

Evaluating the legacy of landscape history: extinction debt and species credit in bird and small mammal assemblages in the Brazilian Atlantic Forest

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Running title: Extinction debt and species credit

Word count - summary: 283; main text: 5,002; acknowledgements: 77; references: 1,252 and figure legends: 297.

Number of figures: 4

Number of references: 47

Summary

1. There is now an extensive literature on extinction debt following deforestation. However, the potential for species credit in landscapes that have experienced a change from decreasing to expanding forest cover has received little attention. Both delayed responses should depend on current landscape forest cover and on species life history traits, such as longevity as short-lived species are likely to respond faster than long-lived species.

2. We evaluated the effects of historical and present-day local forest cover on two vertebrate groups with different longevities – understory birds and non-flying small mammals – in forest patches at three Atlantic Forest landscapes. Our work investigated how the probability of extinction debt and species credit varies (1) among landscapes with different proportions of forest cover and distinct trajectories of forest cover change, and (2) between taxa with different lifespans.

3. Our results suggest that the existence of extinction debt and species credit, as well as the potential for their future payment and/or receipt, are not only related to forest cover trajectory but also to the amount of remaining forest cover at the landscape scale. Moreover, differences in bird and small mammal lifespans seems to be insufficient to affect differently their probability of showing time-delayed responses to landscape change.

4. *Synthesis and applications.* Our work highlights the need for considering not only the trajectory of deforestation/regeneration but also the amount of forest cover at landscape scale when investigating time-delayed responses to landscape change. As many landscapes are experiencing a change from decreasing to expanding forest cover, understanding the association of extinction and immigration processes, as well as their interactions with the landscape dynamic, is a key factor to plan conservation and restoration actions in human-altered landscapes.

47 Keywords: habitat fragmentation, habitat loss, habitat regeneration, landscape structure,
48 landscape dynamics, landscape connectivity, extinction threshold.
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1. Introduction

Habitat loss and fragmentation has been recognized as a major cause of global biodiversity loss (Foley *et al.* 2005). Species extinction following this process can be almost immediate in some cases (Stouffer, Strong & Naka 2009), but often it takes a considerable amount of time for declining populations to disappear (Brooks, Tobias & Balmford 1999; Lindborg & Eriksson 2004; Vellend *et al.* 2006), resulting in what is termed an extinction debt. Extinction debt is the number of extant species that are predicted to go extinct because the threshold condition for their persistence is no longer satisfied (Tilman *et al.* 1994) and the time taken for a community to reach a new, and reduced, number of species after an environmental disturbance is known as relaxation time (Diamond 1972).

Extinction debt and relaxation time can be calculated directly from data on regular long term monitoring of species occurrence after habitat loss and fragmentation (e.g. Ferraz *et al.* 2003). However, as such long term data-series are rarely available, extinction debt has been predominantly evaluated using alternative approaches (see Kuussaari *et al.* 2009). The most frequently used method investigates the effects of past and present-day landscape structure (i.e. habitat cover and configuration) on current species diversity. Extinction debt is assumed to be present when current species diversity is better described by past rather than by present-day landscape structure (e.g. Lindborg & Eriksson 2004). Although the magnitude of extinction debt cannot be estimated, this approach can successfully detect them as well as indicate relaxation time (e.g. Krauss *et al.* 2010).

Studies investigating extinction debt until now have assumed that the dynamic of landscape change is a unidirectional process of habitat loss and fragmentation (e.g. Brooks, Tobias & Balmford 1999). However, the history of fragmented landscapes can be much more complex as present-day landscape structure may be the result of alternating periods of habitat

contraction and expansion. An alternation from decreasing to expanding forest area, i.e. forest transition, has taken place over a century or more in several European countries and in North America (Rudel *et al.* 2005) and has been recently suggested for tropical regions, including the Brazilian Atlantic Forest (Baptista & Rudel 2006). Taking into account this complex change in habitat cover is of foremost importance to understand the legacy of landscape history on current patterns of biodiversity.

Improvements in landscape structure such as habitat expansion are expected to benefit species conservation. However, just as in the case of extinction debt following deforestation, the positive effects of those improvements in landscape structure should take some time to become evident and result in a species credit. Species credit (*sensu* Hanski 2000) is the number of species that will eventually benefit from a positive landscape change. Forest regeneration is expected to result in a species credit as it increases immigration rates across the landscape allowing re-colonisation of forest patches by species that have already gone locally extinct (Hanski 2000) and the rescue of declining populations in forest patches (Brown & Kodric-Brown 1977; Hanski 2000). As a consequence of the time-delayed responses, if the current species diversity in a landscape that has expanded in habitat cover is better described by past than by present-day landscape structure, a species credit can be assumed.

It is worth noting though that re-colonisation of forest patches by species that have already gone locally extinct may only take place if conspecific populations have survived in nearby patches (Hanski 2000; Pardini *et al.* 2010). Thus, species credit should only be received in the future if the total amount of habitat in the landscape is not (or has not gone during its history) below a critical extinction threshold (Hanski 2000; Pardini *et al.* 2010). Similarly, extinction debt is less likely to exist in severely fragmented landscapes than in less transformed landscapes, since species extinctions across the landscape are expected to occur faster in the

former. By contrast in highly forested landscapes, where many species should be able to persist across the landscape, both extinction debt and species credit are unlikely. Thus both debt and credit are most likely to exist and be paid and/or received in the future in landscapes that have undergone intermediate amounts of habitat loss and fragmentation and where many species might be persisting close to their species-specific extinction threshold at the landscape scale (Hanski & Ovaskainen 2002; Pardini *et al.* 2010). However, the probability of a landscape showing an extinction debt or species credit may also depend on other landscape characteristics such as time following landscape change (Vellend *et al.* 2006) and habitat quality throughout the landscape.

Additionally, delayed responses should depend on the life history traits of species, especially longevity. Short-lived species have already passed through many generations since landscape change and are likely to respond fast (but see Burel 1992; Petit & Burel 1998), while long-lived species produce fewer generations after landscape change and might respond slowly (Brook, Sodhi & Ng 2003; Lindborg 2007; Metzger *et al.* 2009; Krauss *et al.* 2010). The effect of longevity should be observed more strongly among habitat specialist species, since habitat generalists are able to occupy altered anthropogenic habitat and should not respond (either rapidly or slowly) to changes in native habitat (Pardini *et al.* 2009, 2010).

Here, we evaluated the effects of historical and present-day forest cover on the richness of two vertebrate groups – forest-dependent understorey birds and non-flying small mammals – in three landscapes from the highly imperilled Atlantic Forest of Brazil (Ribeiro *et al.* 2009). The study landscapes present a wide variation in the current total amount of forest cover which is a result of alternating periods of forest contraction and expansion in the past four decades. Thus, if the current variation in the number of forest-dependent species among patches is better described by historical than present-day local forest cover, an extinction debt or a species credit may be

assumed. Considering no change of forest quality over time, if landscape forest cover has shrunk we assumed an extinction debt; if it has expanded we assumed a species credit. Our work investigated how the existence of extinction debt and species credit varies (1) among landscapes with different amounts of forest cover and distinct trajectories of landscape change, and (2) between taxa with different lifespans. Despite the lack of detailed information about longevity for birds and small mammals, there are some accounts in the field showing that understorey bird species can live up to 10 years (e.g. Brawn, Karr & Nichols 1995) while most non-flying small mammals have a maximum life-span of two years (e.g. Viveiros de Castro & Fernandez 2004). As those accounts indicate that birds live considerably longer than small mammals, we considered the first group as long-lived and the latter as short-lived. Additionally, as changes in individual species abundance are likely to precede changes in species richness, we have also investigated the effects of historical and present-day forest cover on the abundance of individual bird and small mammal forest-dependent species.

2. Materials and Methods

2.1. Study area

The study was conducted in three ~10,000-ha fragmented Atlantic Forest landscapes located on the Atlantic Plateau of São Paulo, Brazil (Fig. 1). The whole region of the Atlantic Plateau was once covered with Atlantic forest classified as Lower Montane Atlantic Rain Forest (Oliveira-Filho & Fontes 2000), but much of the region is now reduced to secondary forest patches in different stages of regeneration (Ribeiro *et al.* 2009; Lira *et al.* 2012). The altitude in the Atlantic Plateau of São Paulo varies between 600–1,100 m above sea level with steep hillslopes, mountain with moderate to gentle hillslopes, and alluvial plains; the annual rainfall is between 1,350–2,000 mm and the mean annual temperature varies from 15°C to 22°C (www.cpa.unicamp.br).

In the study landscapes, remaining forest patches are composed of intermediate to old second-growth forest while the matrix habitat surrounding forest patches is dominated by agriculture and cattle pastures. All three landscapes are at a similar distance to the “Serra do Mar”, which contains the largest continuous tract of Atlantic forest (1,109,546 ha) remaining in Brazil (Ribeiro *et al.* 2009), and are separated from each other by distances of up to 120 km. Although similar in terms of topography, relief, climate, type of forest, and type of human-use (see Table S1 in Supporting Information), the study landscapes differ in the proportion of forest cover, varying from 11%, to 31% and 49% (Fig. 1). Hereafter, the studied landscapes are referred as 10, 30 and 50% forest cover (FC) landscapes.

Present-day total amount of forest cover in each study landscape is a result of the balance between deforestation and forest regeneration over the past five hundred years of human occupation. We were able to directly quantify forest dynamics in the study landscapes over the past four decades (1960s to 2000s) using forest cover maps based on aerial photographs and

SPOT 5 satellite images from three different dates, early 1960s (1962), 1980s (1978–1981) and 2000s (2000–2005). For each decade (1960s, 1980s and 2000s), satellite image polygons with a texture pattern consistent with current areas of dense arboreal vegetation, with canopy height usually > 10 m and with occasional to common emergent trees up to 30–35 m, were classified as forested areas (Lira *et al.* 2012).

2.2. Bird and small mammal sampling

Birds and small mammals were surveyed in a set of forest patches within each landscape. Birds were sampled in a total of 53 forest patches: 17 in the 10% and in the 30% FC landscape, and 19 in the 50% FC landscape (Banks-Leite *et al.* 2011; Martensen *et al.* in press). Each patch was sampled using 10 mist nets (12 m length, 2.5 m high, 31 mm mesh) in a straight line and located at least 50 m from the forest edge. Capture sessions were conducted from 2001 to 2002 in the 30% FC landscape, from 2004 to 2005 in the 10% FC landscape and from 2005 to 2007 in the 50% FC landscape and all forest patches were sampled in the dry and wet season. All captured birds were identified to species in the field and marked with a numbered aluminium band provided by Center of Research for Conservation of Wild Birds (CEMAVE-IBAMA) and released in the vicinity. There was a small variation in sampling effort among landscapes; the mean effort per forest patch was 699 net-hours (SD = 21.7) in the 10% FC landscape, 537 net-hours (SD = 6.2) in the 30% FC landscape and an equal sampling effort of 680 net-hours per forest patch in the 50% FC landscape. However, there is no reason to expect that these differences would generate biased estimates of bird community since similar ecological patterns would have been obtained with only 340 net-hours (Banks-Leite *et al.* 2012).

Small mammals were sampled in 15, 20 and 15 patches in the 10, 30 and 50% FC landscapes respectively (Pardini *et al.* 2010). Four capture sessions of eight days each were

conducted in each forest patch, two per summer during two consecutive summers, totalling 352 trap-nights in each forest patch. Trap lines within patches comprised a 100-m sequence of 11 pitfall traps (60 L), separated by 10 m and connected by a plastic fence. Capture sessions were conducted during the summers of 2001–2002 and 2002–2003 at the landscape with 30% of forest cover and, in the other two landscapes, during summers of 2005–2006 and 2006–2007. Animals were marked with numbered tags at first capture.

2.3. Data analysis

Only forest-dependent species were considered in the analysis as habitat generalist species are not expected to be sensitive to forest cover modification (Pardini *et al.* 2009, 2010) and, consequently, focusing on the species richness of an entire assemblage may mask important differences among species in their likelihood of showing an extinction debt (Kuussaari *et al.* 2009) or species credit. Following Brooks, Tobias & Balmford (1999), we considered as forest-dependent birds those species listed by Stotz *et al.* (1996) as occurring only in forest habitats. All species occurring in naturally disturbed or human-created habitats or in non-forest habitats, even when they occur in primary forest as well, were excluded from the analysis. Following Pardini *et al.* (2010), we considered as forest-dependent small mammals those species with geographical distributions restricted to the two Brazilian forested biomes (Atlantic forest and Amazon forest) and not occupying the core areas of the adjacent savanna-like biomes (Cerrado and Caatinga); species occupying the savanna-like biomes were considered as habitat generalists and were excluded from the analysis.

Bird species richness in each forest patch was calculated as the observed number of forest-dependent species while small mammal species richness was calculated as the average number of forest-dependent species observed in the two sampling years to avoid overestimating

the number of species present simultaneously in each patch (Pardini *et al.* 2010) as there was high turnover of species between years (Felinks *et al.* 2011). The abundance of individual bird and small mammal forest-dependent species in each forest patch was calculated as the sum of the number of individuals recorded. To assess the effects of historical and present-day local forest cover on individual species, we selected species with more than five individuals captured and that were recorded in more than three forest patches in a given landscape (following Banks-Leite, Ewers & Metzger 2010).

For each landscape and date, we measured the amount of forest cover in a circle of 800 m radius around each sampling point using forest cover maps and the Fragstats software (McGarigal & Marks 1995). Hereafter, the amount of forest cover surrounding surveyed sites is referred as local forest cover. We selected an 800 m scale based on previous information about the spatial scale at which bird and small mammal species respond to local forest cover (Umetsu *et al.* 2008; Boscolo & Metzger 2009).

2.4. Statistical analysis

To investigate the effects of historical (1960s and 1980s) and present-day (2000s) local forest cover on the number of forest-dependent species or on individual species abundance, we used variation partitioning (Legendre & Legendre 1998). As local forest cover was highly correlated across years, we used variation partitioning to measure how much of the variation in species richness or individual species abundance could be attributed exclusively to past or present-day local forest cover (unique contributions) and how much of this variation is indifferently attributed to past and present-day local forest cover (shared contributions). As inspection of model residuals showed that Poisson errors and log link function provided the best fit for regressions models of species richness and species abundance, we used Generalised Linear

232 Models for the analyses. We report the explained deviance (pseudo- R^2) as a measure of the
233 explanatory power of the models and the probability obtained from a chi-squared test as a
234 measure of statistical significance (Crawley 2007). All analyses were repeated separately for
235 each taxa or individual species \times landscape combination and statistical analyses were performed
236 using the software R 2.12.1 (R Development Core Team 2010).
237

3. Results

We recorded a total of 117 bird species and 30 small mammal species at the three study landscapes, but only 51 and 18 were classified as forest-dependent species, respectively, and considered in the analysis (see Tables S2 and S3 in Supporting Information). Bird richness in forest patches at the 10% FC landscape is significantly lower than at the 50% FC landscape, while the number of species in forest patches at the 30% FC landscape is similar to the number observed in forest patches at the 10% and 50% FC landscapes (Fig. 2). Small mammal richness per forest patch at the 10% FC landscape varied from zero to two and was significantly lower than at the 30% and 50% FC landscape, where mean richness per forest patch varied from three to seven and from three to 7.5, respectively (Fig. 2).

Between the 1960s and 1980s, total amount of forest cover at the 10 and 50% FC landscapes decreased, while the 30% FC landscape increased slightly. The opposite trend was observed between the 1980s and 2000s; forest regeneration was greater than deforestation at the 10 and 50% FC landscapes and, as a consequence, the total amount of forest cover increased. By contrast, the percentage of forest cover at the 30% FC landscape was drastically reduced between the 1980s and 2000s, showing that considerable deforestation has occurred in recent decades after a period of stable forest cover. On the other hand, both the 10% and 50% FC landscapes have experienced a similar forest cover trajectory – historical deforestation followed by recent forest regeneration (Lira *et al.* 2012; Fig. 1). Floristic data collected in one of the study landscapes suggests that an intermediate successional stage can be achieved within 15–20 years of regeneration (Durigan *et al.* 2008); thus we believe that the forest expansion observed between 1980s and 2000s at the 10 and 50% FC landscapes added forest patches with a similar level of condition to the patches that were already present in the landscape. The temporal change

in the amount of forest cover surrounding surveyed sites in a given landscape was similar to the temporal variation in the total amount of forest cover at the landscape scale (Fig. 3).

The current abundance of forest-dependent bird and small mammal species was not always predicted by variation in local forest cover. Among the species in which variation in abundance was explained by local forest cover, the relative importance of historical and current local forest cover varied widely (see Table S4 in Supporting Information). The abundance of five out of seven bird species at the 10% FC landscape was better explained by the unique effect of local forest cover in the 1980s. At the 30 and 50% FC landscapes, the effects of past and present-day local forest cover varied widely among bird species. The abundance of six out of ten species at the 30% FC landscape was better explained by historical local forest cover (1960s or 1980s) and the effects of past and present-day local forest cover on the abundance of seven out of fifteen species was mostly in the shared contribution among them (see Table S4). For small mammals, the abundance of two out of three species at the 10% FC landscape and of four out of five at the 30% FC landscape were better explained by present-day local forest cover. At the 50% FC landscape, the effects of historical and current local forest cover on species abundance varied widely among small mammal species (see Table S4).

The current distribution of species richness within each study landscape was not always predicted by variation in local forest cover as attested by the regression models (see Table S5 in Supporting Information). Neither present-day (2000s) nor historical (1960s and 1980s) local forest cover seems to be important in explaining species richness of small mammals at the 10% FC landscape. On the other hand, current distribution of richness of birds within the three study landscapes and of small mammals within the 30% and 50% FC landscapes were associated with variation in local forest cover despite the low level of explained deviance (Fig. 4, Table S5).

The importance of the unique contributions of historical and present-day local forest cover and their shared contribution varied widely among taxa \times landscape combinations for which the variation in species richness was explained by forest cover. Bird richness at the 10% FC landscape was better explained by the unique effect of the local forest cover in the 1980s, suggesting that the number of birds at the 10% FC landscape is still reflecting the lower local forest cover of 20 years ago and not the higher forest cover that exists nowadays. No evidence of time-delayed responses to local forest cover change was detected for birds and small mammals at the 30% FC landscape as species richness was better explained by the unique effect of present-day local forest cover. Finally, unique effects of past and present-day local forest cover explained just 2–6% of the variance in the number of birds and small mammals at the 50% FC landscape; it was impossible to disentangle the effects of past and present-day local forest cover on species richness as most of their influence was in the shared contribution (correlation) among them (Fig. 4, Table S5).

4. Discussion

Although a considerable body of work on extinction debt following habitat loss and fragmentation has been accumulated (see references in Kuussaari *et al.* 2009), until now little attention has been given to the potential for species credit following a change from decreasing to expanding forest cover (but see Cristofoli *et al.* 2010; Piqueray *et al.* 2011). Moreover, most studies on time-delayed responses do not take into account the landscape-scale context, which is expected to influence the existence of extinction debt and species credit as well as the potential for their future payment and/or receipt. Although inferences are limited by the small sample size at the landscape scale, our results suggest that the existence of extinction debt and species credit as well as the potential for their future payment and/or receipt depend not only on the forest cover trajectory but also on the amount of remaining forest cover at the landscape scale. This highlights the need for considering landscape dynamics as well as landscape-scale context in future studies on time-delayed responses to land-use and land-cover change.

Accumulated evidence suggests that the probability of extinction debt should decline over time following landscape change (Vellend *et al.* 2006) and should exhibit a non-linear relationship with the strength of the landscape change, with extinction debt being higher at landscapes with intermediate levels of habitat loss where many species persist close to their species-specific regional extinction threshold (Hanski & Ovaskainen 2002). Therefore, among our study landscapes, extinction debt is theoretically more likely to occur at the 30% FC landscape which is the only one that has experienced a recent forest cover contraction (2,160 ha, i.e. 33%, of forest were lost between the 1980s and the 2000s) and currently presents an intermediate amount of total forest cover (30%). However, we found no evidence of extinction debt for either birds or small mammals in this landscape, since forest-dependent species richness was best explained by the unique contribution of present-day rather than past local forest cover.

The absence of an extinction debt at the 30% FC landscape may suggest that both vertebrate groups possess the potential to react quickly to deforestation (in less than ~20 years). Short-lived small mammals have passed through many generations since forest cover contraction and, as a consequence, any extinction debt has probably been already paid (but see Burel 1992; Petit & Burel 1998). Species with longer generation times might persist for longer in a modified landscape as they have spent fewer generations near a critical extinction threshold (Brook, Sodhi & Ng 2003; Lindborg 2007; Krauss *et al.* 2010). Although birds have longer generation times than small mammals, our results suggest that the difference in their life cycles seems to be insufficient to affect differently their probability of showing an extinction debt. An extinction debt was particularly clear for trees at the 30% FC landscape (Metzger *et al.* 2009), suggesting that very long-lived species take longer to disappear following an environmental disturbance.

It is important to highlight that extinction debt has been previously suggested for birds in the Atlantic Forest (Brooks, Tobias & Balmford 1999; Metzger *et al.* 2009). Differently from this study, Brooks, Tobias & Balmford (1999) have estimated extinction debt based on the species–area relationship which is an approach that can produce overestimates of extinction rates from habitat loss (He & Hubbell 2011). On the other hand, Metzger *et al.* (2009) have found for the 30% FC landscape that the number of forest interior bird species was better explained by the present-day forest connectivity but that total abundance was better explained by the combination of present-day forest connectivity and the rate of change in forest connectivity between the 1980s and 2000s. Those results suggest a time-delayed response to landscape modification by total bird abundance but no lag-effects evidence for species richness. As our analyses on individual species have shown, the effects of past and present-day local forest cover at the 30% FC landscape varied widely among individual bird species. Indeed, the abundance of six species are still reflecting the lower forest cover of the 1960s or the 1980s, and we believe that this result could

possibly be driving the observed pattern for total abundance reported by Metzger *et al.* (2009). According to those results, habitat loss and fragmentation at the 30% FC landscape affected some individual species abundances and because changes in species abundance are likely to precede changes in species richness, those effects can lead to species extinction in the future.

In contrast to the 30% FC landscape, deforestation at the 10% and 50% FC landscapes occurred earlier (from the 1960s to the 1980s), suggesting that the potential bird and small mammal extinction debts should have already been paid. More recently (between the 1980s and the 2000s), however, those landscapes experienced a forest cover expansion, but the potential positive effects of forest regeneration were only evident for birds at the 10% FC landscape.

The total amount of forest cover at the 10% FC landscape has probably been below the regional extinction threshold for many species (Andr n 1994; Pardini *et al.* 2010; Hanski 2011) for at least 40 years and, as a consequence, the number of species in this landscape is lower than in the other two study landscapes especially for small mammals. We found no evidence of small mammal species credit in this highly deforested landscape and also no relationship between species richness and present-day local forest cover, which we attribute to the fact that most forest-dependent small mammals are already extinct at the landscape scale (Pardini *et al.* 2010). On the other hand, current richness of forest-dependent birds in forest patches at the 10% FC landscape is still reflecting the lower local forest cover of 20 years ago; probably a result of low connectivity associated to an impoverished species pool at the landscape scale. This result indicates a potential species credit of forest-dependent birds in forest patches at the 10% FC landscape. However, it is important to highlight that such low levels of forest regeneration (~300 ha) might not be sufficient to halt population decline or to support local species recovery (Hanski 2000; Schrott, With & King 2005); i.e. species credit may not be received. Moreover, although it was not possible from our forest cover mapping to detect differences in successional

stages (i.e. forest quality) between new (recently regenerated) and old forest patches, it is plausible to assume that they do exist since age of regeneration and land-use trajectory are factors, amongst others, that are important in determining forest quality. Thus it may not be just the amount of forest regeneration but also the quality of the regenerating forest that might not be sufficient to promote species recovery.

Although there was great forest contraction (~2,500 ha) at the 50% FC landscape between the 1960s and the 1980s, the forest expansion (~2,900 ha) experienced between the 1980s and 2000s was probably enough to prevent or revert previous local extinctions through recolonization and rescue-effect. Thus the current number of forest-dependent birds and small mammals in forest patches at the 50% FC landscape might be a result of the interaction between extinction and immigration rates (Jackson & Sax 2010). Such a capacity of quick recovery without any human intervention is indeed expected to occur in highly forested landscapes, well above the regional extinction threshold of many species (Pardini *et al.* 2010).

In summary, our results highlight three main aspects. First, the dynamics of forest cover change in tropical landscapes is not necessarily unidirectional and, as a consequence, either extinction debt or species credit are possible. Second, the existence of extinction debt and species credit, as well as the potential for their future payment and/or receipt, seems to depend not only on forest cover trajectory but on the amount of remaining forest cover at the landscape scale. A small forest regeneration – such as the one observed at the 10% FC landscape – or the (lower) quality of the regenerating forest might not be sufficient to revert extinctions following deforestation at landscapes where the total amount of forest cover has dropped below the regional extinction threshold a long time ago i.e. species credit might not be received. Third, forest-dependent species of two vertebrate groups with different longevity – birds and small mammals – respond in a fairly similar way to landscape change. Thus, our findings highlight the

need to consider landscape dynamics, landscape-scale context, and groups with stronger differences in longevity in future studies on time-delayed responses to land-use and land-cover change.

As many landscapes are experiencing a change from decreasing to expanding forest cover, such studies on the potential for extinction debt and species credit are extremely valuable to guide conservation and restoration strategies. The ability to identify landscapes that still have not paid their extinction debt can prevent future species loss through landscape management such as habitat restoration. On the other hand, the existence of species credit indicates that a future biodiversity gain is expected from recent natural regeneration. In addition, our work suggests that landscape context may influence the potential for debt and credit to be paid or received, indicating that forest cover at the landscape scale is indeed a good predictor of landscape resilience and of the effectiveness of local management actions (Pardini *et al.* 2010).

Acknowledgments

We are deeply thankful to A.C. Martensen and A. Bueno for providing part of the data on birds and small mammals, respectively, and A. Simonetti, A.M.G. Teixeira, T. Olitta and M.C. Ribeiro for the interpretation of aerial photographs and satellite images. We are also grateful to D. Reuman, L.C. Oliveira, two anonymous reviewers and the associate editor for helpful comments on this manuscript. Research support was provided by CNPq, CAPES, Instituto de Biociências/USP, Imperial College London, SELVA and BIOCAPSP.

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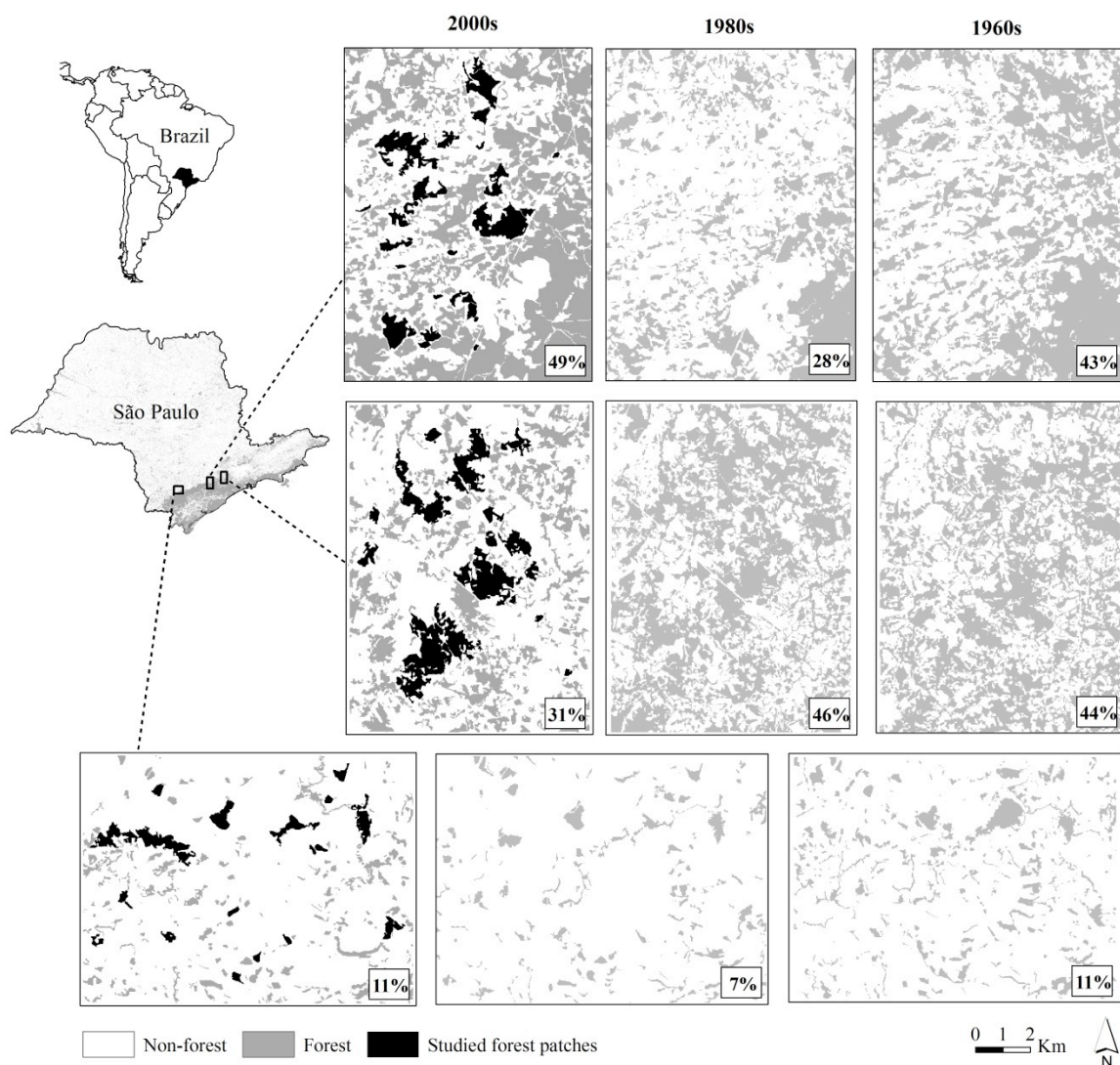
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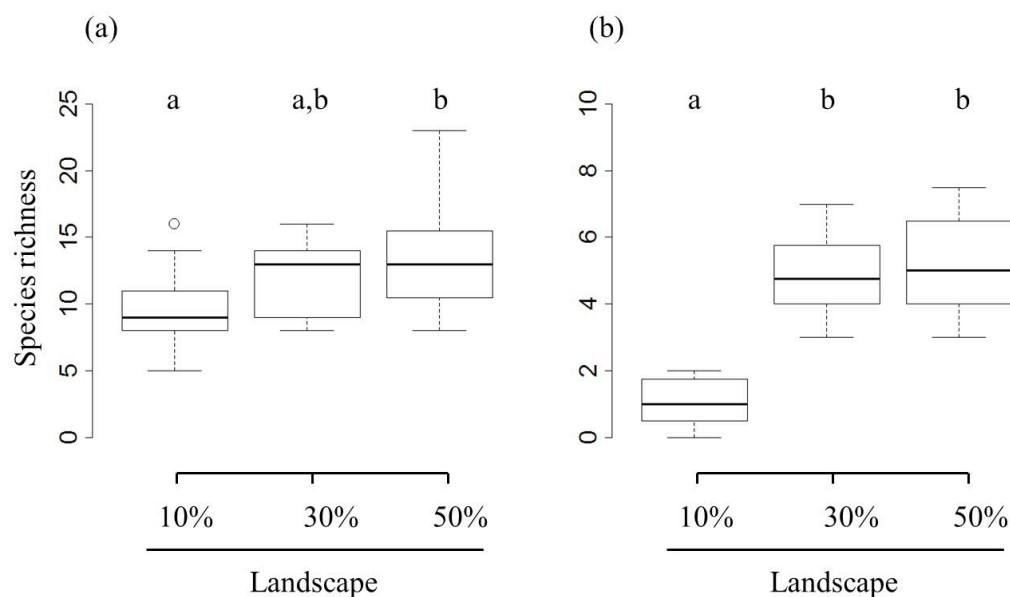


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540 Figure 1: Location of the three studied Atlantic Forest fragmented landscapes in the State of São
 541 Paulo (Brazil) and their forest cover dynamics between the 1960s and 2000s (from right to left).
 542 The percentage of forest cover is shown at the bottom of each forest cover map. Fragments in
 543 black in the 2000s maps were sampled for birds and mammals.

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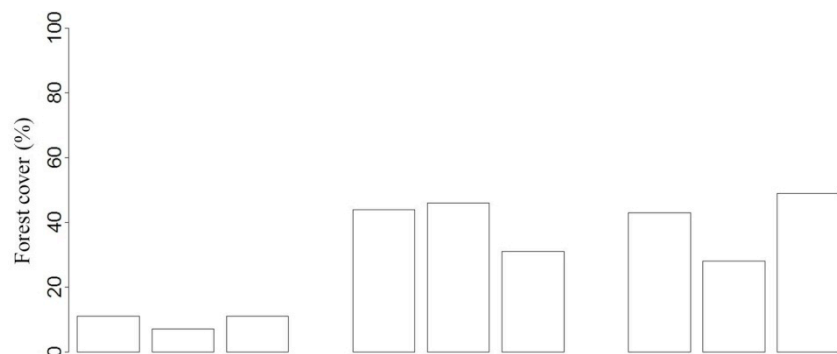


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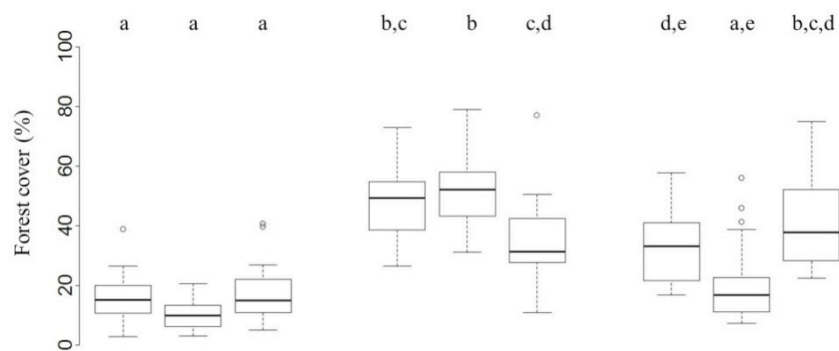
547 Figure 2: Species richness of forest-dependent birds (a) and small mammals (b) in forest patches
 548 at three Atlantic Forest fragmented landscapes with different percentages of forest cover. The
 549 main horizontal line shows the median, boxes represent quartiles and whiskers depict either the
 550 maximum or 1.5 times the interquartile range of the data (whichever is smaller). Points are
 551 outliers. Landscapes that do not have a letter in common differ significantly in species richness
 552 (Tukey's honest significant differences test: $P < 0.05$).

553

(a)



(b)



(c)

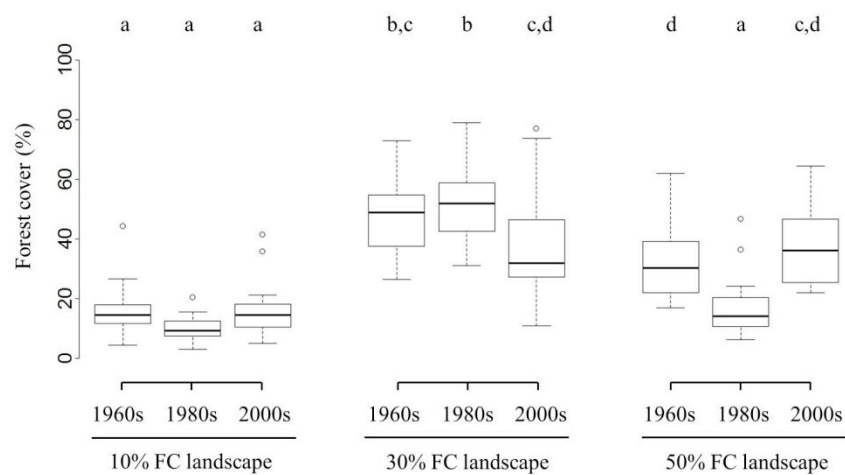
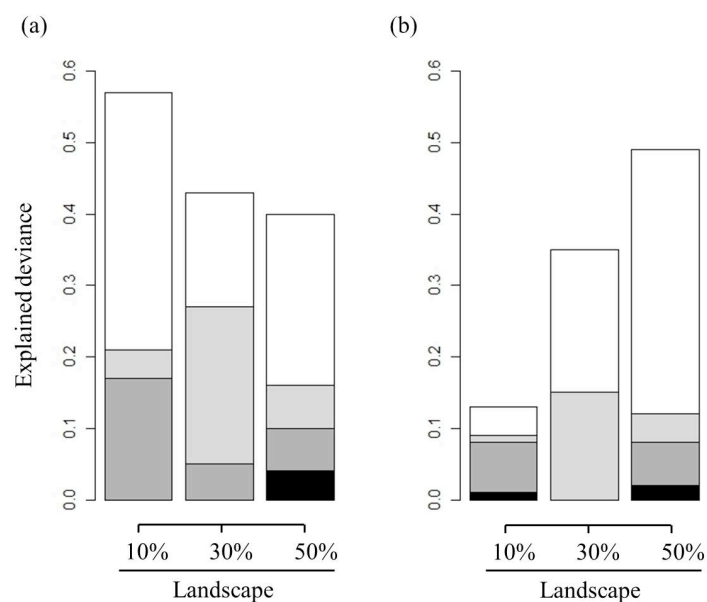


Figure 3: Forest cover (%) dynamics in three Atlantic Forest fragmented landscapes, São Paulo-Brazil (a) and the consequent variation of forest cover (%) in a circle of 800 m radius around

557 sampling points where birds (b) and small mammals (c) were sampled. The main horizontal line
558 shows the median, boxes represent quartiles and whiskers depict either the maximum or 1.5
559 times the interquartile range of the data (whichever is smaller). Points are outliers. Classes that
560 do not have a letter in common differ significantly in forest cover (Tukey's honest significant
561 differences test: $P < 0.05$).
562



564 Figure 4: Explained deviance of forest-dependent species richness by historical (1960s and
 565 1980s) and present-day (2000s) local forest cover at the three studied landscapes (10, 30 and
 566 50% forest cover landscapes) for (a) birds and (b) small mammals. Total explained deviance is
 567 subdivided in shared – white bars – and unique contributions: 1960s in black, 1980s in dark grey
 568 and 2000s in light grey.

570 **Supporting Information**

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

572 **Table S1.** Characteristics of three study fragmented Atlantic forest landscapes.

573 **Table S2.** List of forest-dependent bird species captured.

574 **Table S3.** List of forest-dependent small mammal species captured.

575 **Table S4.** Effects of historical and present-day local forest cover on individual species
576 abundance.

577 **Table S5.** Effects of historical and present-day local forest cover on forest-dependent species
578 richness.