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Comparing species and measures of landscape structure as indicators of conservation importance

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Summary

1. The use of indicators to identify areas of conservation importance has been challenged on several grounds, but nonetheless retains appeal as no more parsimonious approach exists. Among the many variants, two indicator strategies stand out: the use of indicator species and the use of metrics of landscape structure. While the first has been thoroughly studied, the same cannot be said about the latter. We aimed to contrast the relative efficacy of species-based and landscape-based indicators by: (i) comparing their ability to reflect changes in community integrity at regional and landscape spatial scales, (ii) assessing their sensitivity to changes in data resolution, and (iii) quantifying the degree to which indicators that are generated in one landscape or at one spatial scale can be transferred to additional landscapes or scales.

2. We used data from more than 7000 bird captures in 65 sites from six 10 000-ha landscapes with different proportions of forest cover in the Atlantic Forest of Brazil. Indicator species and landscape-based indicators were tested in terms of how effective they were in reflecting changes in community integrity, defined as deviations in bird community composition from control areas.

3. At the regional scale, indicator species provided more robust depictions of community integrity than landscape-based indicators. At the landscape scale, however, landscape-based indicators performed more effectively, more consistently and were also more transferable among landscapes. The effectiveness of high resolution landscape-based indicators was reduced by just 12% when these were used to explain patterns of community integrity in independent data sets. By contrast, the effectiveness of species-based indicators was reduced by 33%.

4. *Synthesis and applications*. The use of indicator species proved to be effective; however their results were variable and sensitive to changes in scale and resolution, and their application requires extensive and time-consuming field work. Landscape-based indicators were not only effective but were also much less context-dependent. The use of landscape-based indicators may allow the rapid identification of priority areas for conservation and restoration, and indicate which restoration strategies should be pursued, using remotely sensed imagery. We suggest that landscape-based indicators might often be a better, simpler, and cheaper strategy for informing decisions in conservation.

Key-words: Atlantic Forest, biodiversity indicators, habitat fragmentation, habitat loss, landscape metrics, surrogates, Umbrella Index

Introduction

Interest in the use of biodiversity indicators has been rising rapidly in recent years. Since 2002, when 188 government Parties to the Convention on Biological Diversity (CBD) agreed 'to achieve by 2010 a significant reduction of the current rate of biodiversity loss' and to develop indicators to monitor progress towards this target (Mace & Baillie 2007), the study of biodiversity indicators has attracted considerable attention (e.g. Billeter *et al.* 2008; Cabeza, Arponen & Van Teeffelen 2008; Mattfeldt, Bailey & Grant 2009). However, for every study

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supporting the general use of indicators (e.g. Mac Nally & Fleishman 2004; Rodrigues & Brooks 2007), there is probably an equivalent number of studies arguing against their widespread use (e.g. Andelman & Fagan 2000; Caro 2003). In fact, the controversy and difficulties of using biodiversity indicators are so large that limited progress was made in developing indicators sets to measure progress towards the CBD's 2010 target before 2010 arrived (Walpole *et al.* 2009).

There are several reasons why indicators used for identifying areas for conservation do not uniformly work as an effective surrogate of biodiversity. Indicator species are sometimes selected based on characteristics such as charisma for the general public, or having a large area requirements or body size, which do not inevitably confer on the species that possess them a high correlation with local diversity or extinction threat (Hockey & Curtis 2009). As a result, the use of species selected for these reasons is frequently no more effective than employing a random selection of species (Andelman & Fagan 2000; Caro 2003; Grenyer *et al.* 2006; Cabeza, Arponen & Van Teeffelen 2008). Other issues that may affect the efficacy of the indicator species strategy, and the comparability of the results across studies, are the lack of standardization of the statistical methods used to select indicator species, variation in data resolution, and the spatial and temporal scale of the sampling design that is used for indicator selection (Weaver 1995; Grenyer *et al.* 2006; Billeter *et al.* 2008; Cabeza, Arponen & Van Teeffelen 2008), as well as the region and extent of the study area (Fleishman *et al.* 2002; Hess *et al.* 2006).

An approach that has received less attention than the use of indicator species is the use of structural indicators, such as landscape metrics or other environmental variables, to identify areas for conservation (Noss 1999; Lindenmayer *et al.* 2002; Faith 2003). In particular, the use of landscape metrics has distinct methodological advantages in that the data are relatively easy to obtain via satellite imagery (Turner *et al.* 2003), and that there are freeware programmes available for quantifying landscape metrics (e.g. Fragstats; McGarigal & Marks 1995). However, the use of landscape metrics also has a number of drawbacks. For example, the ecological processes linking many landscape metrics with on-the-ground measures of biological condition are often not clear (Ewers *et al.* 2009; Lafortezza *et al.* 2010), and species with different life-histories respond differently to the same spatial patterns of habitat (Noss 1999; Fahrig 2003; Banks-Leite, Ewers & Metzger 2010). Consequently, landscape-based indicators may suffer from similar problems to those described for species-based indicators and, until fully validated against empirical data, interpretations of change in landscape-based indicators are no more than a speculative exercise (Noss 1999; Lafortezza *et al.* 2010).

Nonetheless, the low efficacy of biodiversity indicators cannot be solely blamed on the choice of indicators. Biodiversity indicators, as the name reveals, are used to indicate 'biodiversity', a buzzword which encompasses several meanings but that, within this context, is often used to describe species richness (Caro & O'Doherty 1999). There is mounting evidence showing that species richness holds little biological information and is highly sensitive to differences in sampling effort and to the invasion of matrix species into habitats of conservation concern (Gotelli & Colwell 2001; Su *et al.* 2004; Barlow *et al.* 2007). In fact, when assessing the effects of tropical forest degradation on multiple taxa, studies have shown that it is more important to consider the patterns of community turnover rather than species richness (Barlow *et al.* 2007; Basset *et al.* 2008). Patterns of community turnover can be particularly informative when they are measured against a reference condition, such as the community composition found in pristine conditions, as it gives an idea of the quality or integrity of a community (Ewers *et al.* 2009; Lafortezza *et al.* 2010). Measures of community integrity, or the more broadly-defined 'ecological integrity', have been poorly applied in terrestrial and forest systems (Ewers *et al.* 2009), for which few indicators of integrity have been developed so far (Gardner 2010).

In this study, we compared the relative efficacy of species-based and landscape-based indicators for identifying areas for conservation, using bird community integrity as a case study. Our goals were to: (i) compare the relative efficacy of species-based and landscape-based indicators at identifying sites with the highest community integrity at a regional and landscape scale, (ii) assess how changes in data resolution (abundance vs. presence–absence data for indicator species, and coarse vs. fine pixel size for landscape-based indicators) alters the efficacy of the two types of indicators and (iii) assess the ability with which indicators selected to reflect patterns in one area or scale to successfully predict community integrity in other areas and at different spatial scales.

Materials and methods

STUDY AREA

The study was conducted in the Atlantic Plateau of the State of São Paulo, Brazil (Fig. 1). Sampling was conducted in six 10 000-ha landscapes, three of which were fragmented but varied in the total amount of native rainforest (approximately 10%, 30% and 50% of forest cover) while the remaining three had continuous forest cover (approximately 90%; hereafter referred to as 'control areas' (Appendix S1, Supporting Information). We sampled a total of 12 sites in the control areas (four sites in each area) and 53 patches in the fragmented landscapes; 17 patches in the 10% and in the 30% FC landscapes, and 19 patches in the 50% FC landscape. Forest patches were selected to vary from 2 to 150 ha in size in all fragmented landscapes (Appendix S1, Supporting Information).

BIRD SAMPLING

The understorey bird community was sampled using 10 mist-nets (12-m length, 31-mm mesh) per site and with a standardized protocol for an average of 637 net-hours (SD = 76). In total, between March 2001 and March 2007 we performed more than 41 000 mist-net-hours in the three fragmented landscapes and adjacent continuous landscapes (Appendix S1, Supporting Information).

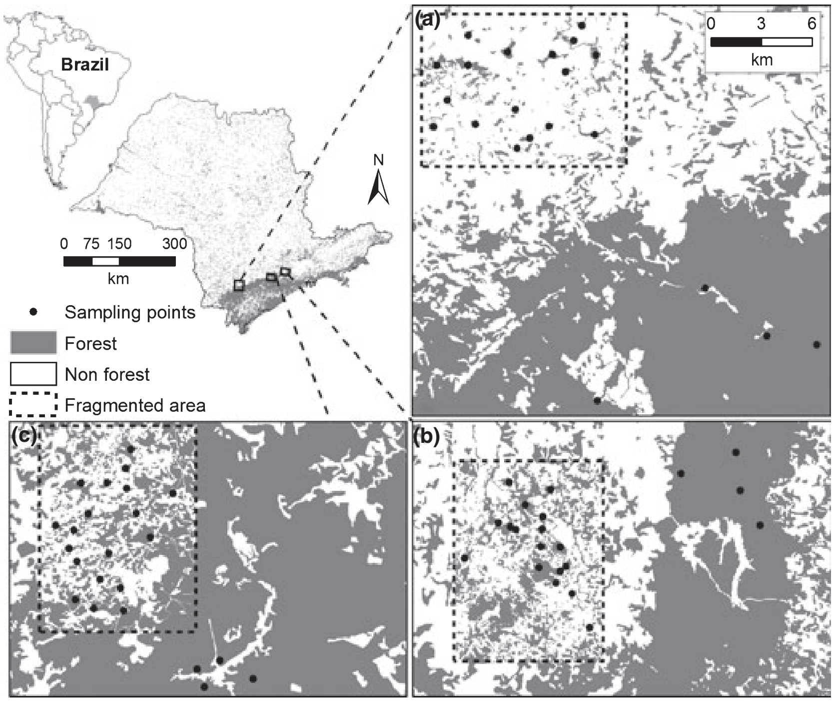

Fig. 1. Map of the study area in the state of São Paulo, Brazil, showing the location of the fragmented landscapes (dotted lines) and adjacent continuous forest, and the sampling sites where understory birds were captured (circles). Panel (a) depicts the 10% FC landscape, panel (b) – 30% FC landscape, panel (c) – 50% FC landscape.

STATISTICAL ANALYSIS

All analyses were conducted using R v2·7·1 (R Development Core Team 2008).

Assessing bird community integrity

Changes in bird community integrity were assessed by using community composition observed in control sites as a reference condition, and quantifying the extent to which species composition in disturbed sites deviated from these reference sites in the multidimensional space (Appendix S1, Supporting Information). Bird community composition was measured with a Principal Coordinate Analysis (PCoA) performed on a Bray-Curtis dissimilarity matrix (Appendix S1, Supporting Information). Changes in bird community integrity were measured at two spatial scales: at the regional scale by using all 53 patches from the three fragmented landscapes in a single ordination, and at the landscape scale by analysing each fragmented landscape separately, always using the paired control landscapes as the reference sites (box on Fig. 2).

Developing indicator sets at different data resolutions and spatial scales

Species-based indicators. We used the Umbrella Index (UI) developed by Fleishman, Murphy & Brussard (2000) to determine the indicator value of each species and thereby select a 'best' set of indicator species in an ecological and quantitative framework. The UI of individual species was calculated as the sum of that species' medium rarity (1-|0·5-P|, where P is the proportional occurrence), mean percentage of co-occurring species and disturbance sensitivity (Fleishman, Murphy & Brussard 2000). The proportional occurrence (P) of each species is calculated by summing the number of sites in which the species is present and dividing by the total number of sites sampled. The mean percentage of co-occurring species is calculated by averaging the species richness (S_{site} − 1) in each site from which the target species was recorded and dividing by the highest recorded species richness among all sites (S_{max} – 1). While the first two criteria were calculated as reported in Fleishman, Murphy & Brussard (2000), disturbance sensitivity criterion had to be modified (Appendix S1, Supporting Information). We performed single regressions between the abundance of each bird species in forest fragments and the gradient of community composition, as represented by the scores of PCoA axis 1. To avoid circularity in these estimates, for each correlation we ran a separate ordination including all recorded species but the one being tested. Because species abundance does not regularly follow normal distributions, we used Generalised Linear Models (GLM) using Poisson errors and then calculated the treatment deviance relative to the null deviance of the model (analogous to the R^2 measure in regression models and hereafter referred to as 'explained deviance'). We used explained deviance as the measure of species' sensitivity to human disturbance for calculating the UI.

We repeated the procedure described above to build indicator sets at the regional and landscape scale, and with high- and low-data resolution (paths 1–8, Fig. 2). To build indicator sets with low data resolution, we collapsed the matrix of species abundances into presence–absence, resulting in a loss of ecological information about the relative abundances of species. The use of presence–absence data required us to recalculate the measure of disturbance sensitivity in the UI, which had been previously calculated using species abundances (Appendix S1, Supporting Information).

Landscape-based indicators. Landscape metrics were calculated on maps with 10 m resolution (Appendix S1, Supporting Information)

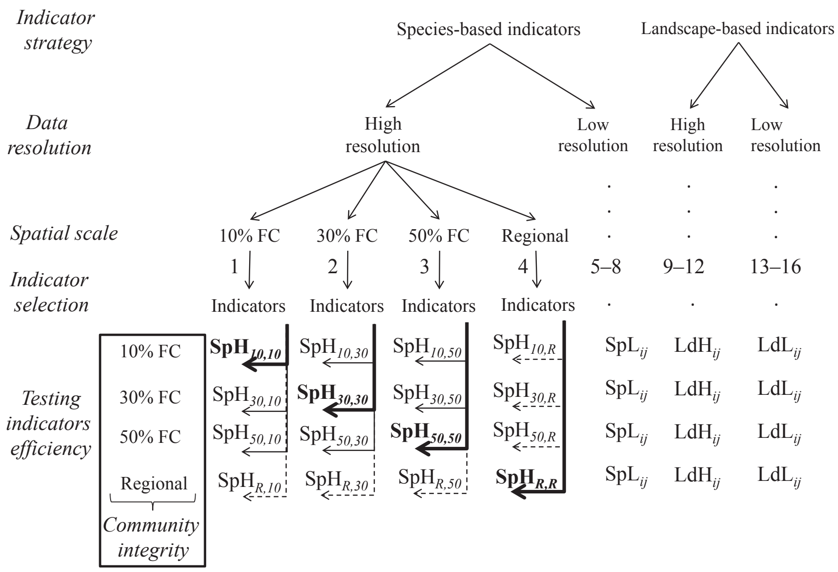

Fig. 2. Schematic representation of the analysis. The acronyms 'SpH', 'SpL', 'LdH' and 'LdL' represent the analyses used for assessing the efficacy of indicators using indicator species with high and low resolution, and landscape-based indicators with high and low resolution, respectively. Subscripts were reported as 10, 30, 50 and R to represent the 10, 30, 50% FC landscapes and the Regional data set, respectively. Paths 1 to 16 represent the selection of indicator sets. Paths $SpH_{10,10}$, $SpH_{30,30}$, $SpH_{50,50}$ and $SpH_{R,R}$ (as well as $SpL_{10,10}$, $SpL_{30,30}$ and so on), depicted in thick arrows, represent the selection and tests of endogenous indicators. All remaining paths depicted in continuous thin arrows (such as $SpH_{30,10}$, $SpH_{50,10}$, $SpH_{10,30}$) represent analyses using exogenous indicators. Paths depicted in dotted lines represent cross-scale validations of selected indicators, where we tested the transferability of indicators from the landscape to the regional scale and *vice versa*. The subscript *j* refers to the data set used to select the indicators, and *i* refers to the data set used to assess the efficacy of the indicators selected using data set *j*.

using Fragstats 3.3 (McGarigal & Marks 1995) and were selected to represent a wide range of environmental variables that are known to affect birds such as patch area, edge effects, connectivity and the proportion of forest cover (Martensen, Pimentel & Metzger 2008; Banks-Leite, Ewers & Metzger 2010). To build the set of landscape-based indicators, we calculated the size, perimeter and shape of patches, the core area of patches using edge penetration distances of 20, 50 and 100 m (following Laurance 2004), contiguity index, proximity index in the range of 20, 50 and 100 m (following Awade & Metzger 2008) and the proportion of forest cover in circles of radii of 300, 500 and 800 m around sampling points (following Boscolo & Metzger 2009). Because of high correlations among all landscape metrics (Table S1, Supporting Information), we performed a principal components analysis (PCA) to obtain 13 uncorrelated axes that represented all the variation in the landscape metrics (Table S2, Supporting Information). PCA axes were obtained by log-transforming all variables which incorporated a measure of patch area, and scaling all *N* metrics to have a zero mean and unit variance.

Again, we built indicator sets for the regional and landscape scale, and for high- and low-data resolution (paths 9 to 16, Fig. 2). For the latter, we degraded the resolution of the 10-m pixel map into a 30-m pixel map, similar to the resolution of a Thematic Mapper Landsat image, from which landscape metrics were then calculated. Because of the changes in resolution, two out of the 13 landscape metrics could not be calculated in 30-m pixel images, thus we only obtained 11 PCA axes.

Selecting the most parsimonious indicator sets and testing their efficacy

We first assessed the efficacy with which indicators selected from a data set would represent changes in community integrity of the same data set (hereafter 'endogenous indicators'; Fig. 2). Our use of the term 'efficacy' is intended to represent the ability of an indicator set to represent changes to the integrity of the bird community, and is measured as the goodness of fit from regressions of indicator values against changes in community integrity.

We performed a two-step procedure to select the set of indicators species and test for its effectiveness in representing changes in community integrity. First, we included in the indicator set only those species that had an UI greater than the mean plus one standard deviation of the distribution of UI values (following Fleishman, Murphy & Brussard 2000). Then, we assessed the efficacy of that indicator set in a multiple linear regression (GLM with Gaussian errors), where the response variable was the PCoA axis representing changes in community integrity and the explanatory variables were the indicator species (Appendix S1, Supporting Information).

To build the sets of landscape-based indicators and test their efficacy, we used backwards stepwise regression to select the minimum adequate set, and then assessed the efficacy of that set. As with the selection of species-based indicator sets, here the PCoA axis was again the response variable representing community integrity and the PCA axes representing changes in landscape metrics were the explanatory variables. The most parsimonious model was selected with the use of AIC (Burnham & Andersen 1998).

Testing for indicator transferability across landscapes and across scales

Indicators that are highly transferable are those that, once selected from data at one location or spatial scale, are effective at accurately reflecting changes in community integrity in other locations or scales. Thus, this analysis assessed the efficacy with which the indicator set selected from one data set would represent changes in community integrity in a spatially independent data set(s) (hereafter 'exogenous indicators'). As before, we used multiple regressions to estimate indicator transferability across landscapes and to test for indicator transferability across scales (Fig. 2). We regressed the indicator set determined from one landscape or scale against the PCoA axis reflecting community integrity in a different landscape or scale, with the transferability of an indicator reflected by measures of goodness of fit from this regression (Appendix S1, Supporting Information).

Comparing the relative efficacy of species-based and landscape-based indicators

We used the adjusted R^2 from the multiple regressions described above as a measure of the explanatory power, or efficacy, with which a given indicator set was able to reflect changes in community integrity, while correcting for differences in model complexity. At the regional scale, we only had one value of adjusted R^2 from each indicator strategy and data resolution, so the explanatory power of different models was compared directly. However, at the landscape scale we had three replicates of landscapes. Given the low number of comparisons, we chose to report effect sizes (*d*) as a measure of the magnitude of a difference (Cohen 1988). Following Rosenthal & Rosnow (1991), we computed *d* from the value of the *t*-test of the differences between two means ($d = 2t/\surd\upsilon$), where υ is the degrees of freedom of the *t*-test, although we used a paired *t*-test in which the comparisons of indicator sensitivity were nested by landscape. For instance, to assess differences in the sensitivity of indicator species when modifying data resolution, we first calculated the *t*-value of the difference in adjusted R^2 from the following analyses depicted in Fig. 2: ($SpH_{10,10}$-$SpL_{10,10}$) + ($SpH_{30,30}$-$SpL_{30,30}$) + ($SpH_{50,50}$-$SpL_{50,50}$) + ($SpH_{R,R}$-$SpL_{R,R}$). From this paired *t*-test, we were able to calculate the effect size *d*. Effect sizes were interpreted in terms of the average percentile standing of one group mean relative to the other, in which an effect size larger than 1·7 shows that the mean of one group is past the 95·5 percentile of the other group (similar to a one-side *P*-value = 0·05) (Cohen 1988).

We used a similar approach to compare the transferability of species-based and landscape-based indicator sets using high- and low-data resolutions across landscapes and spatial scales. We subtracted the adjusted R^2 of models built with exogenous indicators from the adjusted R^2 of models built with endogenous indicators and compared this difference across strategies (Appendix S1, Supporting Information). These tests are designed such that a positive or negative *t*-value indicates that the use of exogenous indicator sets yields a gain or loss in explanatory power respectively.

Results

We captured a total of 6264 individuals (excluding recaptures) of 140 bird species in the fragmented and control landscapes, of which 23 were only captured in the control landscapes. The 50% FC landscape had the highest species richness (total number of species observed = 87, rarefied species richness per 1500 individuals = 85·9), while a lower richness was found in the 30% FC landscape (observed = 62, rarefied = 61·2) and 10% FC landscape (observed = 69, rarefied = 60·3).

INDICATOR EFFICACY AT REGIONAL AND LANDSCAPE SCALES

Based on high-data resolution

At the regional scale, six species had UI scores above the cut-off value of 1·82 and were thus selected as indicators (Table S3, Supporting Information). The set of indicator species was well correlated with changes in community integrity (adjusted $R^2 = 0{\cdot}73$, $F_{6,46} = 24{\cdot}08$, $P < 0{\cdot}0001$, Fig. 3a). The best set of landscape-based indicators contained a similar number of variables (five PCA axes) and also resulted in a significant, but slightly weaker, relationship (adjusted $R^2 = 0{\cdot}58$, $F_{5,47} = 15{\cdot}16$, $P < 0{\cdot}0001$, Fig. 3c, Tables S4 and S5 in Supporting Information).

We found a different pattern when analysing the data at the landscape scale. In all three landscapes (10, 30 and 50% FC), landscape-based indicators outperformed the efficacy of species-based indicators (Fig. 3a,c). Sets of landscape-based indicators explained an average of 90% (SD = 0·07) of the variation in ecological integrity, whereas sets of indicator species explained an average of 70% (SD = 0·08) across the three landscapes; a difference that can be considered significant ($d = 3{\cdot}9$, percentile > 97·7).

Based on low-data resolution

Reducing data resolution had variable and spatial scale-dependent impacts on the effectiveness of species-based indicators, and a consistently negative impact on that of landscape-based indicators (Fig. 3b,d). At the regional scale, the use of species presence–absence data yielded a stronger indicator set (adjusted $R^2 = 0{\cdot}86$, $F_{7,45} = 45{\cdot}06$, $P < 0{\cdot}0001$) than originated from abundance data (Fig. 3a,b), while at the landscape scale the reduction in data resolution yielded weaker results ($d = 2{\cdot}35$, percentile > 97·7). For landscape-based indicators, the reduction in data resolution from a 10-m to a 30-m pixel image led to a reduction in their efficacy both at the regional scale (adjusted $R^2 = 0{\cdot}54$, $F_{4,48} = 16{\cdot}40$, $P < 0{\cdot}0001$, Fig. 3c,d) and at the landscape scale ($d = 14{\cdot}32$, percentile > 97·7).

INDICATOR TRANSFERABILITY ACROSS LANDSCAPES, SPATIAL SCALES AND DATA RESOLUTIONS

Across landscapes, the efficacy of high resolution indicator species in representing changes in community integrity decreased by an average of 33% when using exogenous indicators (Fig. 3a). By contrast, high resolution landscape-based indicators had significantly higher transferability across landscapes and resulted in an average loss of efficacy of just 12% ($d = 2{\cdot}61$, percentile > 97·7, Fig. 3c). When using low-resolution data, however, there was little difference in the transferability of species-based and landscape-based indicators (mean loss in explanatory power was 15% and 24% respectively, $d = 0{\cdot}53$, percentile < 69·0, Fig. 3). Across spatial scales, species-based indicator sets selected using landscape-scale data sets performed poorly when tested on regional data (mean loss in efficacy = 26%), a trend that was not observed for landscape-based indicators which showed a lower loss of explanatory power (mean loss in efficacy = 10%, $d = 4{\cdot}01$, percentile > 97·7, Fig. 3). On the other hand, both species and landscape-based indicators selected using regional data with high resolution data lost a similar, and considerable, amount of

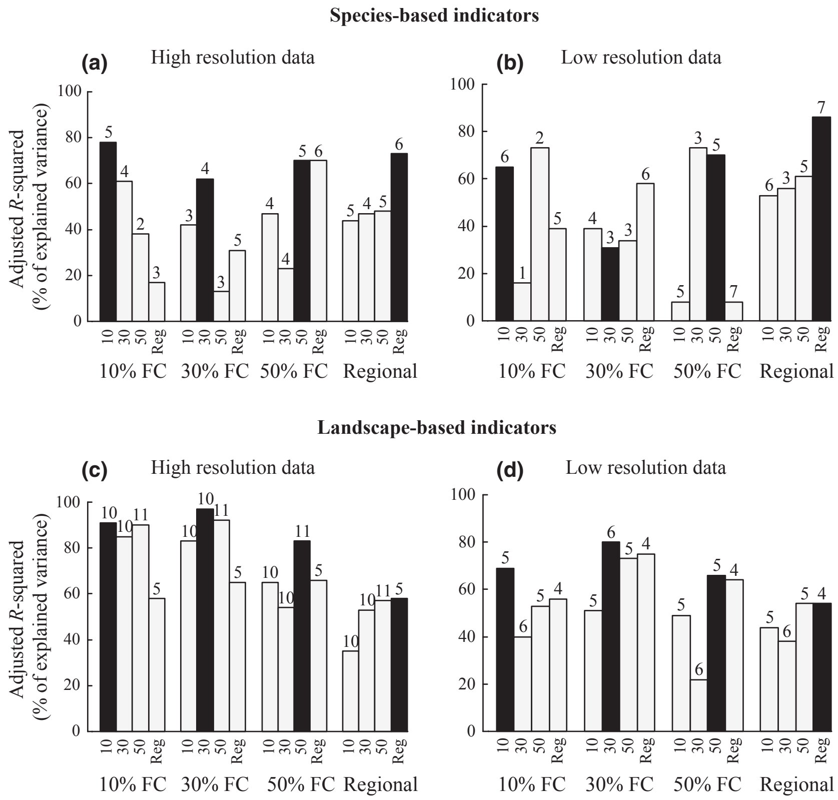

Fig. 3. Sensitivity of species-based (a, b) and landscape-based (c, d) indicators to changes in bird community integrity, when generated using high resolution (a, c) and low resolution data (b, d). Adjusted R^2 values represent the explanatory power or efficacy of indicators. Within each panel, each set of four bars shows the data set used to create indicators, and the bars within each group show the data set used for testing the efficacy of indicators. Black bars show the efficacy of endogenous indicators, and white bars show the transferability of exogenous indicators. As an example, bars in panel (a), running from left to right, represent the results from the analyses performed on paths $SpH_{10,10}$, $SpH_{30,10}$, $SpH_{50,10}$, $SpH_{R,10}$, $SpH_{10,30}$, $SpH_{30,30}$, $SpH_{50,30}$, and so on (Fig. 2). Numbers on the top of the bars show the number of variables included in the indicator set. See Table S4 in Supporting Information for values and significance levels.

explanatory power when applied to the landscape scale (mean loss in explanatory power = 31% and 27% respectively, d = 0·38, percentile < 66·0). The transferability of indicator species across scales was not only poor for high resolution data; it was also poor and variable for low-resolution data (an overall average efficacy loss of 25%), while landscape-based indicators built from low-resolution data had a consistently high transferability both from the regional to landscape scale and *vice-versa* (mean loss in efficacy = 7% and 9% respectively).

Discussion

It would be expected that information on the occurrence and abundance of bird species would generate the best indicators of bird community integrity, but we found that indicators based on remotely sensed landscape metrics consistently outperformed indicator species in predicting community integrity. Using subsets of 13 original landscape metrics, we were able to explain an average of 90% of the variation in bird community integrity at the landscape scale, compared to just 70% using indicator species. Moreover, the results from landscape-based indicators were less variable and more transferable across landscapes and scales than those obtained from indicator species (Fig. 3).

Despite the clear superiority of landscape-based indicators, it would be incorrect to conclude that the use of indicator species would be a ‘flawed’ strategy for selecting areas of conservation importance in the Atlantic Forest. In fact, results achieved for indicator species were amongst the strongest in the published literature (adjusted R^2 values ranging from 0·31 to 0·86); results which are similar in strength to those in which indicators species were used as surrogates of species richness and species complementarity (Mac Nally & Fleishman 2004; Rodrigues & Brooks 2007). Had we not directly compared the use of indicator species to the use of landscape-based indicators, we would almost certainly have concluded that indicator species are an effective strategy that should be pursued. However, we also found that indicator species yielded variable outcomes and had poor transferability; two characteristics that are strongly undesirable when using indicators to design a conservation strategy (Hess *et al.* 2006).

The transferability of indicator species selected using high-data resolution was low, resulting in an average 33% loss in the ability of those indicators to reflect patterns of community integrity in independent data sets. These results corroborate previous findings that changes in the observational scale and study region strongly affect the effectiveness of using indicator species as surrogates of species richness (Weaver 1995; Hess *et al.* 2006; Billeter *et al.* 2008). This outcome has partly a biological basis and is probably due to the three fragmented landscapes having a different degree of habitat loss. For instance, some species selected as good indicators for one landscape were not even captured in other landscapes, either because they were too forest-dependent and thus only occurred in the 50% FC landscape (e.g. *Myrmotherula gularis,* Spix), or because they were too disturbance-dependent and only occurred in the 10% FC landscape (e.g. *Arremon taciturnus,* Hermann). It is likely that indicators selected from replicate landscapes with similar proportions of forest cover would show much higher transferability, as has been shown in other biomes (Mac Nally & Fleishman 2004; Betrus, Fleishman & Blair 2005). Nonetheless, in a heavily fragmented biome such as the Atlantic Forest, it is important to be able to identify a single set of indicators that can be used across the full gradient of habitat loss and fragmentation. If this is not possible, alternative indicators must be considered.

Landscape-based indicators proved to be a powerful and reliable alternative to the use of indicator species. Although landscape-based indicators performed slightly worse than indicator species as endogenous indicators at the regional scale, this result was more than compensated by their consistently high efficacy at the landscape scale (Fig. 3). Landscape-based indicators had relatively low efficacy when generated with low-resolution data, yet were still comparable in efficacy to species-based indicators based on high resolution data. Perhaps most importantly, the transferability of landscape-based indicators was high in almost all cases, and even when transferability was lower, it was still similar to species-based indicators.

The use of landscape-based indicators has further advantages over the use of indicator species that should not be overlooked. First, landscape metrics can be obtained for any place for which satellite images are available, such as from the free Landsat archive (http://www.landcover.org), while the use of indicator species requires field work that is often expensive and time consuming (Gardner *et al.* 2008). Secondly, landscape metrics always yield one measure per site, while indicator species might go undetected at the time of sampling creating the problem of 'absence of information' (Metzger *et al.* 2008). Thirdly, there are several studies across the world showing how habitat loss and fragmentation affect species and communities, and this knowledge can help direct the selection of structural variables to be used as indicators (Ribeiro *et al.* 2009). As shown in our analysis of birds in the Atlantic Forest, there is high transferability of landscape-based indicators across landscapes and from the landscape to the regional level. Thus, local studies that have identified landscape metrics that are correlated with changes in community composition can be used as indicators for nearby regions or for use at a larger spatial scale.

Landscape-based indicators have many advantages over species-based indicators, but it is important to stress that we would have not reached this result had we not performed an exhaustive biological survey to measure the effects of forest fragmentation and habitat loss on bird community integrity. This emphasizes the importance of resisting the common temptation to determine *a priori* a set of landscape metrics to define patterns of habitat quality with little or no regard to ascertaining the biological relevance of those metrics on the ground (Lafortezza *et al.* 2010). It will always be necessary to conduct field surveys to collect information on the strength of species responses to habitat changes as to identify, select and validate landscape-based indicators (Walpole *et al.* 2009). Furthermore, it is possible that this result was produced because birds show very strong responses to habitat loss, fragmentation and degradation (Ferraz *et al.* 2007; Gardner *et al.* 2008; Martensen, Pimentel & Metzger 2008; Banks-Leite, Ewers & Metzger 2010). If we were studying other taxa that respond to alternative features of the environment at stand or micro-habitat scales that we did not measure (Dixo & Martins 2008), then species indicators may outperform landscape-based indicators. However, there is now considerable evidence showing that the major causes of the widespread loss of biodiversity are habitat loss (Fahrig 2003) and fragmentation (Ewers & Didham 2006), and that different groups of forest-dependent species are similarly affected by these variables (Metzger *et al.* 2009; Pardini *et al.* 2009). Such a consistently observed causal relationship should be regarded as a stronger basis for designing indicators than a simple correlation between species occurrence and high species richness. Therefore, we suggest that landscape-based indicators may be a more parsimonious approach than species indicators in situations where there is large, prior knowledge about the environmental variables that affect species and communities, whereas species indicators may be more parsimonious in situations where there is poor knowledge of the taxon biology.

Our study shows results that are among the strongest patterns ever recorded of the impacts of landscape modification on community composition, and lead us to advocate the use of landscape-based indicators for assessing the conservation value of Atlantic Forest areas. This result is particularly important considering that less than 10% of tropical forests lie within protected areas and that the future of biodiversity will certainly depend on the effective conservation and management of human-dominated landscapes, many of which are highly fragmented and degraded (Gardner *et al.* 2009; Ribeiro *et al.* 2009). Landscape-based indicators may thus be used by scientists and practitioners for developing conservation and/or restoration strategies in fragmented landscapes; they can help to identify areas of high conservation value, which can then be preserved, or to identify sites where values can be enhanced by restoration. Additionally, landscape-indicators can also indicate which strategies should be pursued to increase the value of these sites (e.g. increase connectivity, reduce edge effects).

Finally, it is more practical for governments and other conservation stakeholders to identify fragments and landscapes of high conservation value using satellite imagery than it is to embark on a search for a 'best' indicator taxon that will often show poor spatial congruence with species richness or composition of other taxa. In a time when strategies for conservation have to be identified hastily, the use of landscape-based indicators seems to be cheapest cost-effective strategy for identifying priority areas for conservation and restoration.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. PCoA plot of community composition (cited in Appendix S1 only).

Table S1. Correlation matrix of landscape metrics.

Table S2. Loadings of PCA axes onto the landscape metrics.

Table S3. List of selected indicator species.

Table S4. List of PCA axes selected as landscape-based indicators.

Table S5. Adjusted R^2 values and significance levels for all models.

Appendix S1. Supplementary information on Materials and methods.

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