



## Research

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# How do habitat amount and habitat fragmentation drive time-delayed responses of biodiversity to land-use change?

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Land-use change is a root cause of the extinction crisis, but links between habitat change and biodiversity loss are not fully understood. While there is evidence that habitat loss is an important extinction driver, the relevance of habitat fragmentation remains debated. Moreover, while time delays of biodiversity responses to habitat transformation are well-documented, time-delayed effects have been ignored in the habitat loss versus fragmentation debate. Here, using a hierarchical Bayesian multi-species occupancy framework, we systematically tested for time-delayed responses of bird and mammal communities to habitat loss and to habitat fragmentation. We focused on the Argentine Chaco, where deforestation has been widespread recently. We used an extensive field dataset on birds and mammals, along with a time series of annual woodland maps from 1985 to 2016 covering recent and historical habitat transformations. Contemporary habitat amount explained bird and mammal occupancy better than past habitat amount. However, occupancy was affected more by the past rather than recent fragmentation, indicating a time-delayed response to fragmentation. Considering past landscape patterns is therefore crucial for understanding current biodiversity patterns. Not accounting for land-use history ignores the possibility of extinction debt and can thus obscure impacts of fragmentation, potentially explaining contrasting findings of habitat loss versus fragmentation studies.

## 1. Introduction

Land-use change is a main driver of biodiversity loss, primarily via loss and fragmentation of habitat [1]. Where habitat is lost, species' populations decline and might eventually go extinct; a phenomenon widely observed [2,3] and with strong theoretical underpinnings in population ecology [4]. Additionally, as habitat is lost, landscapes become more fragmented, containing higher numbers of typically smaller and more isolated patches [5]. Metapopulation theory [6] and island biogeography theory [7] suggest that fragmentation negatively impacts

species' populations and overall species richness. Finally, fragmented landscapes contain more edge habitat [8], which exerts pressure on many species, for instance by degrading habitat quality, altering biophysical conditions, changing species interactions or increasing human–wildlife conflicts [5,9,10].

Yet, edge habitats also increase landscape heterogeneity, and therefore, species richness may increase near edges [11]. Recent reviews indicate that the effect of habitat fragmentation on biodiversity, independent of habitat amount, is weak and could even be positive sometimes [3,11,12]. This suggests that species primarily respond to the extent of habitat in the landscape (i.e. the habitat amount hypothesis [3]) and not to fragmentation (i.e. habitat patch configuration). The resulting debate about the relative importance of habitat fragmentation, and whether the effects of fragmentation on biodiversity are negative or positive, has been heated [3,13–15]. This debate has potentially major consequences for conservation [16]. If fragmentation affects biodiversity negatively, protecting large habitat patches, and corridors between them, should be prioritized [17]. On the contrary, if habitat amount is the main determinant of biodiversity, several small habitat patches will have the same conservation value as an equally large, single patch [11,12,18], and greater emphasis should be put on protecting the largest amount of habitat, regardless of connectivity and patch size.

Available evidence on the relative effects of habitat amount versus fragmentation on biodiversity, however, remains inconclusive [16], especially at broader spatial scales [13]. Several factors contribute to this. First, fragmentation effects may differ at the patch scale versus landscape scale, because some processes acting at landscape scales cannot be captured when studying individual patches (e.g. interactions with wide-ranging species, habitat diversity across patches). Second, different effects can be found when focusing on habitat specialists (e.g. forest-dependent species) versus generalists or the entire community [10]. Third, fragmentation effects consist of edge effects and isolation effects, and focusing on only one aspect may not capture the full impact of fragmentation [19,20]. Finally, the time period over which habitat fragmentation is studied may greatly impact conclusions [16,20], yet most studies are based on contemporary landscape data.

This focus only on contemporary landscapes is particularly worrisome given increasing evidence for time-delayed responses of biodiversity to habitat transformation [21–24]. Species do not always react to habitat transformation immediately and may persist for decades in transformed landscapes [22]. Such time-delayed responses can create extinction debt, i.e. number or proportion of extant species predicted to go extinct due to past landscape transformation [25]. The probability of communities showing time-delayed responses depends on species' life-history traits, as well as other factors related to landscape transformation (e.g. magnitude of landscape change or time since transformation [22,26]). Understanding time-delayed responses and extinction debt is critical to delineating a window of time for conservation to avert such extinctions [22]. Surprisingly though, most fragmentation studies have ignored time-delayed effects [15,19].

A typical limitation of studies that have investigated time-delayed effects of habitat loss and fragmentation on biodiversity is that they assessed land-use change on only one or a few snapshots in time, typically with long periods between them [21,24,27]. However, land-use change often occurs gradually, meaning that estimated time-delayed responses might remain undetected or appear to be overly long when

considering few snapshots. Previous studies also typically assumed that time-delayed response is the *same* for habitat loss and habitat fragmentation. This is potentially problematic because the effects of past habitat loss may be more immediate than those of fragmentation. In fact, long-term fragmentation experiments found effects of fragmentation to magnify over time [20,28]. To our knowledge, no study has investigated whether time-delayed responses of biodiversity to habitat loss and habitat fragmentation differ.

Advances in satellite data availability and processing now enable landscape change to be reconstructed at high spatial and temporal resolutions [29]. Here, using the Landsat archive since 1985, we systematically test for time-delayed effects of habitat loss and habitat fragmentation on birds and mammals in the Argentine Dry Chaco over a period of 31 years. The Chaco provides an interesting case study due to its dynamic land-use history and recent high deforestation rates [30]. We assessed two research questions:

1. Are contemporary or past landscape patterns more important in determining contemporary bird and mammal communities?
2. Are time-delayed responses more prominent for habitat loss or habitat fragmentation?

We predicted that contemporary bird and mammal communities would be affected by past landscape patterns, because extinction debts are likely to not yet be paid in landscapes where habitat transformation has occurred recently, such as the Chaco. We also predicted that time-delayed responses would be more prominent for habitat fragmentation as the effects of habitat fragmentation can take a long time to manifest on the landscape.

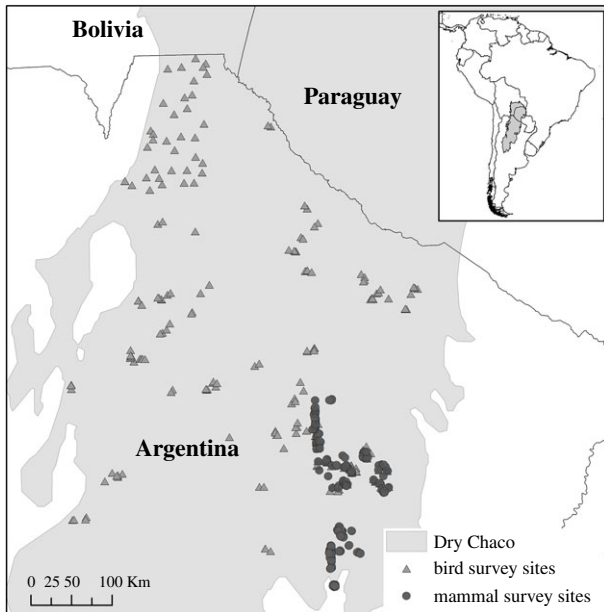
## 2. Methods

### (a) Study area

The Gran Chaco is the largest subtropical/tropical dry forest in South America, covering parts of Argentina, Paraguay, Bolivia and Brazil. The region is rich in biodiversity, harbouring over 500 birds, 150 mammals, 120 reptiles and 100 amphibians [31]. We focused on the Argentine Dry Chaco (approx. 21 million ha, figure 1), an area with a highly seasonal climate (precipitation: from 450 to 900 mm; temperature:  $-7^{\circ}\text{C}$  to  $+42^{\circ}\text{C}$ ) [32]. Natural vegetation is dominated by woodlands with a few interspersed natural grasslands [33]. Much of the regions' natural vegetation has been converted to agriculture, especially after 2000, mainly for cattle ranching and soya bean cultivation [34]. This has resulted in widespread woodland loss and fragmentation [30,35], which in turn has been the main cause of defaunation [24,36].

### (b) Biodiversity data

We surveyed birds and mammals at 431 sites (figure 1) selected to represent gradients of land use and woodland cover. We recorded birds at 233 sites during three field surveys between 2009 and 2014 [37–39], with a mean distance of 4.7 km between sites (standard deviation: s.d. = 6.5 km). We conducted point counts at each site (two to nine point counts per site; see electronic supplementary material, appendix S1). Here, we only considered species that use woodland as their main habitat, as this is by far the dominant natural vegetation in the area and we wanted to test for time-delayed responses to woodland loss and fragmentation. We discarded migrant species to avoid seasonal effects and species associated with the Andean Cloud forest (i.e. Yungas) that were only recorded in the Chaco-Yungas ecotone.



**Figure 1.** Survey sites for birds and mammals in the northern Argentine Dry Chaco.

We surveyed mammals during two field surveys between 2013 and 2016, using a total of 198 camera-trap stations [39,40]. The mean distance between adjacent sites was 1.44 km (s.d. = 1.74). We set cameras off trail where possible, to reduce detection bias associated with targeted sampling [41]. Cameras were active between 14 and 84 trapping days (mean = 39.8 days), with a total sampling effort of 7883 trapping days (see electronic supplementary material, appendix S2). We only considered woodland-dependent mammal species.

We did not assess spatial autocorrelation among sampling sites, as common tests (e.g. spatial correlograms of model residuals) are difficult to apply in an occupancy framework [42,43]. However, spatial autocorrelation is not a problem, as the independence assumption of occupancy models relates to the observation process, not to the occupancy process, and it can be accounted for with an appropriate sampling design (e.g. random sampling, as in our case) [44]. Additionally, overlapping landscapes have been shown to not violate the independence assumption [45].

### (c) Landscape predictors

We calculated landscape scale metrics of habitat amount and fragmentation, meaning that they described the spatial characteristics of entire landscapes, not individual patches [11]. We extracted predictors for circular landscapes centred around each sampling site. Based on sensitivity analyses (electronic supplementary material, appendix S3), we used a 4 km radius for birds and a 2 km radius for mammals. For each of the circular landscapes, we mapped woodland cover for each year between 1985 and 2016 based on Landsat composite metrics derived at a spatial resolution of 30 m in Google Earth Engine [46]. We used an extensive database of training samples [30] and hand-digitized deforestation polygons between 2014 and 2016 from GUYRA Paraguay <http://guyra.org.py/informe-deforestacion>. We used these training data to parameterize a time-calibrated random forest classifier and classified 31 annual woodland loss maps between 1985 and 2016 [47]. Each map used satellite data from that year and the previous year, to ensure consistency between years. We validated these maps following best-practice procedures [48] (average overall accuracy = 90%; standard error = 0.6%, see electronic supplementary material, appendix S4 and figure S1).

We calculated one landscape predictor representing habitat amount: *percentage of woodland*. To characterize fragmentation, we calculated three predictors: *percentage of edge*, *patch density*

and *cohesion index*. A detailed description of these landscape metrics is provided in figure 2 and electronic supplementary material, appendix S5. We calculated all metrics for each landscape and for every year between 1985 (first woodland map) and 2016 (last year of biodiversity sampling). To define the contemporary time period, we related each site to the landscape predictors of the year when biodiversity was sampled (e.g. sites sampled in 2015 were related to the predictors from 2015). We then derived a time series of past landscape predictors 24 years back in time (i.e. landscape patterns from 1 year prior to sampling, 2 years prior to sampling, etc.). We used a maximum time period of 24 years because this is the time span between the oldest Landsat-based woodland map (1985) and the oldest biodiversity sampling (2009) in our dataset.

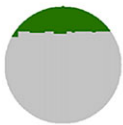











### (d) Modelling framework

We used hierarchical Bayesian multi-species occupancy models [43,49] to assess the influence of our landscape predictors on bird and mammal communities. Occupancy models estimate detection probability, providing a key advantage when working with elusive species. Estimating detection probability requires sites to be visited on multiple occasions within a period closed to changes in occupancy [44]. For mammals, we defined a sampling occasion as seven consecutive camera-days [50,51]. We discarded sites surveyed less than 14 camera-days to have a minimum of two occasions per site and assumed communities to be closed (no site-level species extinction or colonization) for a maximum of 12 sampling occasions (84 days). This resulted in an average of 5.69 occasions (s.d. = 3.07). For birds, we used spatial occasions instead of temporal occasions by treating each point count as one sampling occasion [44]. This resulted in an average of 7.21 occasions (s.d. = 2.26).

Multi-species occupancy models are an extension of single-species occupancy models [52], in which community occupancy is estimated from the occupancy of all individual species, and where species-specific parameters are drawn from a common, community-level distribution. We used data augmentation to account for species that could theoretically be present but were unobserved [49]. Based on the literature [53–55], and species observed during other field surveys, we added eight bird and two mammal species (electronic supplementary material, tables S1 and S2).

Our hierarchical community model therefore had three levels: (i) a level related to the augmented community, in which the occurrence of observed or unobserved species  $k$  ( $w_k$ ) is represented by a Bernoulli process ( $w_k \sim \text{Bernoulli}[\omega]$ , where  $\omega$  indicates the probability of a species belonging to the sampled community); (ii) an ecological process in which the true occurrence of species  $k$  at site  $i$  ( $z_{ik}$ ) is a latent state variable represented by a Bernoulli process ( $z_{ik} \sim \text{Bernoulli}[w_k * \Psi_{ik}]$ ,  $\Psi_{ik}$  represents the occupancy probability) and (iii) an observation process, in which the detection of species  $k$  for occasion  $j$  at site  $i$  is represented by a Bernoulli process ( $y_{ijk} \sim \text{Bernoulli}[z_{ik} * p_{ijk}]$ ,  $p_{ijk}$  represents the detection probability and is conditional on the site being occupied, i.e.  $z_{ik} = 1$ ).

Occupancy and detection probabilities therefore varied by species and were additionally influenced by site characteristics. We first fitted the detection model by including only predictors that may affect detection, using a null occupancy model with no parameters. For birds, we used *observer* and *openness*, and for mammals, we included *camera-trap*, *sampling effort*, *temperature* and *precipitation* as predictors influencing detection (table 1). After excluding correlated predictors (table 1), we compared all possible detection models using the Watanabe–Akaike information criterion (WAIC) [56]. Next, we fitted the occupancy model by adding landscape predictors while keeping the best-fitting detection model constant. We used uninformative priors and ran 10 parallel chains of 100 000 Markov chain Monte Carlo (MCMC) iterations, discarding the first 50 000 iterations as the

landscape metric	definition	low	medium	High
<b>habitat loss</b>				
<i>percentage of woodland</i>	measures the amount of habitat in the landscape			
<b>habitat fragmentation</b>				
<i>percentage of edge</i>	measures the proportion of edge habitat in the landscape			
<i>patch density</i>	measures the number of patches in the landscape			
<i>cohesion index</i>	measures the structural connectedness of patches in the landscape			

**Figure 2.** Landscape metrics used to measure habitat amount and habitat fragmentation in our landscapes (4 km buffers for birds, 2 km buffers for mammals; green = woodland; grey = matrix). Further description on metrics calculation is provided in electronic supplementary material, appendix S5. (Online version in colour.)

**Table 1.** Predictors used for modelling the detection probability of birds and mammals in the Argentine Chaco.

predictor	description	hypothesis
<b>BIRDS</b>		
survey	observer identity	experience and knowledge of the observers may influence detection probabilities
openness	presence or absence of trees at the sampling site	presence of trees may decrease detection probability
<b>MAMMALS</b>		
camera-trap	camera-trap survey	different camera-trap brands and deployments may lead to different detection probabilities
sampling effort	number of days that the camera-traps were active	detection probability increases with increasing survey effort
temperature <sup>a</sup>	mean temperature of the month when the cameras were active	mammals may be less active when it is too cold or too hot, thus decreasing detection probability
temperature (quadratic form) <sup>a</sup>	mean temperature of the month when the camera-trap was active	mammals may be less active during extreme temperatures (i.e. too hot and cold), thus decreasing detection probability
precipitation <sup>a</sup>	mean precipitation of the month when the camera-trap was active and the month before	mammals may move more during the dry season looking for water, thus increasing detection probability

<sup>a</sup>Predictors marked with a were correlated ( $r \geq 0.6$ ). We retained *precipitation*, as it had the lowest WAIC in a univariate model.

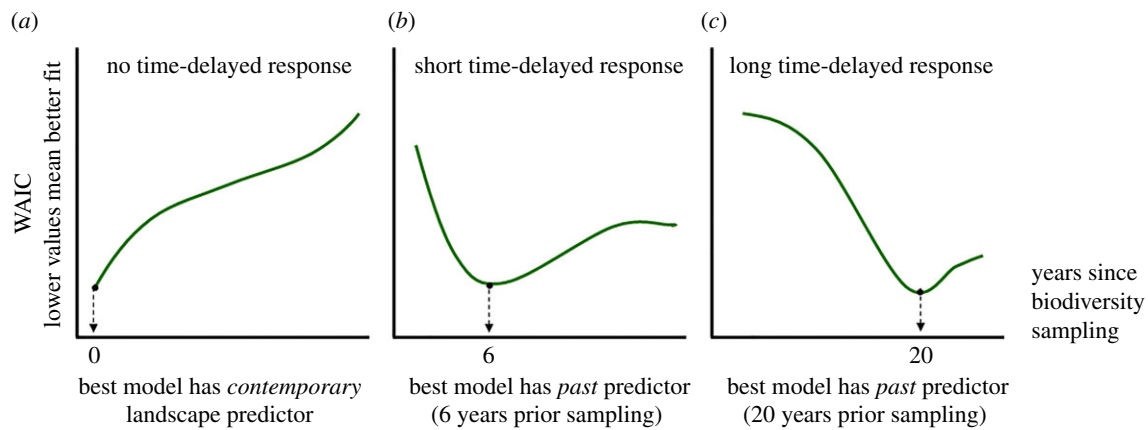
burn-in process and thinning by 10. We assessed model convergence using visual inspection (trace and density plots of MCMC chains) and the Gelman–Rubin statistic, where values less than 1.1 indicated convergence [57]. Model codes are provided in electronic supplementary material, appendix S6 and S7.

### (e) Exploring time-delayed responses to habitat loss and fragmentation

To test whether bird and mammal communities showed time-delayed responses to habitat loss and habitat fragmentation, we

analysed the relationships between contemporary community occupancy probability (i.e. mean occupancy across all species) and (1) contemporary landscape predictors (i.e. year of biodiversity sampling) and (2) past landscape predictors (i.e. 1–24 years prior to sampling). We investigated each landscape predictor individually in terms of its influence on community occupancy separately for birds and mammals. We built 25 univariate models for each landscape predictor and taxon: one model including the landscape predictor of the year when biodiversity was sampled (contemporary model) and 24 models using past landscape predictors. As a result, we fitted 200 models; 100 models (25 years  $\times$  4 landscape predictors) per taxon (electronic





**Figure 3.** (a–c) Approach for assessing time-delayed responses to habitat loss and habitat fragmentation. We concluded that a time-delayed response to habitat loss or to habitat fragmentation was present when any of the models including past landscape predictors (i.e. 1–24 years prior to biodiversity sampling) fitted better (i.e. lower WAIC) than the contemporary model (i.e. predictors from the year of biodiversity sampling).

supplementary material, tables S4 and S5). To assess which model out of the 25 models for each landscape predictor performed best, we compared them by calculating WAIC for each model. We additionally fitted a smooth line to the WAIC values by using the locally estimated scatterplot smoothing method, to visualize the trend in model performance across years. We inferred a time-delayed response to habitat loss or habitat fragmentation when any of the past models fitted better than the contemporary model [21,22,24] (figure 3). Finally, we assessed the effects of habitat amount and habitat fragmentation on birds and mammals by examining the beta coefficients of our univariate models.

We additionally built three bivariate models which included *percentage of woodland* and a fragmentation metric (*percentage of edge* or *patch density* or *cohesion index*). This allowed us to estimate the effect of habitat amount, while accounting for the effect of habitat fragmentation and vice versa. We built the bivariate models using (i) contemporary landscape predictors (i.e. year of biodiversity sampling) and (ii) predictors of the best-fitting models (i.e. predictors of the univariate models with the lowest WAIC).

### 3. Results

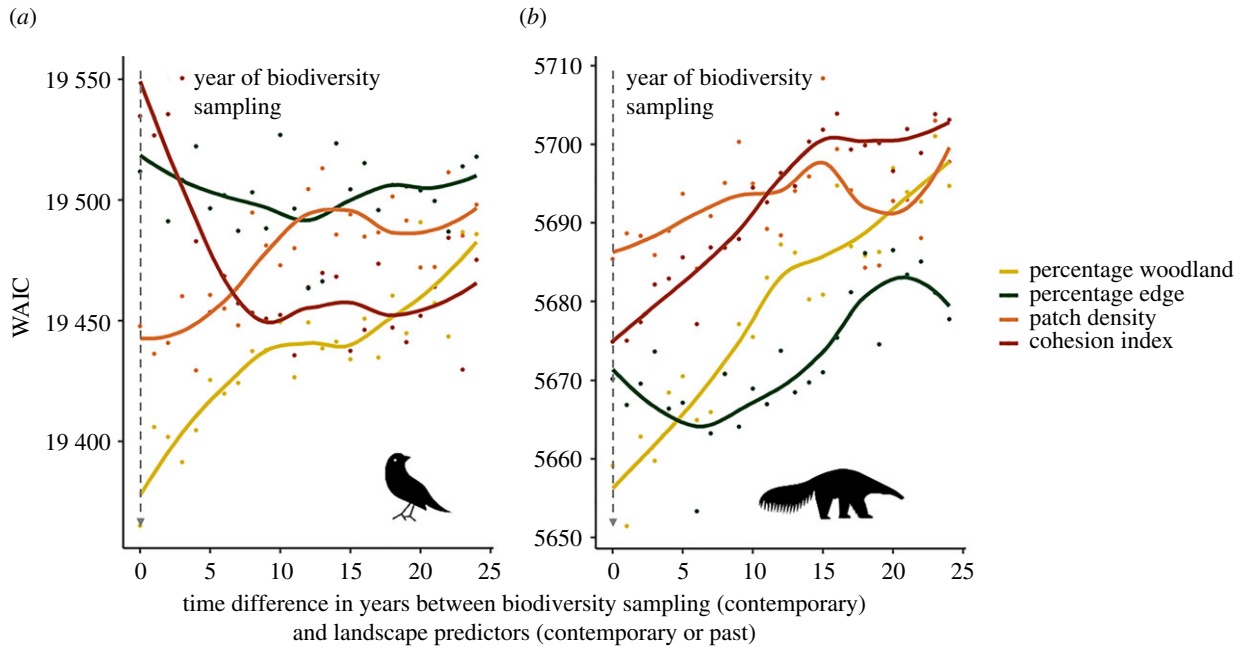
We detected a total of 29 woodland-dependent bird species and 18 woodland-dependent mammal species (electronic supplementary material, tables S1 and S2). The best-fitting detection model for the bird dataset included *survey* and *openness* (electronic supplementary material, table S3). The probability of detecting a bird species, given its occurrence at a site, varied among the three surveys and increased when trees were present at the sampling site ( $\beta = 2.21$ ; 95% Bayesian credible intervals (CRI) = 1.93, 2.52). For mammals, the best-fitting detection model contained *camera-trap* and *precipitation* (electronic supplementary material, table S3), indicating that detection probability varied depending on camera-trap brand and set-up at the sampling site, and increased with increasing precipitation ( $\beta = 0.11$ ; 95% CRI = -0.03, 0.29).

For habitat amount, we found that community-level occupancy probabilities for bird and mammal communities were more strongly influenced by contemporary habitat amount than by past habitat amount (figure 4). The model including a contemporary *percentage of woodland* (i.e. year of biodiversity sampling) had the lowest WAIC for birds (electronic supplementary material, table S4). For mammals, the model

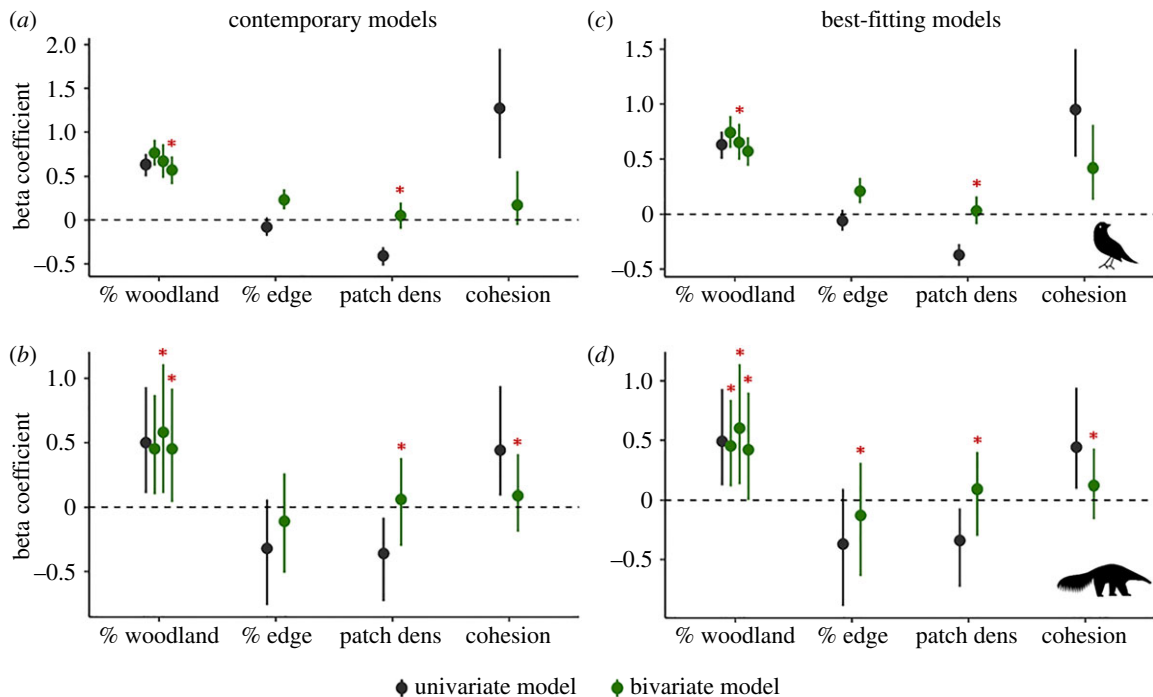
with the lowest WAIC included *percentage of woodland* from 1 year prior to sampling, followed by the model including a contemporary *percentage of woodland* (electronic supplementary material, table S5). *Percentage of woodland* was positively related to bird and mammal occupancy (figure 5).

Regarding the temporal effect of habitat fragmentation, past fragmentation predictors explained bird and mammal occupancy better than did contemporary fragmentation predictors in most cases. For birds and *percentage of edge*, models including variables from 12 and 13 years prior to sampling were the best models (i.e. lowest WAIC; figure 4 and electronic supplementary material, table S4). For *patch density*, the model including the landscape metric from 4 years prior to sampling had the lowest WAIC values (figure 4 and electronic supplementary material, table S4). For *cohesion index*, the bird occupancy models based on past landscapes (from 4 to 24 years prior to sampling) were consistently better than the models including contemporary landscapes, with the model including *cohesion index* from 23 years prior to sampling having the lowest WAIC value (figure 4 and electronic supplementary material, table S4). For mammals, models based on *percentage of edge* for past landscapes had a lower WAIC than the model including a contemporary *percentage of edge*, with the model with *percentage of edge* from 6 years prior to sampling having the lowest WAIC (figure 4 and electronic supplementary material, table S5). Past *patch density* (specifically from 6 years prior to sampling) also explained contemporary mammal occupancy better than contemporary *patch density* (figure 4 and electronic supplementary material, table S5). Finally, *contemporary cohesion index* was a better predictor of mammal occupancy than any *cohesion index* for past landscape configurations (figure 4 and electronic supplementary material, table S5).

The effect of habitat fragmentation on occupancy varied depending on the taxa and landscape metric. The effect of *percentage of edge* on bird occupancy changed from negative to positive when adding *percentage of woodland* to the model, i.e. in the bivariate model (figure 5). For mammals however, the effect of edge was always negative (both in the univariate and bivariate model), indicating that occupancy decreased with increasing edge habitat (figure 5). For both birds and mammals, the effect of *patch density* also changed from negative in the univariate model (i.e. occupancy was lower in patchier



**Figure 4.** Model performance of the annual multi-species occupancy models for birds (a) and mammals (b). Model performance is measured using WAIC, and thus, lower values indicate higher performance. Each graph shows the performance of models using contemporary biodiversity data, and contemporary (year 0) or past (year 1–24) predictor variables. A smooth line fitted to the WAIC values visualize the trend in model performance for models with landscapes variables from landscapes increasingly longer ago. (Online version in colour.)



**Figure 5.** Influence of landscape predictors on bird and mammal occupancy for univariate and bivariate models. Plots show the standardized beta coefficients and 95% Bayesian credible intervals (95% CRI) for all predictors. The effect of a predictor on occupancy was considered to be significant when the 95% CRI did not overlap zero (dashed line). Beta coefficients for *percentage of woodland* in bivariate models represent three models in the following order: (i) *percentage of woodland* + *percentage of edge*, (ii) *percentage of woodland* + *patch density* and (iii) *percentage of woodland* + *cohesion index*. (a,b) Beta coefficients of the contemporary models (i.e. predictors from the year of the biodiversity sampling). (c,d) Beta coefficients of the best-fitting models (i.e. top models in electronic supplementary material, tables S4 and S5). Red stars indicate that the predictor is correlated with another predictor ( $r \geq 0.6$ ). For both taxa, the effect of *percentage of woodland* on occupancy did not vary greatly when comparing the univariate with the bivariate models. However, the effect of fragmentation differed when comparing univariate and bivariate models. (Online version in colour.)

landscapes) to positive in the bivariate model (i.e. occupancy was higher in patchier landscapes) (figure 5). Finally, *cohesion index* always (i.e. univariate and bivariate model) had a

positive effect on occupancy, indicating that the probability of occupancy increased in more connected landscapes (figure 5). It is important to highlight that these patterns (i.e. the change in

magnitude and direction of beta coefficients) were essentially the same for both the contemporary and best-fitting models (figure 5).

## 4. Discussion

Habitat loss is a main driver of biodiversity loss, but the importance of habitat fragmentation remains debated [16]. Available evidence regarding fragmentation effects remains inconclusive despite considerable research efforts [3,15,58]. Yet understanding the impact of fragmentation is critically important, given that land-use change has fragmented most ecosystems around the globe [20,28]. Time-delayed effects of fragmentation are a possible explanation for contrasting results of fragmentation studies, but remain overlooked in the habitat loss versus fragmentation debate [15,16].

We provide, to the best of our knowledge, the first systematic assessment of the influence of contemporary and past habitat amount and fragmentation on biodiversity. Two key insights emerge from this work. First, we found that contemporary biodiversity was influenced by past landscape patterns, suggesting that birds and mammals in the Chaco respond to landscape transformation with a time delay. Second, we found evidence for time delays for most of our models including habitat fragmentation predictors, yet not for those models including habitat amount. This supports the hypothesis that time-delayed responses are driven by habitat fragmentation and that the effects of fragmentation take time to manifest. This time delay potentially explains contrasting findings of previous fragmentation studies, and it provides a window of opportunity for conservation to avert extinctions, as species may persist in fragmented landscapes for years.

We found strong evidence that contemporary occupancy of both taxa was related to past landscape patterns, suggesting that birds and mammals have delayed responses to land-use change. Several studies have recently suggested that time-delayed effects of landscape transformation might be common, especially in regions where large-scale deforestation occurred recently [22,23], such as in the Amazon [59], the Brazilian Atlantic Forest [27], the Kakamega Rainforest in Kenya [60] or the Argentine Chaco [24]. Importantly, we found time-delayed responses of birds and mammals to habitat fragmentation, but not to habitat loss. This should contribute to understanding the effects of fragmentation on biodiversity, as few studies have separated the effect of habitat loss from habitat fragmentation when assessing time-delayed responses to landscape change [21,27]. These studies, however, relied on a few snapshots in time and were unable to estimate differences in the duration of the time-delayed response between habitat loss and habitat fragmentation [21,24,27].

Our finding that the impacts of fragmentation can take time to manifest adds further support to evidence from long-term fragmentation experiments [20,61] that found strongest biodiversity declines with a time delay (e.g. species richness declines across different experiments were more evident 10 years after habitat fragmentation [20]). Indeed, many of the effects of fragmentation on biodiversity can take a long time to manifest. For example, changes in microclimate near forest edges lead to a gradual change in vegetation structure [62], which can have knock-on effects on species' interactions (e.g. increasing nest predation risk for birds [63]).

We also found interesting differences between birds and mammals regarding the estimated time-delayed response to habitat fragmentation, as this delayed response was shorter for mammals than for birds. A potential explanation for this is the high hunting pressure that mammals experience along woodland edges [64,65]. Rural people in the Argentine Dry Chaco prefer hunting mammals over birds [66]. Indeed, hunting pressure increased for almost all mammal species in the Chaco in the last decades [67]. The same reason could explain why birds showed time-delayed responses to connectivity (*cohesion index*) while mammals did not: birds have a higher capacity to cross open areas compared to mammals. This is because mammals have a higher mortality risk when moving between woodland patches, as hunters often kill mammals when they cross open areas, such as agricultural fields or woodland clearings [50,67,68]. Together, these findings suggest that mammals may disappear faster in fragmented landscapes than birds.

Regarding the joint and individual effects of habitat amount and habitat fragmentation on biodiversity, we found that habitat amount, *percentage of woodland* in our case, was an important predictor of bird and mammal occupancy, meaning that the resources that woodlands provide (e.g. food, refuge) are essential for both taxa. This adds further evidence to a growing number of studies that highlight the importance of habitat extent for biodiversity [14,69]. Estimating the relative importance of habitat fragmentation was challenging though, as most of the fragmentation metrics were correlated with *percentage of woodland*. Therefore, we here only discuss the results of the models including weakly correlated ( $r < 0.6$ ) landscape predictors, as collinear predictors may give biased estimates of true effects [70]. Both in univariate and bivariate models, *percentage of edge* had a negative effect on mammal occupancy, again most likely due to the hunting pressure that mammals experience along woodland edges [64,65]. Surprisingly, however, the effect of *percentage of edge* on bird occupancy changed from negative to positive when adding *percentage of woodland* to the model (i.e. bivariate model). This suggests (i) variable interactions, (ii) a possible positive effect of fragmentation, yet also (iii) that fragmentation becomes marginally important once controlling for habitat amount [3,14]. Finally, *cohesion index* had a positive effect on bird occupancy, highlighting that forests are key for biodiversity protection in the Chaco, a finding in accordance with previous work in this region [50] and other tropical deforestation frontiers [71]. Overall, we found that the effects of fragmentation become weaker when adding *percentage of woodland* to the model, both in the contemporary and in the best-fitting models. This suggests that the relative effects of habitat amount and fragmentation do not change markedly over time.

Our systematic assessment of time-delayed effects of habitat loss and fragmentation in the Chaco relied on a large biodiversity dataset, made full use of the Landsat archive to ensure consistent landscape predictors and used occupancy models to account for imperfect detection. Still, some limitations need mentioning. First, we could not consider matrix permeability, although the type of agricultural matrix might influence species occurrence [72]. Second, we used *patch density* to quantify the number of patches in our landscapes—including landscape metrics that capture the effect of patch size would be interesting but would require a patch scale study [13]. Finally, we built univariate models because our goal was to assess the relationship, over time, of habitat

amount or habitat fragmentation on bird and mammal occupancy. Exploring the combined effect of these variables is interesting, and we therefore ran bivariate regression models by including both habitat amount and fragmentation. However, correlation between some of the landscape metrics (see electronic supplementary material, figure S2) suggests possible bias in the model coefficients [70], and we therefore caution against over-interpreting them. An experimental approach [14,58] or path analysis [70] would be necessary to quantify the relative importance of habitat loss versus habitat fragmentation for time-delayed effects. Here, we limit our study to analysing the relationship between occupancy and habitat amount over time on the one hand, and occupancy and habitat fragmentation over time on the other.

Our work has two main implications for conservation. First, our findings highlight the importance of habitat amount for birds and mammals, meaning that protection of woodland patches should be prioritized to avoid short-term local extinctions (e.g. expanding protected areas). Second, our study showed that fragmentation effects take time to manifest, resulting in a fragmentation-driven extinction debt. This provides a window of opportunity, as fragmented landscapes may still contain a high percentage of species which may otherwise go extinct if restoration activities are not implemented swiftly. Therefore, increasing landscape connectivity (e.g. restoring natural vegetation patches in the agricultural matrix) may help to prevent the loss of species vulnerable to extinction, as occupancy will keep decreasing even if no further fragmentation occurs. Additionally, to prevent local extinctions of mammals, edge effects should be diminished (e.g. expanding forested areas through active restoration actions or anti-poaching campaigns).

Our study also informs the debate on the relative importance of habitat amount versus fragmentation. We found habitat amount to be the most important driver of contemporary biodiversity patterns. However, the effects of habitat fragmentation were also significant and, importantly, took more time to manifest. Conclusions regarding the effects of

habitat fragmentation have often been based on snapshots of landscapes, typically from the time when biodiversity was sampled. Our study provides further evidence that contemporary habitat fragmentation may not be a strong predictor of species richness [15], that time-delayed responses to habitat fragmentation can be strong [20], and that landscape history should be considered when assessing contemporary biodiversity patterns [22,23]. Considering time-delayed responses seems particularly important in regions where landscapes have undergone recent and widespread changes [23]. This is the case for many subtropical and tropical deforestation frontiers, where extinction debt due to recent landscape fragmentation is likely large and not paid in full, and a positive impact of fragmentation on overall richness might be the result. By contrast, where landscapes have been transformed long ago, extinction debt has likely been paid [22,23]. Overall, this suggests that land-use history might at least explain partly the diverging conclusions from meta-analytical work on the effects of habitat fragmentation.

**Data accessibility.** Biodiversity data and landscape predictors available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.9zw3r22c5> [73]. Model codes and detailed modelling results are included in the electronic supplementary material. Our woodland cover maps are based on publicly available remote sensing imagery.

**Authors' contributions.** A.S.P. and T.K. designed the study; J.D., G.G.P., B.G.V., L.M., M.E.M. and P.V.Z. collected field data; M.B. and F.P. provided data; A.S.P. carried out the statistical analyses and drafted the manuscript; C.B. participated in data analyses. All authors contributed to the writing, gave final approval for publication and agreed to be held accountable for the work performed therein.

**Competing interests.** We declare we have no competing interests.

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## References

1. Tilman D, Clark M, Williams DR, Kimmel K, Polasky S, Packer C. 2017 Future threats to biodiversity and pathways to their prevention. *Nature* **546**, 73. (doi:10.1038/nature22900)
2. Brooks TM *et al.* 2002 Habitat loss and extinction in the hotspots of biodiversity. *Conserv. Biol.* **16**, 909–923. (doi:10.1046/j.1523-1739.2002.00530.x)
3. Fahrig L. 2013 Rethinking patch size and isolation effects: the habitat amount hypothesis. *J. Biogeogr.* **40**, 1649–1663. (doi:10.1111/jbi.12130)
4. Wiegand T, Revilla E, Moloney KA. 2005 Effects of habitat loss and fragmentation on population dynamics. *Conserv. Biol.* **19**, 108–121. (doi:10.1111/j.1523-1739.2005.00208.x)
5. Fahrig L. 2003 Effects of habitat fragmentation on biodiversity. *Ann. Rev. Ecol. Evol. Syst.* **34**, 487–515. (doi:10.1146/annurev.ecolsys.34.011802.132419)
6. Hanski I. 1998 Metapopulation dynamics. *Nature* **396**, 41–49. (doi:10.1038/23876)
7. MacArthur R, Wilson E. 1967 *The theory of island biogeography*. Princeton, NJ: Princeton University Press.
8. Broadbent EN, Asner GP, Keller M, Knapp DE, Oliveira PJ, Silva JN. 2008 Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. *Biol. Conserv.* **141**, 1745–1757. (doi:10.1016/j.biocon.2008.04.024)
9. Laurance WF *et al.* 2002 Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conserv. Biol.* **16**, 605–618. (doi:10.1046/j.1523-1739.2002.01025.x)
10. Pfeifer M *et al.* 2017 Creation of forest edges has a global impact on forest vertebrates. *Nature* **551**, 187–191. (doi:10.1038/nature24457)
11. Fahrig L. 2017 Ecological responses to habitat fragmentation per se. *Ann. Rev. Ecol. Evol. Syst.* **48**, 1–23. (doi:10.1146/annurev-ecolsys-110316-022612)
12. Watling JI *et al.* 2020 Support for the habitat amount hypothesis from a global synthesis of species density studies. *Ecol. Lett.* **23**, 674–681. (doi:10.1111/ele.13471)
13. Fahrig L *et al.* 2019 Is habitat fragmentation bad for biodiversity? *Biol. Conserv.* **230**, 179–186. (doi:10.1016/j.biocon.2018.12.026)
14. Melo GL, Sponchiado J, Cáceres NC, Fahrig L. 2017 Testing the habitat amount hypothesis for South American small mammals. *Biol. Conserv.* **209**, 304–314. (doi:10.1016/j.biocon.2017.02.031)
15. Fletcher Jr RJ *et al.* 2018 Is habitat fragmentation good for biodiversity? *Biol. Conserv.* **226**, 9–15. (doi:10.1016/j.biocon.2018.07.022)
16. Miller-Rushing AJ, Primack RB, Devictor V, Corlett RT, Cumming GS, Loyola R, Maas B, Pejchar L. 2019 How does habitat fragmentation affect biodiversity? A controversial question at the core of conservation biology. *Biol. Conserv.* **232**, 271–273. (doi:10.1016/j.biocon.2018.12.029)



17. Worboys G, Francis WL, Lockwood M. 2010 *Connectivity conservation management: a global guide*. London, UK: Earthscan Ltd.
18. Fahrig L. 2020 Why do several small patches hold more species than few large patches? *Global Ecol. Biogeogr.* **29**, 615–628. (doi:10.1111/geb.13059)
19. Ewers RM, Didham RK. 2006 Confounding factors in the detection of species responses to habitat fragmentation. *Biol. Rev.* **81**, 117–142. (doi:10.1017/S1464793105006949)
20. Haddad NM *et al.* 2015 Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci. Adv.* **1**, e1500052. (doi:10.1126/sciadv.1500052)
21. Krauss J *et al.* 2010 Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. *Ecol. Lett.* **13**, 597–605. (doi:10.1111/j.1461-0248.2010.01457.x)
22. Kuussaari M, Bommarco R, Heikkinen RK, Helm A, Krauss J, Lindborg R *et al.* 2009 Extinction debt: a challenge for biodiversity conservation. *Trends Ecol. Evol.* **24**, 564–571. (doi:10.1016/j.tree.2009.04.011)
23. Lira PK, de Souza Leite M, Metzger JP. 2019 Temporal lag in ecological responses to landscape change: where are we now? *Curr. Landscape Ecol. Rep.* 1–13.
24. Semper-Pascual A *et al.* 2018 Mapping extinction debt highlights conservation opportunities for birds and mammals in the South American Chaco. *J. Appl. Ecol.* **55**, 1218–1229. (doi:10.1111/1365-2664.13074)
25. Tilman D, May RM, Lehman CL, Nowak MA. 1994 Habitat destruction and the extinction debt. *Nature* **371**, 65–66.
26. Figueiredo L, Krauss J, Steffan-Dewenter I, Cabral JS. 2019 Understanding extinction debts: spatio-temporal scales, mechanisms and a roadmap for future research. *Ecography* **42**, 1973–1990.
27. Uezu A, Metzger JP. 2016 Time-lag in responses of birds to Atlantic forest fragmentation: restoration opportunity and urgency. *PLoS ONE* **11**, e0147909. (doi:10.1371/journal.pone.0147909)
28. Crooks KR, Burdett CL, Theobald DM, King SR, Di Marco M, Rondinini C *et al.* 2017 Quantification of habitat fragmentation reveals extinction risk in terrestrial mammals. *Proc. Natl Acad. Sci. USA*. **114**, 7635–7640. (doi:10.1073/pnas.1705769114)
29. Oeser J, Heurich M, Senf C, Flugmacher D, Belotti E, Kuemmerle T. 2019 Habitat metrics based on multi-temporal Landsat imagery for mapping large mammal habitat. *Remote Sens. Ecol. Conserv.*
30. Baumann M *et al.* 2017 Carbon emissions from agricultural expansion and intensification in the Chaco. *Glob. Change Biol.* **23**, 1902–1916. (doi:10.1111/gcb.13521)
31. TNC, FVS, FDSC, WCS. 2005 *Evaluación Ecorregional del Gran Chaco Americano*, Buenos Aires, Argentina: Fundación Vida Silvestre Argentina.
32. Minetti JL, Albarracín SA, Bobba ME, Hernández CM, López ER, Acuña LA, Mendoza E. 1999 *Atlas climático del noroeste argentino*. San Miguel de Tucumán, Argentina: Fundación Caldenius.
33. Baumann M *et al.* 2018 Mapping continuous fields of tree and shrub cover across the Gran Chaco using Landsat 8 and Sentinel-1 data. *Remote Sens. Environ.* **216**, 201–211. (doi:10.1016/j.rse.2018.06.044)
34. Fehlenberg V, Baumann M, Gasparri NI, Piquer-Rodríguez M, Gavier-Pizarro G, Kuemmerle T. 2017 The role of soybean production as an underlying driver of deforestation in the South American Chaco. *Global Environ. Change* **45**, 24–34. (doi:10.1016/j.gloenvcha.2017.05.001)
35. Piquer-Rodríguez M *et al.* 2015 Effects of past and future land conversions on forest connectivity in the Argentine Chaco. *Landsc. Ecol.* **30**, 817–833. (doi:10.1007/s10980-014-0147-3)
36. Periago ME, Chillo V, Ojeda RA. 2015 Loss of mammalian species from the South American Gran Chaco: empty savanna syndrome? *Mamm. Rev.* **45**, 41–53. (doi:10.1007/s10980-014-0147-3)
37. Macchi L, Grau HR, Zelaya PV, Marinero S. 2013 Trade-offs between land use intensity and avian biodiversity in the dry Chaco of Argentina: a tale of two gradients. *Agric. Ecosyst. Environ.* **174**, 11–20. (doi:10.1016/j.agee.2013.04.011)
38. Mastrangelo ME, Gavin MC. 2012 Trade-offs between cattle production and bird conservation in an agricultural frontier of the Gran Chaco of Argentina. *Conserv. Biol.* **26**, 1040–1051. (doi:10.1111/j.1523-1739.2012.01904.x)
39. Decarre J. 2015 Diversity and structure of bird and mammal communities in the semiarid Chaco Region: response to agricultural practices and landscape alterations. PhD thesis, Imperial College London, London, UK. (10.25560/38615)
40. Gómez-Valencia B. 2017 Medianos y grandes mamíferos en fragmentos de bosque de tres quebrachos, sudoeste de la provincia del Chaco. PhD thesis, Universidad De Buenos Aires.
41. Kolowski JM, Forrester TD. 2017 Camera trap placement and the potential for bias due to trails and other features. *PLoS ONE* **12**, e0186679. (doi:10.1371/journal.pone.0186679)
42. MacKenzie D, Nichols J, Royle J, Pollock K, Bailey L, Hines J. 2006 *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*. San Diego, CA: Elsevier.
43. Burton AC, Sam MK, Balangtaa C, Brashares JS. 2012 Hierarchical multi-species modeling of carnivore responses to hunting, habitat and prey in a West African protected area. *PLoS ONE* **7**, e38007. (doi:10.1371/journal.pone.0038007)
44. MacKenzie DI, Nichols JD, Royle JA, Pollock KH, Bailey L, Hines JE. 2017 *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*. San Diego, CA: Elsevier.
45. Zuckerberg B *et al.* 2020 A review of overlapping landscapes: pseudoreplication or a red herring in landscape ecology? *Curr. Landscape Ecol. Rep.* **2020**, 1–9.
46. Gorelick N, Hancher M, Dixon M, Ilyushchenko S, Thau D, Moore R. 2017 Google Earth engine: planetary-scale geospatial analysis for everyone. *Remote Sens. Environ.* **202**, 18–27. (doi:10.1016/j.rse.2017.06.031)
47. Griffiths P, Jakimow B, Hostert P. 2018 Reconstructing long term annual deforestation dynamics in Pará and Mato Grosso using the Landsat archive. *Remote Sens. Environ.* **216**, 497–513. (doi:10.1016/j.rse.2018.07.010)
48. Olofsson P, Foody GM, Herold M, Stehman SV, Woodcock CE, Wulder MA. 2014 Good practices for estimating area and assessing accuracy of land change. *Remote Sens. Environ.* **148**, 42–57. (doi:10.1016/j.rse.2014.02.015)
49. Dorazio RM, Royle JA. 2005 Estimating size and composition of biological communities by modeling the occurrence of species. *J. Am. Stat. Assoc.* **100**, 389–398. (doi:10.1198/016214505000000015)
50. Semper-Pascual A, Decarre J, Baumann M, Busso JM, Camino M, Gómez-Valencia B, Kuemmerle T. 2019 Biodiversity loss in deforestation frontiers: linking occupancy modelling and physiological stress indicators to understand local extinctions. *Biol. Conserv.* **236**, 281–288. (doi:10.1016/j.biocon.2019.05.050)
51. Semper-Pascual A *et al.* 2020 Using occupancy models to assess the direct and indirect impacts of agricultural expansion on species' populations. *Biodivers. Conserv.* **29**, 3669–3688. (doi:10.1007/s10531-020-02042-1)
52. MacKenzie DI, Nichols JD, Lachman GB, Droege S, Andrew Royle J, Langtimm CA. 2002 Estimating site occupancy rates when detection probabilities are less than one. *Ecology* **83**, 2248–2255. (doi:10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2)
53. Canevari M, Vaccaro O. 2007 *Guía de mamíferos del sur de América del Sur* Buenos Aires, Argentina: L.O.L.A. (Literature of Latin America).
54. Del Hoyo J, Elliott A, Sargatal J, Christie D, de Juana E. 2014 *Handbook of the birds of the world alive*. Barcelona, Spain: Lynx Edicions.
55. Short LL. 1975 A zoogeographic analysis of the South American chaco avifauna. *Bull. AMNH* **154**, article 3.
56. Watanabe S. 2010 Asymptotic equivalence of Bayes cross validation and widely applicable information criterion in singular learning theory. *J. Mach. Learn. Res.* **11**, 3571–3594.
57. Gelman A, Stern HS, Carlin JB, Dunson DB, Vehtari A, Rubin DB. 2013 *Bayesian data analysis*. London, UK: Chapman and Hall/CRC.
58. Haddad NM, Gonzalez A, Brudvig LA, Burt MA, Levey DJ, Damschen EI. 2017 Experimental evidence does not support the habitat amount hypothesis. *Ecography* **40**, 48–55. (doi:10.1111/ecog.02535)
59. Wearn OR, Reuman DC, Ewers RM. 2012 Extinction debt and windows of conservation opportunity in the Brazilian Amazon. *Science* **337**, 228–232. (doi:10.1126/science.1219013)
60. Brooks TM, Pimm SL, Oyugi JO. 1999 Time lag between deforestation and bird extinction in tropical forest fragments. *Conserv. Biol.* **13**, 1140–1150. (doi:10.1046/j.1523-1739.1999.98341.x)
61. Cook WM, Yao J, Foster BL, Holt RD, Patrick LB. 2005 Secondary succession in an experimentally fragmented landscape: community patterns across space and time. *Ecology* **86**, 1267–1279. (doi:10.1890/04-0320)

62. Magnago LFS, Rocha MF, Meyer L, Martins SV, Meira-Neto JAA. 2015 Microclimatic conditions at forest edges have significant impacts on vegetation structure in large Atlantic forest fragments. *Biodivers. Conserv.* **24**, 2305–2318. (doi:10.1007/s10531-015-0961-1)
63. Schneider NA, Low M, Arlt D, Pärt T. 2012 Contrast in edge vegetation structure modifies the predation risk of natural ground nests in an agricultural landscape. *PLoS ONE* **7**, e31517. (doi:10.1371/journal.pone.0031517)
64. Brashares JS, Arcese P, Sam MK. 2001 Human demography and reserve size predict wildlife extinction in West Africa. *Proc. R. Soc. Lond. B* **268**, 2473–2478. (doi:10.1098/rspb.2001.1815)
65. Cullen Jr L, Bodmer RE, Pádua CV. 2000 Effects of hunting in habitat fragments of the Atlantic forests, Brazil. *Biol. Conserv.* **95**, 49–56. (doi:10.1016/S0006-3207(00)00011-2)
66. Camino M, Cortez S, Altrichter M, Matteucci SD. 2018 Relations with wildlife of Wichi and Criollo people of the Dry Chaco, a conservation perspective. *Ethnobiol. Conserv.* **7**, 1–11.
67. Romero-Muñoz A *et al.* 2020 Increasing synergistic effects of habitat destruction and hunting on mammals over three decades in the Gran Chaco. *Ecography* **43**, 1–13. (doi:10.1111/ecog.05053)
68. Altrichter M. 2005 The sustainability of subsistence hunting of peccaries in the Argentine Chaco. *Biol. Conserv.* **126**, 351–362. (doi:10.1016/j.biocon.2005.06.024)
69. De Camargo RX, Boucher-Lalonde V, Currie DJ. 2018 At the landscape level, birds respond strongly to habitat amount but weakly to fragmentation. *Divers. Distrib.* **24**, 629–639. (doi:10.1111/ddi.12706)
70. Ruffell J, Banks-Leite C, Didham RK. 2016 Accounting for the causal basis of collinearity when measuring the effects of habitat loss versus habitat fragmentation. *Oikos* **125**, 117–125. (doi:10.1111/oik.01948)
71. Lees AC, Peres CA. 2008 Conservation value of remnant riparian forest corridors of varying quality for Amazonian birds and mammals. *Conserv. Biol.* **22**, 439–449. (doi:10.1111/j.1523-1739.2007.00870.x)
72. Mastrangelo ME, Gavin MC. 2014 Impacts of agricultural intensification on avian richness at multiple scales in Dry Chaco forests. *Biol. Conserv.* **179**, 63–71. (doi:10.1016/j.biocon.2014.08.020)
73. Semper-Pascual A *et al.* Data from: How do habitat amount and habitat fragmentation drive time-delayed responses of biodiversity to land-use change? Dryad Digital Repository. (<https://doi.org/10.5061/dryad.9zw3r22c5>)