: Eleanor Slade

Handling Editor: Edward Webb

Abstract

Protecting tropical forests and their biological diversity is a global priority. Understanding if thresholds of forest cover exist beyond which biodiversity displays non-linear declines is key to developing appropriate conservation strategies and policies, but uncertainty remains around the identification and characteristics of these thresholds. We performed a global systematic review of studies using forest cover gradient to identify an ecological threshold across tropical forest ecosystems. Our systematic review finds 68 ecological thresholds reported in 33 peer-reviewed publications. Three main conclusions emerged: first, we show clear geographical gaps in ecological thresholds studies, with 72% of reported thresholds found in South America, over half in Brazil; second, we see ecological threshold studies follow taxonomic biases in line with wider conservation research; and third, there is a lack of homogeneity and comparability in the metrics and sampling designs used to identify a threshold. This global review shows interest in ecological thresholds continues to grow, but further evidence is needed to understand their application in tropical forest management. We identify the main gaps in knowledge and provide guidance to focus research efforts on six key aspects to better understand their potential as a policy-making tool for tropical forest conservation.

Abstract in Spanish is available with online material.

KEYWORDS

biodiversity metrics, conservation evidence, ecological thresholds, forest cover, policy-making, tropical ecosystems

1 | INTRODUCTION

Tropical forests play a major role in conserving biological diversity and providing ecosystem services (Barlow et al., 2018; Ferreira et al., 2018). Covering around 10% of the Earth's surface, they contain over half of the world's known species including 90% of terrestrial bird species (Barlow et al., 2018; Gibson et al., 2011) and are central to climate change mitigation (Gibbs et al., 2007). Estimates suggest the tropics lost 12 million ha of forest in 2018, with the average rate

of loss of intact tropical forests tripling in the last 10 years to 4.3 million ha per year, an area the size of Belgium (Schulte et al., 2019). Deforestation continues to be the main driver of biodiversity loss in the tropics (Maxwell et al., 2016; Morris, 2010a) and the effects of forest loss, habitat fragmentation, and ecosystem degradation on biological diversity are well understood (Giam, 2017; Haddad et al., 2015; Morris, 2010b).

As the implementation period of the Convention of Biological Diversity's (CBD) Strategic Plan for Biodiversity 2011–2020 comes

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to an end (Convention on Biological Diversity, 2019), scientists and policy-makers are discussing new targets to form the basis of national and international plans to protect biological diversity over the next decades (Purvis, 2020; Rounsevell et al., 2020). While the success of global conservation policy processes depends on issues of governance, socioeconomics, and politics, there are also key ecological questions to be addressed in the creation of targets for tropical forests conservation (Green et al., 2019; Noss et al., 2015; Purvis, 2020; Svancara et al., 2005). In creating targets for the protection of forests, such as through protected areas, or for forest restoration, key questions on species responses to forest loss must be understood. How much forest is enough to maintain biodiversity?

Ecological thresholds have emerged over the past 20 years as a potential tool to help design effective conservation action based on preventing forest loss beyond a “break-point,” after which drastic biodiversity declines are observed (Francesco Ficetola & Denoel, 2009). In the context of tropical forest ecosystems, they are increasingly applied as a method of identifying the minimum amount of native vegetation needed to avoid changes to species–habitat relationships, leading to biodiversity loss (Huggett, 2005; Kelly et al., 2015) (Figure 1). They have been used in management decisions in Australia, Brazil, Canada, and the USA (van der Hoek et al., 2015) to define limits to deforestation or set restoration targets. Despite support for ecological thresholds as an important tool to link forest cover loss to thresholds of change (“tipping points”) beyond which ecosystem functioning is at risk (Arroyo-Rodríguez et al., 2020; Banks-Leite et al., 2014; de Oliveira Roque et al., 2018; Johnson, 2013; Lindenmayer & Luck, 2005; I. Melo et al., 2018), strong scientific debate exists around their existence and use in conservation planning (Brook et al., 2013; Foley et al., 2015; van der Hoek et al.,

2015; Lindenmayer & Luck, 2005; Muradian, 2001). Concerns surrounding the threshold concept include criticisms of its use as a “rule of thumb” value applied globally, while based on local or regional evidence (Banks-Leite et al., 2021), and the risk of publication bias meaning studies with negative results are less likely to be published. In addition, some studies investigating the ecological response to forest cover loss may not identify a specific tipping point or non-linear change, as changes to metrics such as species abundance often happen non-linearly in the terrestrial biome (Brook et al., 2013). While tipping points and thresholds for global ecosystem change might not be identifiable, nor useful (Brook et al., 2013), non-linear changes in biodiversity at the landscape scale continue to be investigated (Estavillo et al., 2013; Newbold et al., 2018) as a way to better understand biodiversity responses to specific habitat or ecosystem changes, and anthropogenic drivers, such as forest cover loss.

Given the continued debate around their application to forest conservation policy and management, a compilation of available evidence from tropical ecosystems across the world can help inform conservation decision-making (Adams & Sandbrook, 2013) and forest management practices. To better understand the questions surrounding ecological threshold identification, their characteristics, and use, we conducted a systematic review of approaches and findings of ecological threshold studies from tropical forest landscapes. We present an overview of global evidence and discuss the uncertainties surrounding the existence of forest cover thresholds in tropical regions and the variation in methods used to identify them. This review had the following objectives: (a) to compile existing evidence on ecological thresholds of tropical forest cover; (b) to summarize existing data; (c) to identify methodological approaches and inconsistencies in threshold identification; and (d) to highlight species and regions of particular conservation concern lacking threshold information and for which additional empirical work is most urgently needed.

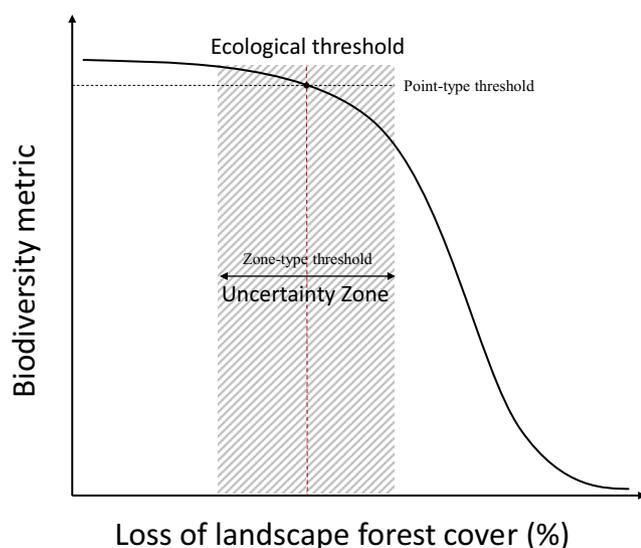


FIGURE 1 Graphical representation of an ecological threshold of forest cover (vertical dashed line); the minimum amount of forest cover required in a landscape to avoid non-linear declines in biodiversity metrics. The gray dashed areas represent the uncertainty zone within which bands or “zone-type” thresholds can be identified

2 | METHODS

2.1 | Search strategy and data collection

We performed a systematic literature review using *SciVerse's Scopus* online bibliographical tool and *Google Scholar* following the “Guidelines for Evidence Synthesis in Environmental Management” established by the Collaboration for Environmental Evidence (CEE) (CEE, 2018). We performed two searches, the first between April and June 2018 and the second search in January 2020. Due to the volume of literature available, search results were restricted to English. Studies were selected to fit the following criteria: (i) study conducted in tropical terrestrial ecosystems (as defined by Olson et al. 2001); (ii) study analyzed an ecological metric as a response to landscape forest cover change; (iii) study recorded forest cover gradient; (iv) the analysis aimed to identify a numerical forest cover threshold, expressed as percentage forest cover. Considering the selection criteria, we designed a search string using sub-strings divided into six categories (see Supporting Information).

TABLE 1 Grouped biodiversity metrics used as a response variable to forest cover change in ecological threshold identification, and related ecological threshold statistics

Biodiversity metric	Thresholds identified (N = 68)	Mean ecological threshold (% FC)	SE
Community composition	6	34.46	4.56
Dispersal	1	58.40	0.00
Functional diversity	2	27.35	7.35
Genetic diversity	2	35.50	4.50
Occurrence	5	42.00	7.84
Phylogenetic diversity	3	28.13	1.87
Predation	1	20.00	0.00
Species abundance	17	48.50	4.33
Species richness	31	42.58	2.98
TOTAL	68	41.90	

Abbreviations: FC, forest cover.

The search strategy resulted in 3593 initial results (Table S1). We included all peer-reviewed literature from 1970 to January 2020. An initial screening was performed reviewing the title and the abstract of each peer-reviewed study to determine whether the subject and scope of the article fit the defined search criteria. This screening produced 289 peer-reviewed articles, of which we reviewed abstract, methods, and results to determine whether the study reported quantitative threshold information (percent forest cover) following the criteria outlined above. Keywords were used as search terms during the screening process: “forest cover”, “cover”, “%”, “percentage,” and “threshold.” To ensure representation of all regions and avoid possible effects of reporting bias, additional targeted searches were carried out for regions with tropical forest ecosystems of conservation concern which were lacking data: SE Asia and Central Africa. Following this method, one additional reference was added in December 2018 (Kupsch et al., 2019). In addition to the publications captured by the search strategy aimed at selecting those reporting on numerical thresholds, we also scanned reference lists of relevant review papers (see Supporting Information for further details). Our systematic review resulted in 33 identified peer-reviewed papers containing information on 68 ecological thresholds of forest cover.

Although interested in the links between habitat structure and biodiversity responses, we restricted our analysis to studies concerning direct effects of forest cover; those reporting exclusively on fragmentation were not included. Evidence shows the effect of habitat loss and habitat fragmentation can be independent and affect populations in different ways (Fahrig, 2003; de Oliveira Roque et al., 2018), so, to ensure clarity in interpretation of the results, we focused on empirical or modeling studies assessing landscape-scale forest cover loss only.

Prior to this analysis, we carried out a pilot study using the same approach to answer the research question for the Atlantic Forest biome in Brazil (Laurance, 2009), allowing for the refinement of search terms to best fit the research aims using a smaller geographic area and a more complete data pool. The results of the Atlantic Forest search string were tested against an existing list of peer-reviewed articles stemming from expert discussions and literature search. We then carried out three pilot searches using the extended search

string for the global analysis to ensure maximum inclusion of relevant results, while considering the practicalities related to the number of papers to be screened (see Supporting Information for more details). To test the accuracy of the review process, co-authors reviewed a subset of the initial results to test for discrepancies in the screening process and data extraction, each screening six randomly selected papers and sharing the extracted data and threshold interpretation.

2.2 | Data extraction

A database of ecological thresholds of forest cover was created using threshold data extracted from the final 33 relevant peer-reviewed articles. The following key information was recorded for each article:

2.2.1 | Biodiversity metric

We define a biodiversity metric as an ecological measure of biodiversity (e.g., species richness, phylogenetic diversity, and abundance). Biodiversity metrics reported by authors were grouped into 9 general metrics used in analysis (Table S2 and Table 1).

2.2.2 | Ecological threshold

We define an ecological threshold as the threshold of forest cover beyond which non-linear changes in biodiversity are recorded, following definitions established in the literature (Huggett, 2005; Kelly et al., 2015). Each threshold was selected as an independent data point if one of the following conditions was met: (i) unique biodiversity metric used or (ii) unique species characteristics (e.g., level of specialization) or (iii) unique sample area or (iv) unique location of study site, that is, thresholds identified in the same peer-reviewed article were classed as independent if the threshold was recorded using different metrics and/or species as the dependent variable, in a different geographic location, or using a sampling area of a different size. Threshold values were extracted as reported by the authors, and in cases of zone-type

thresholds (when a band was given as a threshold rather than a single number), the mid-point value was used for analysis.

2.2.3 | Forest cover gradient

We recorded the gradient of forest cover used in analysis to identify a biodiversity response, measured as minimum to maximum percentage landscape forest cover within the study region.

2.2.4 | Geographic region

We used the GEO/IPBES¹ regional classification (Brooks et al., 2016) to identify regions and sub-regions in which studies were conducted.

2.2.5 | Species class

Species used in analysis were classified as reported by authors. Species are classed as amphibians, birds, insects, mammals, plants, or “mixed” when analysis used species from multiple classes to identify an ecological response (amphibians $N = 1$, birds $N = 23$, insects $N = 3$, mammals $N = 22$, plants $N = 15$, mixed $N = 4$).

2.2.6 | Ecological specialization

Species used in analysis were classified by level of specialization as reported by authors. Species are classed as specialist or generalist.

2.2.7 | Location of study site

The geographic location of the study as reported by authors.

2.2.8 | Sample area

We define the “sample area” as the size of the site in which forest cover was measured (km^2) in each peer-reviewed publication. Typically studies either use multiple sample areas with varying levels of forest cover which are compared, or they use a gradient of forest cover within one sample area, to identify a biodiversity response.

2.2.9 | Study region

Size (if reported) of the region within which sample areas are located, and which represents the area over which forest cover gradient is calculated. The study region often contains multiple study sites where forest cover is measured, and the gradient in forest cover emerges from differences in forest cover between those sites.

2.2.10 | Species sample size

The number of species used in analysis to detect an ecological threshold using biodiversity metrics measured against forest cover change (e.g., individual species such as Jamaican fruit bat, or species groups (families) such as *phyllostomid* bats).

2.3 | Analysis

First, we summarized the available data on ecological thresholds, globally, and regionally. A Shapiro–Wilk normality test (Ghasemi & Zahediasl, 2012) was used to assess the distribution of the ecological threshold data. We calculated the 95% confidence interval for ecological threshold values using the bootstrap method for non-normal data (Jung et al., 2019; Wang, 2001), using the R “boot” package (Canty & Ripley, 2019). Second, we used descriptive statistics to understand the patterns in ecological thresholds and investigated variation in ecological thresholds identified using different biodiversity metrics, in different geographic regions with different sizes of sample area and different forest cover gradients used. Third, we used nested linear mixed effect models to investigate the influence of six parameters on ecological threshold identification, using the R “lme4” package (Bates et al., 2015): sample area, species class, location of study site, ecological specialization, species sample size, and forest cover gradient. Due to the nature of the dataset and data collection method, we applied a random nesting effect to account for the fact that (A) multiple thresholds are identified in the same region and (B) in the same paper. “Region” and “Paper ID” (representing the paper from which a threshold was extracted) were used as random effects. We performed this analysis using the full dataset, and also performed two sub-analyses to look at the effect of five parameters on threshold identification for the two most representative groups: birds ($N = 23$) and mammals ($N = 22$). The “ANOVA” function from the R “CAR” package was used to compare model fit (Fox & Weisberg, 2019). All data and statistical analyses were conducted in R Studio v3.6.2 (R Core Team 2013). ArcMap v10.6 (ESRI 2011) was used to create a global map of ecological threshold studies.

3 | RESULTS

3.1 | Existing evidence on ecological thresholds in tropical forests

Our systematic review identified 68 individual ecological thresholds extracted from 33 peer-reviewed studies which fit the selection criteria, covering six regions (Figure 2) (see Supporting Information). We find evidence of both “point-type” and “zone-type” thresholds (Huggett, 2005; F. P. L. Melo et al., 2013). Zone-type thresholds use *zones* or *bands* instead of a single number to define a range of forest cover values within which ecological changes are observed (e.g., 30–40%, rather than 35%) when single numeric break points could not

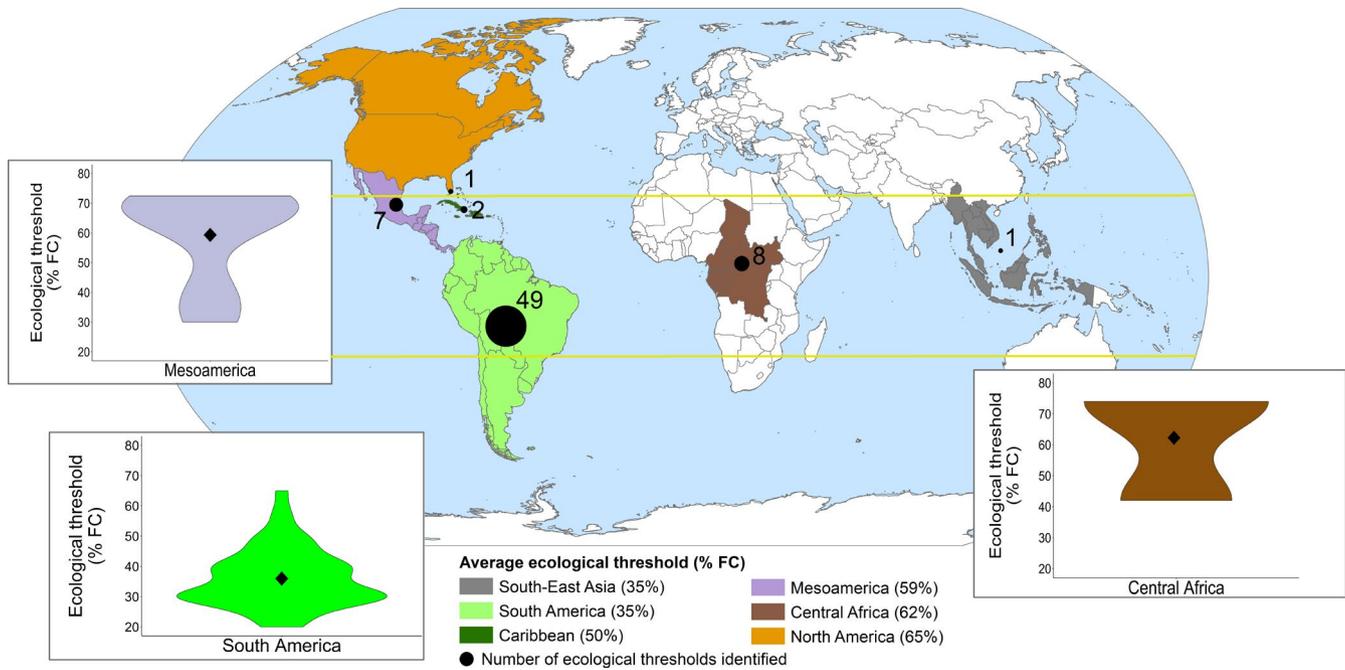


FIGURE 2 Average ecological threshold (percent landscape forest cover) and number of thresholds identified (black circles) in each sub-region (using the GEO regional classification; Brooks et al., 2016). Countries with no identified ecological thresholds of forest cover are shown in white. Violin plots represent the distribution of ecological threshold values for regions with enough existing data (black diamond shows mean value). Tropics of Capricorn and Cancer are shown in yellow. Note: one ecological threshold was included in the USA for tropical hardwood hammock (Armentano et al., 2002) from the Florida Keys region (Main et al., 2011)

be identified. Of the 33 reviewed articles, three reported range or zone-type thresholds (Estavillo et al., 2013; Martensen et al., 2012; Pardo et al., 2018), with most identifying a single numerical threshold of percentage of forest cover. The average ecological threshold beyond which non-linear biodiversity declines are observed is 41.9% forest cover (95% CIs 38.08–45.82, SE = 1.97) (Figure S1) across all studies.

Ecological threshold studies are geographically biased (Figure 2); 82% of ecological thresholds published to date have been identified in the Neotropics, 49 in South America, 7 in Mesoamerica, and 2 in the Caribbean (Figure 2) (Table S5). Central Africa and SE Asia are severely under-represented, with only eight and one ecological threshold identified, respectively. We see regional ecological thresholds vary from 35% forest cover in SE Asia ($N = 1$) and South America ($N = 49$) to 62% in Central Africa ($N = 8$). There is also wide variation in the number of species used in threshold analyses, ranging from single species to large datasets of over 500 species. There is a clear gap in ecological threshold data for plants and invertebrates. Twenty-three thresholds were identified for birds, 22 for mammals, 15 for plants, three for insects, and only one threshold was reported for amphibians (figures do not total 68 due to 4 thresholds being calculated using combined mammal and bird data).

Our results indicate the variance in ecological thresholds identified may be affected by the location of the study in which analysis was conducted (Table 2). Model comparison reveals the location of the study site has the strongest effect on the variance of the data across the full database ($p = 0.0007$ ***) (Table 2) and for the

mammal sub-group ($N = 22$; $p = 0.0006$ ***) (Table 3). Within the sub-group of ecological thresholds identified for birds ($N = 23$), none of the tested fixed effects significantly affected ecological thresholds results (Table 3). In addition, we see nesting effects in the ecological thresholds database (as multiple thresholds are reported within the same paper and for the same region, mostly Brazil ($N = 44$; ecological threshold = 35% forest cover)). Adding "Region" and "Paper ID" as random variables results in a higher mean ecological threshold (49.8% forest cover) compared with the global average calculated without nesting effects (41.9% forest cover).

3.2 | Threshold detection methods

Ecological thresholds in the reviewed studies are identified by measuring biodiversity over a gradient of forest cover and finding a point where biodiversity metrics show a non-linear decline as a response to forest cover loss. A wide variety of biodiversity metrics are used, with authors mainly reporting on species richness (46%; $N = 31$) and species abundance (25%; $N = 17$) (Figure 3, Table 1, Table S2). The methods used to identify this break-point also vary, with most studies applying modeling techniques such as generalized linear models, piecewise regression models (Muggeo, 2003; Toms & Lesperance, 2003), and logistic models (Kupsch et al., 2019) (Table S3). Empirical studies in which authors visually analyses and compare biodiversity metrics between sample areas with varying levels of forest cover are used in six studies (Table S3) (Balkenhol et al., 2013; Benchimol et al. 2017; Bergman et al., 2006; Boesing

Fixed effects	All data (N = 68)			
	AIC	Df	Pr (>ChiSq)	Chi-square
Null model	556.35			
Sample area	558.19	1	0.692	0.16
Species class	561.80	5	0.473	4.55
Location of study site	546.34	11	0.0007***	32.01
Ecological specialization	558.23	1	0.727	0.12
Species sample size	553.50	1	0.028*	4.85
Forest cover gradient	555.79	1	0.110	2.56

TABLE 2 Results of model comparison between nested linear mixed-effects models evaluating the effect of six variables on ecological threshold identification

Note: Region and Paper ID (representing the paper from which a threshold was extracted) were used as random effects.

Significance codes: 0 "****" 0.001 "***" 0.01 "**" 0.05 ".".

TABLE 3 Results of model comparison between nested linear mixed-effects models evaluating the effect of five variables on ecological threshold identification for two class sub-groups, birds (23), and mammals (22)

Fixed effects	Birds (N = 23)				Mammals (N = 22)			
	AIC	Df	Pr (>ChiSq)	Chi Square	AIC	Df	Pr (>ChiSq)	Chi-square
Null model	194.17	-	-	-	186.09	-	-	-
Sample area	195.96	1	0.645	0.21	187.11	1	0.322	0.98
Location of study site	194.13	4	0.090	8.04	174.58	4	0.0006***	19.51
Ecological specialization	193.69	1	0.116	2.48	185.18	1	0.088	2.92
Species sample size	194.24	1	0.165	1.93	186.80	1	0.256	1.29
Forest cover gradient	194.35	1	0.178	1.82	183.15	1	0.026*	4.95

Note: Results are not comparable across groups (columns). Region and Paper ID (representing the paper from which a threshold was extracted) were used as nesting effects.

Significance codes: 0 "****" 0.001 "***" 0.01 "**" 0.05 ".".

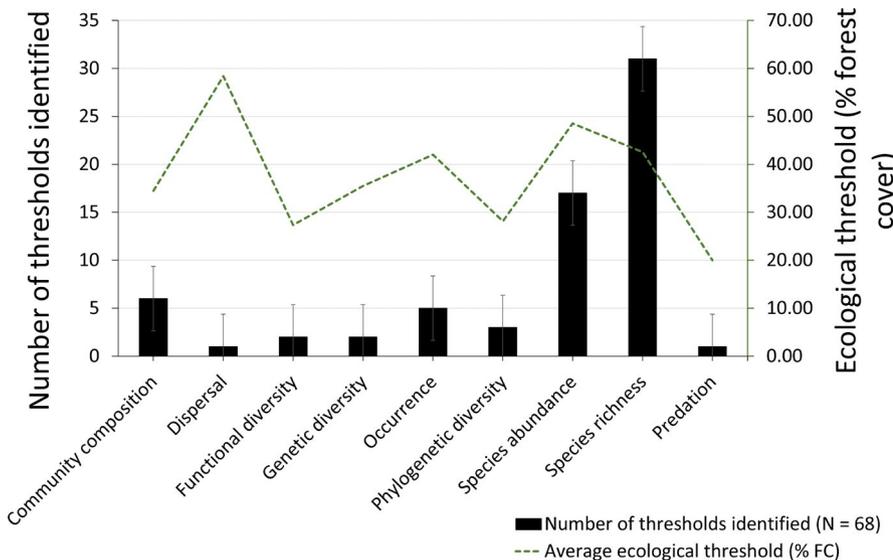


FIGURE 3 Number of ecological thresholds and average ecological threshold identified using different metrics to measure a biodiversity response (N = 68), globally. Error bars show standard error

et al., 2018; Estavillo et al., 2013; Püttker et al., 2013) which identified 9 ecological thresholds (average = 36.5% forest cover). The size of the sample area in which forest cover is measured also varies widely. Studies often use small plots within larger regions to identify a threshold. The average sample area used in ecological threshold studies to measured forest cover and identify a biodiversity

response is 56.06 km² (SE = 18.81) (Table S4); only 13 ecological thresholds from 10 peer-reviewed studies measured forest cover in sample areas larger than 100 km². The gradient of forest cover used to identify a threshold is generally high, with 68% of thresholds measured in landscapes where maximum forest cover was between 80 and 100% (Mean = 81.62%, SE = 2.34). We also find 26% of

thresholds were measured in landscapes with maximum measured forest cover between 45% and 60%.

4 | DISCUSSION

4.1 | Data gaps and research bias in ecological threshold identification

As a promising and easy to communicate concept, ecological thresholds continue to receive attention from the scientific community, and in some regions, are gaining policy traction (Dunning, 2018) leading to calls for landscape forest cover to be kept above 30% or 40% (Arroyo-Rodríguez et al., 2020; Banks-Leite et al., 2014; Estavillo et al., 2013; Fahrig, 2003; Rompré et al., 2010). The 30% threshold value has become widely referred to in landscape ecology since Andrén (1994) identified a threshold of forest cover between 10% and 30% below which habitat fragmentation exerts increased pressures on populations. A policy message of maintaining at least 40% of forest in a landscape was also put forward by Rompré et al., (2010), who found a habitat threshold for bird species with large ranges (using data from boreal and temperate forests) between 30% and 40%, in line with a global review of bird responses to landscape changes which found a threshold at 33.6% forest cover at tropical latitudes ($N = 7$) (I. Melo et al., 2018). Banks-Leite et al., (2014) also identified a 30% threshold for small mammals, amphibians, and birds in Brazil's Atlantic Forest, which has been adopted by regional government (Dunning, 2018). Thresholds for minimum canopy cover (a similar measure, although different to landscape forest cover (Asrat et al., 2018)) at 40% have also been adopted by industry for "Biodiversity-friendly" coffee certification and have shown positive effects on both mammals and birds (Caudill & Rice, 2016).

Despite their increased presence in the scientific literature (Figure 4), the evidence we present highlights a lack of congruence between the metrics and methods used in threshold identification, and indeed the definition of an ecological threshold for biodiversity

itself. In this review, we have used ecological thresholds of forest cover extracted from the reviewed literature as defined by authors. Although there is variation in the analytical methods, biodiversity metrics and landscape characteristics used in identifying thresholds for biodiversity, all authors are consistent in defining a threshold as the level of forest cover (percentage) below which a non-linear or "drastic" change in biodiversity is measured. While we can identify a global average threshold across studies of 42% forest cover, the lack of a clear conceptual framework around identification and reporting of ecological thresholds does not allow for thresholds to be robustly assessed and compared across landscapes (Martin et al., 2009). However, it is clear that the question of *How much is enough?* continues to be highly relevant in conservation research (Arroyo-Rodríguez et al., 2020), and its use as a policy-making tool is increasingly considered in some regions, such as Brazil (Rezende et al., 2018). As empirical evidence to support their existence continues to grow (Figure 4), we draw several meaningful conclusions and identify the main knowledge gaps surrounding ecological thresholds for tropical forests.

First, we find knowledge on ecological thresholds of forest cover is unevenly distributed among species and regions. Data remain biased toward studies conducted in South America and for small mammals and birds. There are clear gaps in knowledge for conservation hotspots in SE Asia and Central Africa (Myers et al., 2000), with only one peer-reviewed study identified in each region, showing ecological threshold literature follows wider patterns of geographic bias in biodiversity research (Di Marco et al., 2017; Trimble & van Aarde, 2012). Threshold studies for pollinating insects or specialist species are also under-represented, and only one out of the 68 identified thresholds assessed the response of a large mammal to forest cover loss (jaguars (Zemanova et al., 2017)). In addition to geographic bias, we find that the evidence is concentrated in specific regions, many within the Atlantic Forest biome, where studies have measured the effects of forest cover loss on different metrics or species groups and reported multiple thresholds using the same study regions (Ávila-Gómez et al., 2015; Kupsch et al., 2019). The non-independence of some observation in our database means

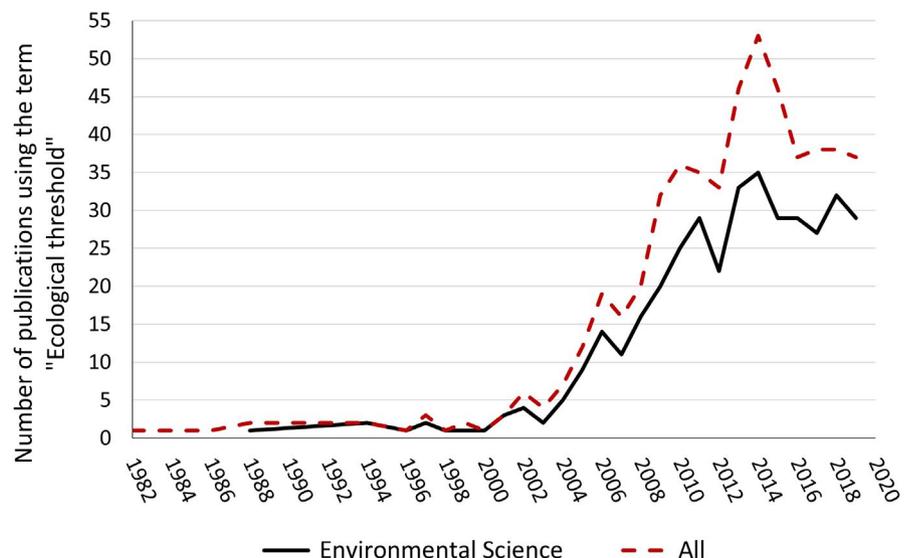


FIGURE 4 Increase in the number of peer-reviewed publications using the term "ecological threshold" per year (1970–2019), for publications in the environmental science field (continuous line, first record in 1988) and for all fields (dashed line, first record in 1982). Measured using Elsevier's *Scopus* bibliographical tool

that comparisons and inferences of the validity of thresholds across different scales and in different locations cannot be made, as thresholds vary for different metrics, landscapes, and/or species (Roque et al., 2018). However, the existence of studies which use some replications of study design and landscape improve our understanding of variation in threshold across taxa (e.g., Ávila-Gómez et al., 2015).

Second, we see variation in the area over which biodiversity responses to forest cover are measured. Conservation interventions often cover large areas and targets and policies can apply to entire countries or biomes (Paloniemi et al., 2012), but we find few analyses quantifying the relationship between forest cover and biodiversity using sample areas larger than 100 km², with 54% of studies using sample areas smaller than 15 km². Some reported study regions, representing the total area over which forest cover gradient is considered, cover entire biomes and reach up to 1.3 million km² (in the case of the Brazilian Atlantic Forest) (e.g. Banks-Leite et al., 2014; Roque et al., 2018), but the sites (sample areas) where forest cover is measured within these regions can be as small as 2 km². In addition to remaining questions around scalability of results and the influence of wider landscape dynamics, nearly half of studies found have total study regions smaller than 500 km² (see Supporting Information), while estimates suggest the average home range size of the mammalian fauna in the Atlantic Forest biome is ~788.4 km² (Bogoni et al., 2018) and tropical forest species in general can have large ranges covering a few thousand kilometers (Pe'er et al., 2014; Purvis et al., 2000). Analyzing the implications of forest loss for species with large range-sizes and dispersal needs, such as large mammals and apex predators, is crucial (Holland et al., 2004), but is currently under-represented in ecological threshold studies. Arroyo-Rodríguez et al., (2020), present guidelines for the use of a 40% forest cover threshold applicable to “most species”, with habitat requirements lower than 1,000 km², and suggest ecological thresholds can be used as a tool in “smaller landscapes” (of less than 3000 km²). We find existing data for most tropical regions is insufficient to support this general threshold. The mismatch between the size of areas where ecological processes are measured and the level at which policy decisions are made continues to be a major challenge in the development of successful conservation interventions (Paloniemi et al., 2012), and the implications for ecosystem functioning of sample area size remain poorly understood (Gonzalez et al., 2020). Thus, the use of ecological thresholds to dictate the minimum amount of forest to keep in a landscape based on sampling of vegetation change in small portions of affected ecosystems should be approached with care (van der Hoek et al., 2015; Lindenmayer & Luck, 2005).

Third, we find few examples of ecological threshold studies using long-term land-use change data to assess the effect of forest loss on biodiversity. Time lags in biodiversity responses are well understood (Norris, 2016), and the lack of studies using long-term forest cover change to investigate a forest cover threshold prevents understanding the nature of these responses and their impacts on tropical forest ecosystems. These delayed responses are likely to be species-specific and differ across regions and scales. Existing time-series datasets of forest cover and biodiversity change could be used to help bridge these knowledge gaps

(e.g. Dornelas et al., 2018; Hansen et al., 2013). The vast majority of studies compared landscapes with different levels of present-day forest cover, with the exception of three studies, which assessed how biodiversity metrics responded to deforestation within a landscape surveyed over time (Bergman et al., 2006; Döbert et al., 2017; Zemanova et al., 2017). The thresholds identified in these studies, incorporating historical data, range from 20% to 80% forest cover, with an average of 48%, slightly higher than the average used across all studies. However, the sample size is insufficient to draw any conclusion about the significance of space for time substitution when inferring the presence of ecological thresholds in response to varying forest cover.

Choosing sample areas which represent gradients of forest cover in human-dominated landscapes often leads to the comparison of biodiversity metrics between sites with different levels of degradation, commonly 10%, 30%, and 50% forest cover (Balkenhol et al., 2013; Martensen et al., 2012; Pardini et al., 2010; Püttker et al., 2013), increasing the chance of a threshold being reported at these levels. Five out of 7 thresholds identified using this methodology reported a threshold at 30% forest cover. The analysis and long-term monitoring of data from dynamic landscapes with varying degrees of degradation is key to address existing knowledge gaps, as the gradient of forest cover directly impacts the point of disturbance at which non-linear biodiversity responses can be recorded. The change in forest cover used to predict ecological responses in the reviewed studies is generally wide enough to allow for identification of a threshold; the average maximum forest cover used is 81%, well above the average threshold of 42%. However, over a quarter of thresholds were identified using study regions where the highest level of forest cover was lower than 60%, limiting threshold identification to values below this. Finally, landscape matrix composition and characteristics can cause variability in biodiversity responses (Pardo et al., 2018) and are likely to influence ecological threshold identification (Boesing et al., 2018; Ricketts, 2001) and should be considered when choosing sample areas and comparing threshold results. As fragmentation and landscape matrix was not a focus of this review (see Methods), the majority of studies found investigate landscape forest cover change as the anthropogenic stressor, without focusing on patch isolation or matrix composition. However, we encourage further work to understand the importance of the landscape and ecological context, combined with forest loss, in creating tipping points for biodiversity.

4.2 | Use of ecological thresholds in policy-making

Clear and scientifically robust biodiversity indicators and targets supported by policy-makers are key in the development of the Post-2020 Biodiversity Agenda (Convention on Biological Diversity, 2019; Purvis, 2020). A decision-making landscape often dominated by a *policy approach* to conservation, where guidelines are based on “political achievability” rather than scientific evidence (Holl, 2017; Svancara et al., 2005), can result in seemingly arbitrary targets with no clear ecological significance. While we agree that the search for

“magic numbers” can sometimes be counter-productive to conservation management decisions (Van Der Hoek, 2014), we also stress that policy-makers need clear and sometimes simplified messages to understand the conservation needs of habitats of critical biodiversity concern, such as tropical forests. Ecological thresholds remain a highly debated concept in ecology (Francesco Ficetola & Denoel, 2009; Groffman et al., 2006; van der Hoek et al., 2015; Lindenmayer & Luck, 2005), and their use may be limited to specific contexts. The concentration of ecological threshold studies conducted in Brazil, and more specifically in the Atlantic Forest biome, shows potential for evidence to be used to inform conservation decision-making in this region. The characteristics of Atlantic Forest's habitats, highly fragmented and degraded, and the high concentration of landscape ecology and biodiversity research in Brazil may have led to a strong research focus on understanding the effect of low forest cover on biodiversity. An average ecological threshold of 33.5% forest cover was found across studies in the biome ($N = 41$), in line with Banks-Leite et al., (2014)'s recommendation to policy-makers of maintaining 30% forest cover in Atlantic Forest landscape planning (Dunning, 2018). The type of policies and policy landscape surrounding the protection and restoration of Brazil's Atlantic Forest also lends themselves to these type of ecological studies (Wiens, 2016) and, while the use of ecological thresholds may not be appropriate in informing global policy processes, this relative consistency across studies should not be ignored. The Atlantic Forest case study should be further examined to understand not only the limits, but also the opportunities, of using ecological thresholds as a conservation tool in other biodiversity hotspots with high levels of forest degradation and human-modified landscapes.

Finally, as highlighted recently by Banks-Leite et al., (2021) and others, we agree there is a lack of evidence to support blanket assumptions and statements about the existence of ecological thresholds of forest cover for biodiversity across the tropics. Here, we have attempted to fill some of these data gaps, but have shown that existing evidence is heavily biased toward South America, and is based on a wide range of ecological metrics and species. Our review finds an average reported ecological threshold across the available literature of 42%. In Latin America, and in Brazil specifically, this threshold is closer to 35%, and when using nesting effects to account for the disproportionate number of thresholds identified in this region, many in the same paper, we see the global average threshold is higher, at 48% forest cover. While these thresholds are helpful and may be relevant to the fragmented landscape existing in some tropical regions, the widespread recognition of the 30 or 40% threshold should be treated with caution. Arroyo-Rodríguez et al., (2020) conclude the concept of maintaining at least 40% forest cover in landscapes applies to temperate forests, and a higher percentage is likely necessary in the tropics and in human-dominated landscapes. Newbold et al., (2018) also identified a higher ecological threshold when modeling biodiversity responses to vegetation removal in tropical ecosystems, showing drastic changes to ecosystem structure are predicted when removal exceeds 50%. Additionally, our review found only one paper on ecological threshold for the Central African region. This paper (Kupsch et al., 2019) identifies ecological thresholds at 74% forest cover for several bird species

groups. Thus, a forest cover threshold of 30–40% may be too low for some under-studied regions and species, risking the creation of conservation policies which do not protect many large mammals and apex predators. As highlighted by others (Banks-Leite et al., 2021), basing forest conservation and/or restoration targets on the amount of protection in a given landscape can be problematic in terms of implementation and ecological outcomes, and we caution the communication of scientific findings in a way which suggests the existence of general thresholds, and their use in policy-making, as current evidence is not enough to support this beyond context-specific examples.

4.3 | Key questions and priorities for future research

The conservation science community increasingly calls for systematic analysis and presentation of conservation evidence (Adams & Sandbrook, 2013) to better understand the needs of the natural world. While we acknowledge the existence of methodological frameworks to address questions in environmental science through systematic approaches (CEE, 2018; Pullin & Knight, 2009), the spread and heterogeneity of existing threshold data hamper formal meta-analysis. Here, we show limited quantitative understanding of the impacts of sample area size and landscape structure on ecological thresholds in tropical forests. Existing evidence supports their use only in specific bio-geographical contexts, as the large variation in biodiversity metrics, study design, landscape composition, and taxa investigated prevents robust comparisons or generalizations across studies (Cooke et al., 2017; Francesco Ficetola & Denoel, 2009; Lindenmayer & Luck, 2005; Martin et al., 2009), beyond South America.

In this paper, we are not advocating for the use of ecological thresholds to determine the minimum amount of forest cover required to avoid all negative biodiversity responses, but it is clear that the loss of species diversity and community integrity can lead to changes in ecosystem functions (Morante-Filho et al., 2015), and that ecological thresholds can be a useful conservation tool at local or regional scales. For example, in the Atlantic Forest, non-linear changes to forest-specialist bird species richness and abundance have been linked to forest cover loss below 45% (Morante-Filho et al., 2015) and changes to forest bird functional diversity were found to occur below 20% forest cover (Boesing et al., 2018). In Malaysian Borneo, non-linear changes to functional dispersal were identified in understory plants when forest cover was below 35% (Döbert et al., 2017). We suggest future studies focus on the relationship between thresholds and species with varying sensitivity to external changes (Van Der Hoek, 2014), such as climate change, as well as landscapes of different characteristics and matrix compositions. Efforts should be made to close data gaps and avoid conservation interventions applying threshold concepts without adequate evaluation of uncertainty (van der Hoek et al., 2015; Suding & Hobbs, 2009), as thresholds are expected to vary widely across species and regions (Rhodes et al., 2008; Van Der Hoek, 2014). With this in mind, we make the following recommendations to focus future research:

4.3.1 | Close geographic data gaps

Research efforts should be focused on tropical forests of critical conservation concern currently lacking threshold information, such as the forests of Central Africa and SE Asia. We should also be aware of the over-representation of South America, and Brazil specifically, in threshold studies and consider this when communicating threshold results and advocating for their use in global or regional conservation policy processes outside this region. Our results infer that the location of the study site impacts ecological threshold identification, but the heterogeneity of the existing data prevents making robust conclusions. Closing data gaps would allow further exploration of the importance of geographic location, critical to improving comparability across studies, and use in decision-making;

4.3.2 | Further investigate the scalability of results and analyses thresholds over larger areas

There remains a clear divergence between the sample areas used to investigate ecological thresholds and the scale at which policy-making for biodiversity conservation operates. Many studies use small sample areas to infer ecological thresholds, while others use gradients of forest cover measured over larger regions. This creates challenges when comparing studies and the predominant use of smaller sample areas leaves unanswered questions about the influence of scale in threshold detection. Investigating the existence of thresholds using the same biodiversity metrics and species at different scales would help advance knowledge (e.g., Ávila-Gómez et al. 2015). A robust analysis of the scale-dependency of these thresholds would require a nested study design where the same biodiversity metrics and forest cover gradients are calculated within a given study region in sample areas of different sizes. Even within single-scale studies, attention should be paid also to the size of the area in which biodiversity responses and forest cover are measured. In addition, the terminology and methodological design used when investigating ecological thresholds should be treated with greater care when discussing and reporting on findings. There is a lack of consistency across studies reporting on ecological thresholds, and within landscape ecology more broadly, on the size and definition of the term “landscape,” which further complicates comparability and interpretation of findings;

4.3.3 | Close taxonomic data gaps and improve species representation

As with wider biodiversity conservation research, mammals and birds form the majority of the species assessed in the reviewed studies. However, our data reveal further bias toward small mammals specifically, with only one threshold study found for a mammal with a large range size (jaguars). If thresholds are to be used in policy-making, it is important to have wider-ranging and specialist species represented and ensure thresholds are high enough to cover

multiple taxonomic groups. Better understanding is also needed on the wider ecological and ecosystem consequences of crossing ecological thresholds of species abundance, richness, and dispersal for different taxa. We suggest studies choose biodiversity metrics and study species in a more systematic way and better represent species of conservation concern and/or most at risk of extinction, and those with an important role in ecosystem functioning. Consistency in the use of measurable biodiversity metrics, for example, species richness or species abundance, could improve the understanding of threshold applicability to different habitats. The most used metrics are currently those concerned with species diversity (e.g., species richness), metrics which capture population dynamics and community composition are also needed and require further attention.

4.3.4 | Improve consistency in analytical methods

We find researchers are using different analytical methods which may affect the detection of thresholds (Francesco Ficetola & Denoel, 2009). We suggest authors carefully evaluate the reporting of an ecological threshold in light of the analytical methods used. Methods such as Threshold Indicator Taxa Analysis (TITAN) can inaccurately identify thresholds (Cuffney & Qian, 2013), and piecewise regression has been suggested as a more robust threshold detection method (Toms & Lesperance, 2003). Other methods, such as logistic regressions or visual comparisons in biodiversity change between sites are also used, but may incorrectly detect a threshold within a band (Francesco Ficetola & Denoel, 2009) or increase uncertainty, leading to inaccurate reporting of a specific threshold and allowing more room for author biases.

4.3.5 | Further investigate the impact of sampling design and landscape composition in threshold detection

This review shows the sampling design and the type of landscape chosen also varies across studies and prevents comparison and use of ecological thresholds in decision-making with confidence. Recorded sampling designs vary from using forest cover measured in small sample areas within larger regions, to comparing habitats with different levels of forest cover within a mixed anthropogenic matrix. We suggest studies are clearer on the impact of the sampling strategy on ecological threshold findings, as measuring non-linear changes in biodiversity as a response to forest cover is likely to have different outcomes depending on landscape matrix, level of anthropogenic disturbance, forest density, and maximum levels of forest cover (Pardo et al., 2018). We suggest more studies use long-term forest cover change data to identify a threshold for biodiversity, considering an appropriate reference level for forest cover, ideally a pristine condition, to sample the widest possible range of forest cover rates, rather than focusing analyses only on the most intact existing landscapes (often highly degraded and fragmented and with

similar levels of forest cover, such as 10%, 30%, and 50%). More research should be focused on understanding the impact of using different sampling designs on threshold detection and variability for tropical forest ecosystems specifically;

4.3.6 | Investigate the relationship between biodiversity responses, thresholds of forest cover, and ecosystem functioning

Our review further suggests that the question presented by (Sutherland et al., 2009) in “One hundred questions of importance to the conservation of global biological diversity” remains one of the key unanswered research areas in tropical forest ecology: “Do critical thresholds exist at which the loss of species diversity, or the loss of particular species, disrupts ecosystem functions and services, and how can these thresholds be predicted?”. The data gaps and lack of consistency in reporting on thresholds hamper efforts to answer this question. Further research is needed to understand the role of different taxa in ecosystem functioning, and focus ecological threshold studies on species with active roles in productivity, seed dispersal, or pollination (Oliver et al., 2015) across different tropical regions.

As tropical forest areas drastically decline in size around the world (Taubert et al., 2018) it is crucial that conservation management decisions are made based on scientific evidence. While global targets continue to be designed and applied, drawing important political, and media attention, (Convention on Biological Diversity, 2019), we show existing evidence on thresholds of forest cover which safeguard biological diversity is non-systematic, taxonomically biased and exists predominantly for the Neotropics. International or national policy targets can be difficult to apply, and evidence of critical thresholds could allow for tailored and landscape-scale interventions which may be more effective in preventing ecosystem collapse and the associated irreversible consequences for biodiversity and for people (Wunder et al., 2014). The scientific community should strive to produce novel, important research which advances the field of knowledge in conservation biology, but should also intend to provide the necessary evidence in the appropriate format and communicate it in a way which can meaningfully impact and assist conservation policy-making. We hope this systematic review and exploration of existing data pushes the scientific community to approach the study of ecological thresholds in a more systematic way, investigating the linkages between forest cover change and biodiversity across landscapes of different sizes and characteristics, within and across regions. With the beginning of a new era in biodiversity target setting, a joint approach to investigate, standardize, and share data on ecological thresholds for tropical forests at larger temporal and spatial scales would allow for their potential as a policy tool to be fully explored.

ACKNOWLEDGMENTS

This work was supported by the UK Natural Environment Research Council [grant number NE/L002485/1].

CONFLICT OF INTEREST

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

AUTHOR CONTRIBUTIONS

Yara Shennan-Farpón involved in conceptualization, methodology, investigation, data curation, formal analysis, writing the original draft, and writing the reviewing and editing. Piero Visconti involved in conceptualization, methodology, and supervision. Ken Norris involved in conceptualization, methodology, supervision, and writing the reviewing and editing.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the UCL Research Data Repository (<https://rdr.ucl.ac.uk/>) at <http://doi.org/10.5522/04/12613205>.

ORCID

Yara Shennan-Farpón  <https://orcid.org/0000-0002-3635-0913>

Piero Visconti  <https://orcid.org/0000-0001-6823-2826>

Ken Norris  <https://orcid.org/0000-0003-0894-245X>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Shennan-Farpón, Y., Visconti, P., & Norris, K. (2021). Detecting ecological thresholds for biodiversity in tropical forests: Knowledge gaps and future directions. *Biotropica*, 00, 1–14. <https://doi.org/10.1111/btp.12999>