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A review of threshold responses of birds to landscape changes across the world

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ABSTRACT. Identifying the threshold of habitat cover beyond which species of birds are locally lost is useful for understanding the biological consequences of landscape changes. However, there is little consensus regarding the impact of landscape changes on the likelihood of species extinctions. We conducted a literature search using Scopus and ISI Web of Knowledge databases to identify studies where bird species were used to estimate threshold responses to landscape changes. We obtained a list of 31 papers published from 1994 to 2018, with 24 studies conducted at temperate latitudes and seven in tropical regions. Nineteen studies were based on species-level assessments, and investigators used a variety of response variables such as probability of detection and occurrence to detect threshold responses. Eight studies were based on communities, and species richness and abundance were primarily used to detect threshold responses. Four studies included both communities and species-level assessments. Methods used to identify threshold responses varied among studies, but most relied on either regression models to visually identify values from graphs or piecewise regression to estimate a specific threshold value. Although the limited number of studies and their variety of approaches and methods prevented a formal meta-analysis, we found that mean threshold responses in studies that reported either a range or a single threshold value were 27.9% at temperate latitudes (range = 1.3–90%; $N = 11$) and 33.6% at tropical latitudes (range = 20–50%; $N = 7$). Considering only studies where single threshold values were reported, the mean habitat cover threshold was 11% for studies conducted at temperate latitudes ($N = 3$) and 29.5% for studies in the tropics ($N = 4$). These crude estimates suggest that tropical species might be more susceptible to habitat loss than temperate species. Although application of the threshold concept is still controversial, the number of studies using this approach is increasing because the results of such studies may have direct application to conservation strategies and restoration of landscapes for bird conservation.

RESUMEN. **Una revisión de las respuestas de umbral de las aves a los cambios de paisaje en todo el mundo**

Identificar el umbral de la cobertura del hábitat más allá de la cual especies de aves se pierden localmente, es útil para comprender las consecuencias biológicas de los cambios en el paisaje. Sin embargo, existe poco consenso respecto al impacto de los cambios en el paisaje sobre la probabilidad de extinción de las especies. Llevamos a cabo una búsqueda bibliográfica utilizando las bases de datos Scopus e ISI Web of Knowledge para identificar estudios en los que se utilizaron especies de aves para estimar las respuestas de umbral a los cambios en el paisaje. Obtuvimos una lista de 31 artículos publicados de 1994 a 2018, con 24 estudios realizados en latitudes templadas y siete en regiones tropicales. Diecinueve estudios se basaron en evaluaciones a nivel de especie, y los investigadores utilizaron una variedad de variables respuesta, como la probabilidad de detección y ocurrencia para detectar respuestas de umbral. Ocho estudios se basaron en comunidades, y la riqueza y la abundancia de especies se utilizaron principalmente para detectar respuestas de umbral. Cuatro estudios incluyeron tanto comunidades como evaluaciones a nivel de especie. Los métodos utilizados para identificar las respuestas de umbral variaron entre los estudios, pero la mayoría se basó en modelos de regresión para identificar visualmente los valores de los gráficos o la regresión por partes para estimar un valor de umbral específico. Aunque el número de estudios es limitado y su variedad de enfoques y métodos impidieron un metanálisis formal, encontramos que las respuestas de umbral promedio en los estudios que informaron un rango o un solo valor de umbral fueron 27.9% en latitudes templadas (rango = 1.3–90%; $N = 11$) y 33.6% en latitudes tropicales (rango = 20–50%; $N = 7$). Teniendo en cuenta solo los estudios en los que se informaron valores únicos de umbral, el umbral medio de cobertura del hábitat fue del 11% para los estudios realizados en latitudes templadas ($N = 3$) y del 29,5% para los estudios en los trópicos ($N = 4$). Estas estimaciones crudas sugieren que las especies tropicales podrían ser más susceptibles a la pérdida de hábitat que las especies templadas. Si bien la aplicación del concepto de umbral todavía es controversial, el número de estudios que utilizan este enfoque va en aumento, debido a que los resultados de dichos estudios pueden tener una aplicación directa a las estrategias de conservación y restauración de paisajes para la conservación de aves.

Key words: Bird conservation, extinction thresholds, habitat loss, piecewise regression, species loss

Human activities are impacting climate and ecosystems across the globe (Bennett and Ford 1997, Brook et al. 2008, Rockström et al. 2009, Sebastián-González et al. 2015). Although habitat loss is recognized as having one of the most severe impact of human activity on biodiversity (Brook et al. 2008), little consensus exists on the extent to which such loss impacts species extinctions. The results of some studies show that biodiversity initially declines proportionally to the amount of suitable habitat in a landscape, but, when availability of habitat declines below a certain level, non-linear changes emerge in response to shrinking patch size and increasing patch isolation, the so-called threshold responses (Andrén 1994, Pardini et al. 2010, Hanski 2011). These responses have been related to synergetic effects (Brook et al. 2008, Pardini et al. 2010, Swift and Hannon 2010), including the 'Allee effect', i.e., a positive relationship between components of individual fitness and numbers or density of conspecifics (Stephens et al. 1999). Determining how species respond to landscape change, such as threshold responses, can improve our understanding of the underlying processes that cause species extinctions and can also be important in identifying conservation and restoration strategies at the landscape scale (Suding and Hobbs 2009).

Lande (1987) defined extinction threshold as the "minimum proportion of suitable habitat distribution through a region that is necessary for population persistence", based on the demographic equilibrium model. Since then, a number of investigators have conducted studies with the aim of better understanding the patterns of species loss across a habitat gradient (e.g., Lawton et al. 1994, Hanski et al. 1996). Notably, Andrén (1994) examined the factors influencing the abundance and distribution of bird and mammal species in landscapes with different degrees of habitat fragmentation and found a threshold of 30% of remaining habitat below which species tended to be more sensitive to habitat alterations. Following Lande's (1987) definition of extinction threshold and the work of Andrén (1994), an increasing number of analyses within the context of thresholds have been used to suggest conservation actions (Banks-Leite et al. 2014, Lima and Mariano-Neto 2014, Ochoa-Quintero et al. 2015, Rodrigues et al. 2016). In addition, threshold values across different taxonomic groups and different regions have been used to identify the presence of warning signals in community metrics across landscape changes before major extinction events are expected to occur (Roque et al. 2018).

According to the State of the World's Birds, one of eight species (i.e., 13%) is threatened with extinction (BirdLife International 2013). Most early studies of bird conservation were conducted at local scales, focusing on habitat fragments. However, beginning in the 1990s, the landscape-scale approach started to appear in the scope of the conservation ecology of birds (Bennett and Ford 1997, Radford et al. 2005). Since then, a growing number of studies have gone beyond the fragment scale, aiming to better understand threats by identifying landscape characteristics such as the amount and configuration of habitat (e.g., Farigh 2003, Shanahan and Possingham 2009, Moura et al. 2013). Notably, an increasing number of studies are reporting thresholds in loss of bird species relative to the amount of habitat loss (e.g., Drinnan 2005, Suorsa et al. 2005, Ochoa-Quintero et al. 2015, Boesing et al. 2018).

For a synthetic understanding of the responses of bird species to landscape changes, examining both the trends and geographical bias of studies investigating thresholds of species loss relative to habitat loss is necessary. We reviewed studies where bird species were used to estimate such putative habitat-cover thresholds. Our objectives were to: (1) present the methods, scale of analysis, and geographical distribution of empirical studies examining threshold responses of birds to landscape structure, (2) summarize their main results, including examining possible effects of latitude on threshold values, and

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(3) discuss the gaps in knowledge and future perspectives in light of bird conservation at the landscape level. In a time characterized by loss of native vegetation in many parts of the world (Hansen et al. 2013, Watson et al. 2016), understanding how loss of habitat impacts birds is increasingly relevant to their conservation.

Literature search. We searched the literature using ISI Web of Knowledge and Scopus databases in March 2018. Given that the term “threshold’ is widely used beyond the field of ecology, we used exact phrases such as deforestation threshold, species loss threshold, fragmentation threshold, extinction threshold, and habitat threshold, and also used related alternatives by changing the order of words (e.g., threshold of deforestation and threshold of species loss). We also included the synonyms tipping point and break*point. We restricted the search to agricultural, biological, and environmental sciences. An initial search retrieved 463 and 2550 records (Scopus and ISI Web of Science, respectively). Of those records, we selected only those that included bird species and only those dealing with environmental thresholds as defined in our introduction (i.e., species putative responses to declines in availability of native habitat and describing abrupt non-linear changes). In addition, to identify publications potentially missing from the databases, we checked the literature cited sections of all the selected papers.

Studies examining responses of birds to landscape structure. We identified 31 papers specifically designed to determine the percentage of suitable habitat at which species or communities abruptly decline at the landscape level (Table 1). Most studies were conducted after 2000, with a steady increase in the number of studies since then (Fig. 1). Of the 31 studies, 24 were conducted in countries located at temperate latitudes, including the United States (10), Canada (five), Australia (five), Sweden (one), Finland (one), Sweden and Finland (one), and Tunisia (one). We found only seven studies that had been conducted in countries in the tropics, including Brazil (five), Ecuador (one), and Panama (one) (Fig. 2).

We can distinguish two different overarching levels to search for bird responses to landscape structure: species level (one or more species analyzed individually) and community level. In total, 19 studies were based on species (six based on a single species and 13 on multiple species; Table 1). In most of these studies, investigators used either the probability of occurrence or occupancy as a response variable (e.g., Jansson and Angelstam 1999, Radford and Bennett 2004, Suorsa et al. 2005, Betts et al. 2010), or something similar such as frequency of occurrence or probability of extinction, absence, colonization, or persistence. Communities were used as the level of analysis in eight studies, with species richness used as a response variable in six of these studies (e.g. Bennett and Ford 1997, Rompré et al. 2009, Table 1). Exceptions to this main trend include studies where community integrity and phylogenetic integrity were used as response variables (Banks-Leite et al. 2014), and where taxonomic, functional, and phylogenetic diversity were used (Boesing et al. 2018). In addition, we found four studies focusing on both communities and single species individually, from which Morante-Filho et al. (2015), Richmond et al. (2015), and Becker et al. (2015) also used guilds as the level of analysis (Table 1).

Regardless of whether studies focused on species or communities, some investigators defined the most influential predictor variable by using a model-averaging process with an array of putative predictor variables (Burnham and Anderson 2002), whereas others used a single predefined predictor variable. In both cases, tree cover or percent cover of native vegetation were the most commonly used predictor variables (Table 1). In addition, Drinnan (2005) used the amount of tree cover, not a percentage, to find a threshold of 4 ha for an urban environment in Australia, and Suorsa et al. (2005) used timber volume as the predictor variable.

In general terms, methods used to identify threshold values have improved over time. Initially, thresholds were inferred arbitrarily from visual inspection of data in a graphic representation of, most often, vegetation cover as predictor of the response variable (e.g., species richness). In total, investigators visually inferred the results from a graphic representation in 15 papers. For example, Radford and Bennett (2004) used logistic regression models and hierarchical partitioning to infer a 5–25% woodland-cover threshold for White-browed

Table 1. List of studies examining bird threshold responses to landscape changes.

Publications	Country[a]	Level of analysis[b]	Response variable[c]	Predictor variable	Threshold value	Inferred/ estimated[d]
Bennett and Ford (1997)	Australia	Community	Richness	Percent tree cover	10%	Inferred
Villard et al. (1999)	Canada	Mult. sp.	P. of presence	Percent forest cover	Not reported	Inferred
Jansson and Angelstam (1999)	Sweden	Species	P. of occurrence	Percent habitat cover	Various	Inferred
Carlson (2000)	Sweden and Finland	Species	Proportion of habitat occupied by the species	Percent habitat cover	13%	Inferred
Radford and Bennett (2004)	Australia	Species	P. of patch occupancy	Percent woodland cover	15-25%	Inferred
Radford et al. (2005)	Australia	Community	Richness	Percent tree cover	10%	Estimated[1]
Drinnan (2005)	Australia	Community	Richness	Remnant area	4 ha	Inferred
Lindenmayer et al. (2005)	Australia	Community and mult. sp.	P. of detection and Richness	Percent vegetation cover	No evidence	Inferred
Guénette and Villard (2005)	Canada	Mult. sp.	P. of presence and occurrence	Percent canopy closure and tree density	70% and 80 stems/ha	Estimated[2]
Suorsa et al. (2005)	Finland	Species	P. of occupancy	Timber volume	152 m^3/ha	Inferred
King et al. (2005)	USA	Species	P. of nest occurrence	Limb-tree density per 0.04 ha	2–6 limb trees	Inferred
Betts et al. (2007)	Canada	Mult. sp.	P. of occurrence	Percent habitat cover	8.6 to 28.7%	Estimated[3]
Poulin et al. (2008)	Canada	Species	P. of nest sites present	Density of snags and trees, and area of mature forest (ha)	127 trees/ha, 56 snags/ ha, and, 10.4 ha of forest	Estimated[2]
Rompré et al. (2009)	Panama*	Community	Richness	Percent tree cover	25%	Estimated[3]
Mordecai et al. (2009)	Ecuador*	Mult. sp.	P. of presence and emigration	Percent canopy cover	21–40%	Inferred
Betts et al. (2010)	USA	Mult. sp.	P. of occurrence	Percent forest cover	1.35–24.55%	Estimated[3]
Zuckerberg and Porter (2010)	USA	Mult. sp.	P. of extinction, absence, colonization, persistence	Percent forest cover	24.36–88.16%	Estimated[3]
Jones et al. (2011)	USA	Mult. sp.	P. of occupancy	Percent forest cover and stand age	Various	Inferred
Martensen et al. (2012)	Brazil*	Community	Richness and mean abundance	Percent forest cover	30–50%	Inferred

Table 1. Continued

Publications	Country[a]	Level of analysis[b]	Response variable[c]	Predictor variable	Threshold value	Inferred/ estimated[d]
Cunningham and Johnson (2012)	USA	Mult. sp.	Frequency of occurrence	Percent tree cover	20–60%	Inferred
van der Hoek et al. (2013)	USA	Mult. sp.	P. of extinction and persistence	Percent forest cover	50.8–91.0%	Inferred
Suarez-Rubio et al. (2013)	USA	Mult. sp.	Abundance	Forest cover and percent forest fragments	Various	Estimated[4]
Banks-Leite et al. (2014)	Brazil*	Community	Community and phylogenetic integrity	Percent forest cover	30% overall	Estimated[3]
Touihri et al. (2014)	Tunisia	Mult. sp.	P. of detection	Tree and snag density	650 stems, 207 snags/ha	Inferred
Ochoa-Quintero et al. (2015)	Brazil*	Community	Richness	Percent tree cover	43%	Estimated[3]
Becker et al. (2015)	USA	Community, mult. sp., and guilds	Abundance and occurrence	Percent land cover	Various	Estimated[4]
Morante-Filho et al. (2015)	Brazil*	Community, mult. sp. and guilds	Richness and abundance	Percent forest cover	44–50%	Estimated[3]
Richmond et al. (2015)	Canada	Community, mult. sp. and guilds	Richness and occurrence	Percent forest cover	4–45%	Estimated[3]
Van der Hoek et al. (2015)	USA	Mult. sp.	P. of extinction	Percent forest cover	7–90%	Estimated[3]
Suarez-Rubio and Lookingbill (2016)	USA	Mult. sp.	Abundance	Percent compactness	Various	Estimated[4]
Boesing et al. (2018)	Brazil*	Community	Taxonomic, functional, and phylogenetic diversity	Percent forest cover	20% overall	Estimated[3]

[a]Countries with * correspond to studies conducted in tropical regions.
[b]Mult. sp. stands for multiple species analyzed individually.
[c]P. stands for probability.
[d]The procedure used to obtain the threshold value. Inferred is when the value is visually identified from the graphic, whereas estimated can be (1) using AIC to find best fit model, (2) using ROC, (3) using piecewise regression, or (4) using TITAN.

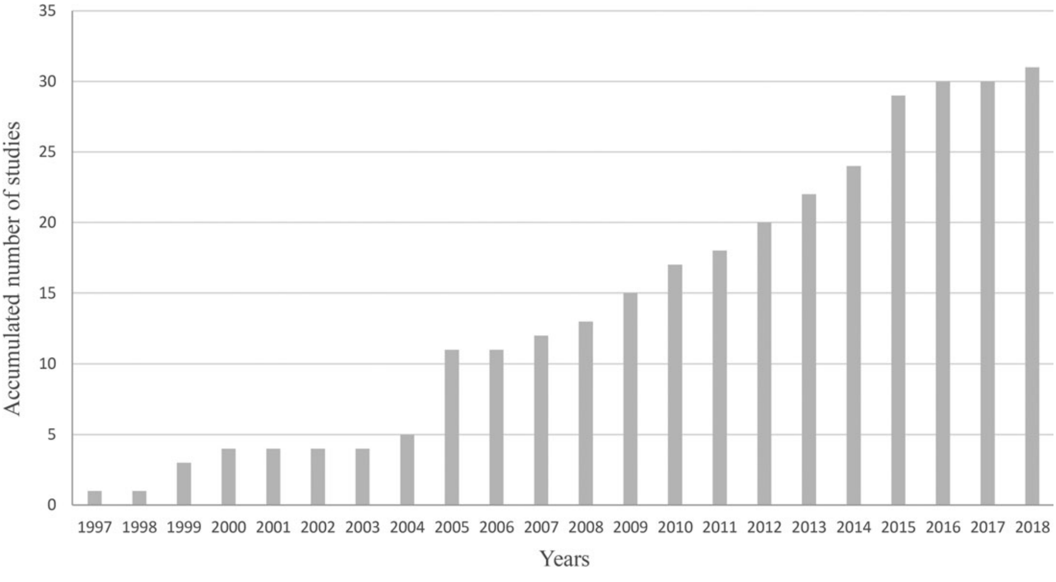

Fig. 1. Accumulated number of studies focusing on threshold responses of birds to habitat loss published since 1997.

Treecreepers (*Climacteris affinis*) in Australia. In the remaining 16 papers, investigators used different methods to statistically estimate threshold values rather than inferring them visually, e.g., Receiver-Operating Characteristic analysis (ROC), Akaike information criterion, and piecewise regressions. Beginning in 2007, based on Muggeo (2003), researchers started using piecewise regressions to estimate threshold values (e.g., Betts et al. 2007, Richmond et al. 2015, Boesing et al. 2018). Currently, this appears to be the most widely used method, with nine of the 16 studies that estimated threshold values using piecewise regressions. The piecewise regression method tests different starting points to find the most parsimonious breaking point (Muggeo 2003). As a result, a specific threshold value is obtained that provides a more objective estimate than if it is visually inferred from a graphic.

Another method used to estimate thresholds is TITAN (Threshold Indicator Taxa ANalysis), with indicator species used to integrate occurrence, abundance, and directionality of taxa responses to landscape changes (Baker and King 2010). To date, investigators have used this approach to identify threshold responses of birds in three studies (Suarez-Rubio et al. 2013, Becker et al. 2015, Suarez-Rubio and Lookingbill 2016). Additional methods have been used to estimate thresholds of habitat loss. For example, Yin et al. (2017) developed a method that identifies rapid changes in species distributions instead of a breaking point, but, to our knowledge, this method has not been used with birds.

Of the 31 reviewed papers, 18 reported either a range or a specific threshold of the percentage of habitat cover, or mixed results with threshold and non-threshold responses. To illustrate the latter case, Morante-Filho et al. (2015) found no response in the richness and abundance of the whole community, but a threshold response on diversity of forest-specialist, frugivorous, and insectivorous birds, and a positive effect on generalist birds. Zuckerberg and Porter (2010) tested for the presence of a threshold for 25 species of forest birds using the New York State Breeding Bird Atlas. They found that thresholds were a common, but not a pervasive, characteristic that defined species responses to changes in forest cover, with 22 species showing extinction threshold responses ranging from 24.4 to 88.2% forest cover. The remaining 13 papers reported an array of results, including thresholds based on habitat characteristics other than habitat percentage (e.g., Jansson and Angelstam 1999, Guénette and Villard 2005), multiple thresholds depending on scale,

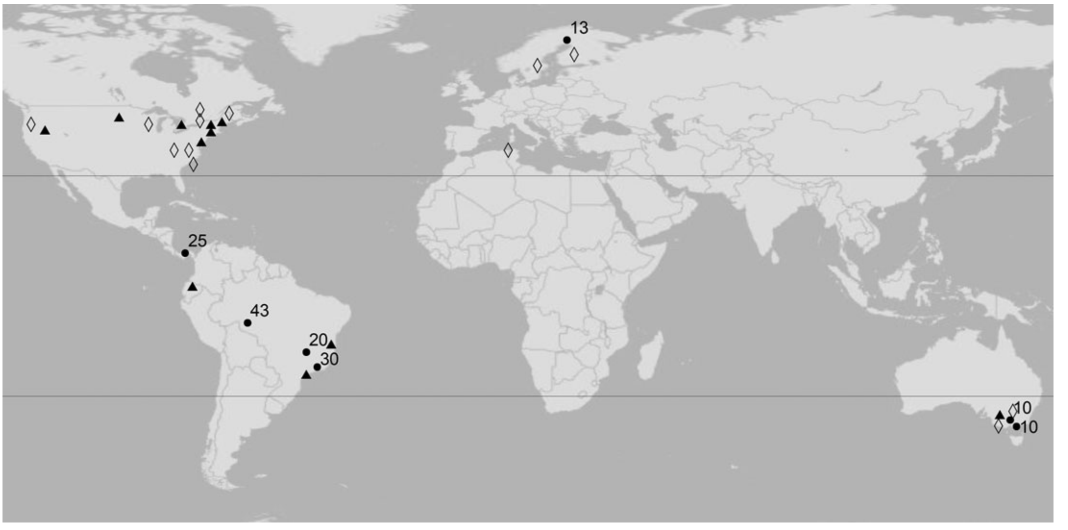

Fig. 2. Location where 31 studies on thresholds of bird species loss as a function of habitat loss were conducted. Black circles represent the seven studies where a single threshold value of percent habitat cover was reported (value shown on the map), diamonds represent 11 studies where a range of percentages of habitat cover were reported, and triangles represent 13 studies where thresholds were reported in a different way (i.e., no-threshold response, tree density, canopy closure, and so on). When the coordinates of study areas were not reported, points indicating locations were estimated based on the description of study areas. Black lines indicate the tropics of Capricorn and Cancer.

species, and response variable (e.g., Suarez-Rubio et al. 2013, Becker et al. 2015, Suarez-Rubio and Lookingbill 2016), and no threshold response by one or more of the evaluated species. For example, Lindenmayer et al. (2005) reported no evidence of any kind of threshold. These authors examined responses of different species of birds and reptiles to native vegetation cover in Australia and argued that, because the choice of both response and predictor variables and the inherent ecological variability of species assemblages may influence the results, the predictive power and practical usefulness of the threshold concept are questionable.

Threshold responses from the 18 studies that reported either a range or a single threshold value ranged from ~ 1 to ~ 90% forest cover (Table 1). The different levels of analysis (species and communities) and the variety of methods used to collect and analyze data (i.e., threshold values inferred from graphs, piecewise regression, ROC, and so on) prevent a proper statistical comparison among studies. However, as a crude approximation, we note a possible trend between studies conducted in temperate regions and those in the tropics. Studies conducted in temperate regions reported lower values (mean = 27.9%, range = 1.3–90%; $N = 11$) than those conducted in the tropics (mean = 33.6%, range = 20–50%; $N = 7$). Comparison of the means (with a t-test using SPSS, version 22) revealed no significant difference between temperate and tropical regions ($P = 0.20$). Considering only the seven studies where single threshold values were reported, the same trend prevailed, but with a significant difference between regions ($P = 0.015$). The mean habitat cover threshold was 11% for studies conducted at temperate latitudes ($N = 3$) and 29.5% for studies in the tropics ($N = 4$; Fig. 3). These crude estimates suggest that tropical species might be more susceptible to habitat loss than temperate species, and there may be more variation in responses of the species and communities in temperate regions as indicated by the wider range of threshold values than in tropical regions. Values from the tropics are more consistent with theoretical threshold studies that suggest a threshold of 30% of remaining habitat, below which species tend to be more sensitive to habitat alterations (Andrén 1994).

Variation in threshold values, especially among studies conducted in temperate regions, may be due to differences in the

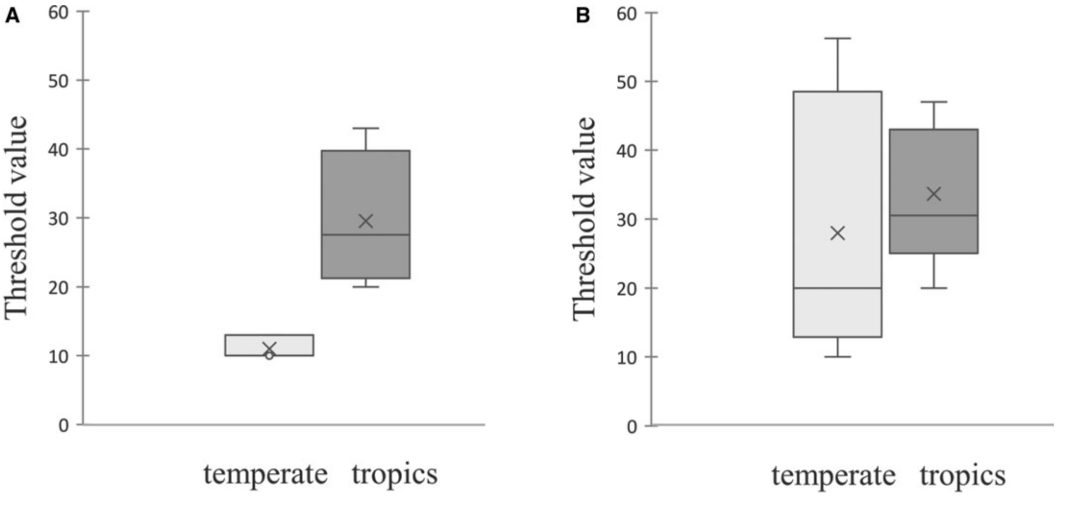

Fig. 3. Comparison of the means from (a) seven studies that reported single threshold values, and (b) 18 studies that reported either a range or a singular threshold values. The lines outside each box represent minimum and maximum values, lines within the boxes are the medians, and 'x' represents the mean of the threshold value for each region.

conservation status of study areas, historical features of land-use changes, or the fact that more studies have been conducted in temperate regions. Variation may also be related to differences in the level of analysis (community or species) or the applied statistical analyses. In the literature, such variability has been acknowledged (Lindenmayer and Luck 2005, Ficetola and Denoël 2009, Estavillo et al. 2013, Boesing et al. 2018, Roque et al. 2018) as being the result of (1) statistical artefacts, (2) interrelated factors of nature, such as different species responses to landscape change, differences in habitat quality, and timing, intensity and extent of the change or, alternatively, (3) variability in the landscape matrix surrounding study areas. Thus, the uncontrolled variables inherent to the nature of this review may affect the results of our comparison between temperate and tropical regions.

Controversy still exists about the effect of the species selected for study and the community and population metrics used in studies of threshold responses. For example, Ochoa-Quintero et al. (2015) reported higher threshold values when including only threatened species, and Rodrigues et al. (2016) found that the threshold responses could drop from near 90% when using abundance to lower than 20% when using richness of aquatic macroinvertebrate communities. These facts highlight that our temperate versus tropical comparison was made only as a preliminary assessment. If the observed difference in threshold values between tropical and temperate regions is genuine, and not related to use of different methods, we suggest that it may be related to the historic climatic conditions that make species that evolved in more stable conditions (i.e., tropics) less resilient to change (Dalsgaard et al. 2011, Sandel et al. 2011). This would explain the observed higher and a narrower range of threshold values in the tropics, and the lower and wider range of thresholds in temperate regions with both resilient and non-resilient species. We hope this review stimulates tests of this proposed hypothesis, i.e., there is a synergetic effect between historical climate stability and habitat destruction on biodiversity.

Identifying threshold values can generate clear recommendations for habitat management and conservation. Although authors of most of the papers we reviewed made general recommendations, some authors made concrete recommendations concerning desirable habitat characteristics and the minimum amount of habitat to be preserved (e.g., Drinnan 2005, Radford et al. 2005, Martensen et al. 2012, Ochoa-Quintero et al. 2015). Notably, the findings and recommendations of Banks-Leite et al. (2014) have now been implemented as the official target for restoration in an environmental resolution legislated by the São Paulo State and a federal decree in Brazil. Banks-Leite et al. (2014) provided scientific evidence that led the Environment Secretariat of the State of São Paulo to prioritize reforestation projects in municipalities with less than 30% forest cover, and to define higher offsetting standards for entrepreneurs in municipalities with less than 30% forest cover. These new rules are part of Resolution SMA 7/2017. Also, these results were incorporated in the official map used by the Brazilian Environment Ministry to help support the Native Vegetation Protection Law (N° 12.651/2012) and the National Policy for Native Vegetation Recovery (resolution n° 8.972/2017), thus being instrumental in the development of an optimal restoration scenario (C. Banks-Leite, pers. comm.).

Gaps of knowledge and future perspectives. Given the relevance for understanding species and the possibility of aiding conservation actions, habitat thresholds of bird species loss are clearly a subject attracting attention from researchers, conservationists, and decision-makers. Nonetheless, we found relatively few empirical studies on this topic. The need for a habitat gradient to identify thresholds may be a practical limitation, as might the time-consuming fieldwork requirements depending on the selected variable.

The geographical distribution of threshold studies, with most conducted in North America (15), South America (six), and Australia (five), but with only a few conducted in Europe (three), Africa (one), and Central America (one), and the lack of studies in Asia, provide evidence of a strong geographical bias (Fig. 2). Consequently, more threshold studies are needed in regions with few or no studies to date. However, we acknowledge that, because our search retrieved only papers in English, we may have missed records of studies conducted, for example, in Asia or Latin America. Amano et al. (2016) acknowledged that, although English is recognized as a global scientific language, ignoring non-English publications may cause biases in our understanding of study systems. Regarding the low number of studies in the tropics compared to temperate regions, we believe that it is crucial to conduct more (comparable) studies in the tropics to test if – and why – threshold values may differ between these regions.

Even though there is an increasing array of literature involving thresholds with different taxonomic groups (Fig. 1), some controversies exist regarding their applicability, e.g., not all species in a community have the same responses (Lindenmayer et al. 2005, Estavillo et al. 2013), and the results of studies may not be transferable across regions, e.g., species may have different threshold responses in different locations (van der Hoek et al. 2013). Also, although the percentage of suitable habitat may be the most important and widely used variable, threshold responses may change with different landscape configurations such as the degree of fragmentation. Notably, some of these challenges have already been addressed (Jansson and Angelstam 1999, Villard et al. 1999, Suarez-Rubio et al. 2013, Van der Hoek et al. 2015). We argue that the applicability of the threshold concept, even though the number of studies is increasing, may benefit from more refined analyses that include the matrix (Boesing et al. 2018), and consider historical land use changes and other variables such as historical climate stability that help identify the mechanisms behind the responses.

Taken together, although the threshold concept is clearly relevant for understanding how current habitat destruction will impact patterns of biodiversity (Ratajczak et al. 2018), there are many challenges to overcome and the concept needs to be used with caution to make sound conservation or management recommendations (Lindenmayer and Luck 2005). However, our review suggests that tropical regions may have higher threshold responses than temperate regions, where the ranges of values is highly variable, indicating that tropical species may be more impacted by habitat alteration. Despite current limitations, identifying thresholds of species loss should improve our understanding of the consequences of landscape transformations on biodiversity and bird species. Further research is vital because agriculture expansion is one the most important threats to birds and biodiversity in general. We urge researchers to further develop the threshold concept and/or conduct large-scale studies using similar methods, allowing unbiased comparisons of species responses to landscape change. Such studies can be translated into conservation practices, given a clear understanding of the political and environmental contexts where they were conducted.

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