

Edge effects and their influence on habitat suitability calculations: a continuous approach applied to birds of the Atlantic forest

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Summary

1. The suitability of human-modified habitats for native species and the response of species to habitat edges are two important ecological processes that affect species and communities in fragmented landscapes. However, field studies generally analyse these two processes separately. We extended a recently proposed continuous approach to link these two processes, using empirical data from birds of the Atlantic forest in Argentina, Paraguay and Brazil.

2. We tested different models for describing the responses of birds (both forest and open-habitat species) to the interior–exterior gradient within different edge types (ecotones). We used two types of data: the first originated from a large data set collected at regional scale using the point-count method and the second originated from a detailed local telemetry study of three bird species.

3. For both data sets, these models successfully described the responses to edges of the majority of species and assemblages and significantly influenced the calculated habitat suitability in both native and anthropogenic habitats. Edge effects were seen in the majority of species; however, the magnitude of these effects was influenced by the ecotone type. At the assemblage level, more species avoided edges in the ecotone with tree plantations compared with open habitats.

4. The effect of edges on the calculated habitat suitability was either positive or negative, depending on the function that best described the response of the species to edges and whether they avoided edges or penetrated into the less-preferred habitat. In general, forest species penetrated deeper into tree plantations but moved only short distances into open habitats.

5. *Synthesis and applications.* Our results demonstrate the impact of edge effects on bird species and communities in fragmented landscapes. Furthermore, the differential penetration capacity of the native forest birds into anthropogenic habitats shows the importance of using a continuous approach to calculate habitat suitability; classic calculation (without considering the distance to the preferred habitat) is likely to bias the calculated suitability and permeability of the hostile matrix and affect our estimations of connectivity.

Key-words: Atlantic forest, birds, distance gradients, ecotone, edge effect, habitat suitability

Introduction

Changes in species abundance and community structure in the ecotone between two contrasting habitats are often termed

‘edge effects’ (Murcia 1995; Ewers & Didham 2006). Edge effects result from alterations in environmental conditions, vegetation structure and composition (Ries & Sisk 2004; Santos *et al.* 2008) and altered biotic interactions such as predation and parasitism (Batáry & Báldi 2004; de Melo, Dirzo & Tabarelli 2006). Recent studies have highlighted the impact of

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edge effects on population dynamics and species persistence in fragmented landscapes, demonstrating that edge effects reduce habitat quality within the remaining patches and the functional connectivity between them (Murcia 1995; Laurence 2000; Hansbauer *et al.* 2008; Banks-Leite, Ewers & Metzger 2010; Gillies & St. Clair 2010).

The capacity of native species to use anthropogenic habitats or to move through them is one of the main determinants of landscape functional connectivity (Tischendorf & Fahrig 2000; Antongiovanni & Metzger 2005; Hansbauer *et al.* 2010; Watling *et al.* 2010; Zurita & Bellocq 2010). Some species may be completely restricted to native habitat cores (often called *habitat specialists*) and perceive anthropogenic habitats as impermeable for dispersal, whereas other species may use a variety of habitats, including anthropogenic habitats, and correspondingly perceive them as highly permeable for dispersal (*habitat generalist species*) (Gillies & St. Clair 2010). Habitat suitability studies often assume that the changes in suitability between different anthropogenic habitats are discrete (e.g. Zurita *et al.* 2006; Watling *et al.* 2010; Zurita & Bellocq *in press*). However, the suitability of anthropogenic habitats could be influenced by the distance to native habitats (Antongiovanni & Metzger 2005), that is, in landscape mosaics, native species may be observed in human matrices merely as a result of the proximity to the native habitat. In such cases, treating suitability separately from distance would bias both the calculated suitability of the matrix and our estimates of functional connectivity.

Edge effects and the suitability of anthropogenic habitats for forest animals have usually been examined in separate studies in different contexts. Ewers & Didham (2006) have shown that most edge-related studies either do not consider distance as a continuous factor or concentrate on one side of the interior–exterior gradient only (usually from the native habitat edge into its interior). However, the responses of species to ecotones and correspondingly to edge effects occur on both sides of an edge. This study uses an adaptation of the approach proposed by Ewers & Didham (2006) for delineating the extent and magnitude of edge effects for species and assemblages. We extend its application by testing its power and comprehensiveness at simultaneously analysing both edge effect and habitat suitability.

We focus our analyses on data from the Atlantic forest of Brazil, Argentina and Paraguay, which is one of the most diverse and one of the most threatened ecosystems in the world (12.7% of the original distribution) (Ribeiro *et al.* 2009). More than 80% of the remaining patches are smaller than 50 ha and are separated by more than 1 km (Ribeiro *et al.* 2009); thus, edge effects are probably among the most important factors affecting native species and communities in the Atlantic forest (Banks-Leite, Ewers & Metzger 2010). An analysis that combines edge effects with the calculation of habitat suitability for different land types can improve our ability to understand the distribution of forest species in fragmented landscapes. The same approach can be extended into analyses of species assemblages.

Materials and methods

GENERAL DESIGN

We used two data sets on birds from three different locations in the Atlantic forest. The first data set was derived from point-count surveys in the Atlantic forest of Argentina and Paraguay. This data set was used to examine the response of forest and open-habitat species to the ecotone between forest and two anthropogenic habitats (tree plantations and open habitats). We extended the results to the assembly level. The second data set, from telemetry surveys of three forest species in Brazil, was used to examine individual responses to a larger number of ecotones. These data indicated activity–density, which is mechanistically an important determinant of density or abundance. Our study combines different mechanisms (behavioural mechanisms vs. relative abundance patterns), ecological levels (individuals, species relative abundances and assemblages) and spatial scales (local vs. regional).

POINT-COUNT SURVEYS

Species abundance data were collected using the point-count technique with a 50 m fixed radius (Bibby, Jones & Marsden 1998). Bird surveys were conducted between 06:00 and 10:00 during the breeding season (September–January) in 2004, 2005 and 2006. The same observer performed all bird counts, recording all birds heard and seen during a 5-min period within a 50 m radius. Only individuals inside the sampled habitat were recorded. The geographical location of each point count was recorded using a global positioning system.

The point counts were separated by a minimum distance of 500 m and distributed over three extensive regions: NW and NE of Misiones province in Argentina (20 000 and 10 000 km², respectively, Fig. 1a) and in SW Paraguay (5000 km², Fig. 1b), encompassing a large proportion of the remaining Atlantic forest in Argentina and Paraguay. Commercial tree plantations dominate NW Misiones; annual and perennial crops and cattle pastures are abundant in NE Misiones; and in Paraguay annual crops and cattle pastures account for 91% of the economically productive areas (Zurita & Bellocq 2010). Native forest covers 45% of both regions of Argentina and 17% in Paraguay (for more details, see Zurita & Bellocq 2010). Point counts were randomly distributed within a given land use, but the sampling effort was similar between land uses; 55% of the bird point counts were located within an open-habitat ecotone and 45% within the tree plantation ecotone.

TELEMETRY SURVEYS

At the individual level and the local scale, we used telemetry data on the Atlantic Plateau of Ibiúna in south-eastern Brazil (23°35′–50′S; 46°45′–47°15′W, Fig. 1c). The study area was a rural landscape covering 10 000 ha, comprising 37% forest cover (31% older and 6% young secondary forest), 60% open areas (mainly agricultural fields), 17% tree plantations (mainly eucalyptus and pine) and 11% human settlements. Fragment sizes in the study area ranged from <1 to 280 ha (for more details, see Metzger *et al.* 2006 and Uezu, Metzger & Viellard 2005).

Mist-nets 100–120 m in length were located within five target patches, ranging from 4 to 53 ha in area. In the largest patch, the distance to the nearest edge was *c.* 300 m. From February 2003 to January 2005, three forest species were captured and radio-tagged at five different sites within the fragmented landscape: *Chiroxiphia caudata* (Shaw & Nodder) (15 cm, 25 gr); *Pyriglena leucoptera* (Vieillot)

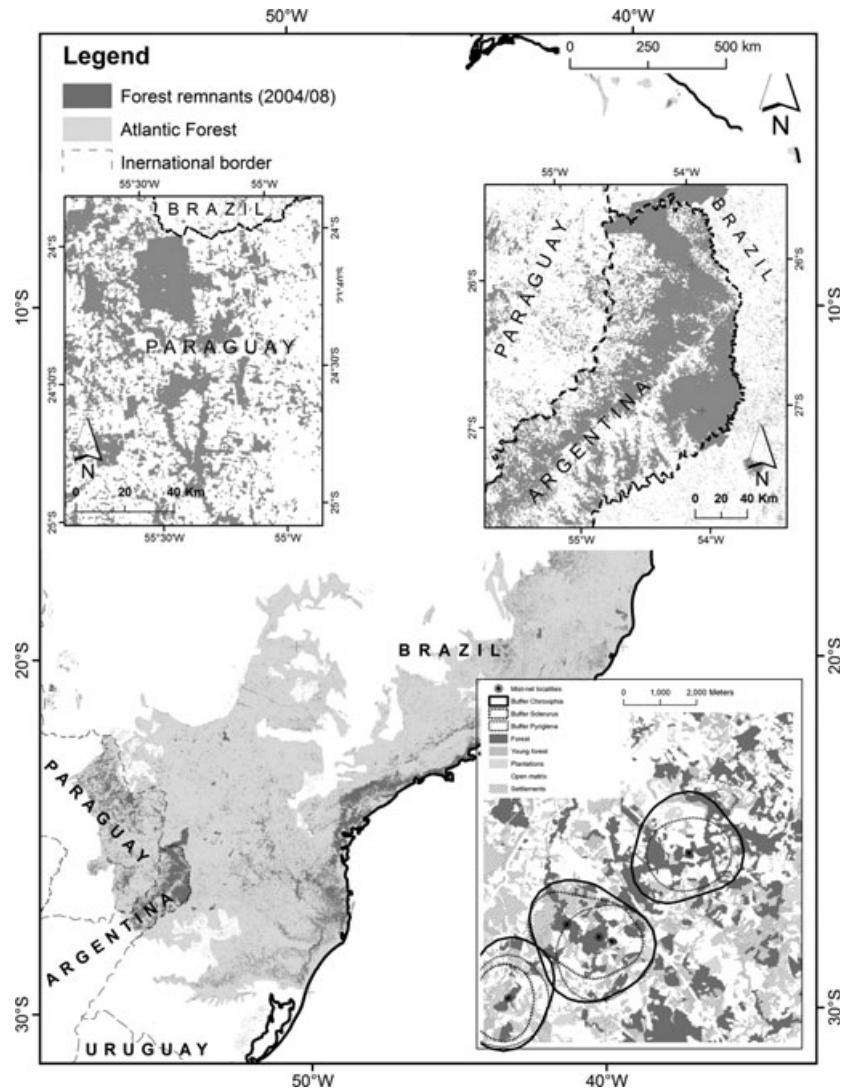


Fig. 1. Study area in Argentina (upper right), Paraguay (upper left) and Brazil (lower right). Light grey indicates the original extent of the Atlantic forest and dark grey the current distribution. In Brazil, buffer areas used to calculate the activity–density of the three different species are marked with dashed and continuous lines surrounding the mist-net localities (circles).

(18 cm, 30 gr); and *Sclerurus scansor* (Ménétries) (18.5 cm, 39 gr). Transmitters (0.43–0.64 gr; Biotrack Ltd, Wareham, UK) were back- or tail-mounted (Kenward 2001). For each individual, we recorded at least one location per day by triangulation from three or more fixed points. For the analyses, we considered home ranges based on ≥ 25 locations and monitored for 10–47 days (depending on the battery life of the transmitter; Hansbauer *et al.* 2008) to assess their maximal observable home range extensions. Thus, we included data for 24 *C. caudata*, seven *P. leucoptera* and eight *S. scansor*.

ALIGNING THE DATA ALONG THE DISTANCE GRADIENT

All geo-referenced sampling points (point counts and telemetry records) were included in a geographic information system with detailed information on landscape composition and configuration (Hansbauer *et al.* 2008, 2010; Zurita & Bellocq 2010). Euclidian distance was estimated from each sampling point (both inside and outside the native forest) to the nearest edge between forest and anthropogenic habitat. In the point-count survey, edges were clustered into two categories: (i) between native forest and tree plantations (mainly *Pinus* spp.) and (ii) between native forest and open areas (clear-cuts, annual crops and cattle pastures). In the telemetry surveys, we considered five edge types between secondary old forest

and either (i) secondary young forest, (ii) tree plantations (*Eucalyptus* spp.), (iii) shrubs, (iv) annual crops or (v) rural settlements (for more details, see Uezu *et al.* 2005; Hansbauer *et al.* 2008).

To align the data across a distance gradient, the sampling points were grouped into categories according to the distance to the nearest edge. Point-count records were grouped into 14 distance categories (both inside and outside forest): 0–50, 50–100, 100–200, 200–400, 400–700, 700–1000 and > 1000 m. We then calculated the proportion of points in which each species was recorded within each distance category. Although abundance data were available (number of records per sampling point count), we simplified them into presence/absence of species at each sampling point (hereafter, ‘relative abundance’) to avoid biases because of the potential counting of similar individuals more than once. Such an approach, which can be considered to be a ‘reporting rate’, could have its own biases of over-estimating the abundance of widely distributed species. This bias could eventually affect the comparison among species (which was not the objective of this study) but not the analysis of the edge response along the distance gradient for individual species.

Activity–density based on the telemetry data represented the number of observation points within a given distance-belt. Here, a larger number of points represented either the increased activity of a given bird in a preferred locality or an area where more individuals were

observed. This approach is typically applied when the number of individuals is small or if the identity of individuals is unknown (e.g. footprint-based studies). The available habitat area was centred on the mist-net locations and defined as two times the observed mean home range diameter of the tracked birds. This criterion was adopted because the relevant area depended on the mist-net locations and the species in question (Hansbauer *et al.* 2008). Thus, we ensured that the density of observation points in each land-use type was analysed within an area that could be considered to be relevant from the perspective of the individuals. This area was divided into 20-m distance clusters from 0 to 100 m (i.e. 0–20, 20–40, etc.), then 100–150, 150–200 and 200–500 m.

In both point-count and telemetry data, we assigned negative signs to distance values inside native forests and positive signs to distances within anthropogenic habitats. We standardized activity–density from the telemetry data using the maximum value for each species within each type of ecotone so that the maximum value was always 1.

DATA ANALYSIS

Following Ewers & Didham (2006), we used five different models to explore the response of species and assemblages to edges. Additionally, we calculated the suitability of the preferred and the non-preferred habitats using asymptotes resulting from those models. We performed regression analyses for these five models, in which the relative abundance or the activity–density of each species was the dependent variable, and the distance to the nearest edge type was the independent variable. In cases where more than one function significantly fitted the data, we used the Akaike's information criteria with a correction for small sample size (AICc; Burnham & Anderson 2002) to select among the different models. The models used were the following:

1. Abundance/activity = Mean

Mean: This model describes species that utilize natural and anthropogenic habitats equally and therefore exhibit no response to edges (generalist species).

2. Abundance/activity = $\beta_0 + \text{Distance} \times \beta_1$

Linear model: This model would best describe circumstances where the response of species to edges extends beyond the sampled range on both sides of the ecotone.

3. Abundance/activity = $\beta_0 \times e^{\beta_1 \times \text{Distance}} + Y_{\min}$

Power model: The power function may be useful for describing the incomplete coverage of the edge response of species in which an asymptote is reached on one side of the ecotone (Y_{\min}).

4. Abundance/activity = $Y_{\min} + ((Y_{\max} - Y_{\min}) / (1 + e^{(\beta_0 - \text{Distance}) \times \beta_1}))$

Sigmoid model: This model describes circumstances in which species respond to edges either gradually or abruptly, and there is thus a discrete change in habitat suitability. Here, the complete range of edge responses of a species is covered by data (i.e. asymptotes are reached on both sides of the ecotone). Y_{\max} and Y_{\min} represent the recalculated suitability of the species in both habitat types beyond the edge effect.

5. Abundance/activity = $Y_{\min} + ((\beta_0 - Y_{\min}) / (1 + e^{(\beta_1 - \text{Distance} + \beta_2 \times \text{Distance}^2) \times \beta_3}))$

Unimodal model: This model describes circumstances in which species prefer edges. In the case in which one habitat is preferred over another, the function will underestimate suit-

ability on one side and overestimate it on the other because the function assigns equal values to the asymptotes on both sides of the ecotone (Y_{\min}). To overcome this limitation, we conducted two separate power regression analyses to find the correct parameters of the asymptotes.

We used the first and second derivatives of the sigmoid and unimodal functions to calculate the *extent* and *magnitude* of the edge effect (see Fig. S1, Supporting information). We calculated the *magnitude* of the edge effect as the difference in the relative suitability (per cent) between the lower and upper asymptotes ($100 \cdot (Y_{\max} - Y_{\min}) / Y_{\max}$). In the case of the sigmoid function, Y_{\max} and Y_{\min} were obtained directly from the function; in the case of a unimodal function, Y_{\max} was calculated from the inflection point of the first derivative. We calculated the *extent* of the edge effect as the distance between both inflection points in the sigmoid and unimodal functions: in the case of the sigmoid function, this was the distance between the maximum and the minimum of the second derivative (i.e. the two inflection points of the function); in the case of the unimodal function, it was the distance between the two maxima of the second derivative.

We defined *penetration* as the potential of species to enter into the non-preferred habitat, calculated as the distance from the edge to the inflection point of the sigmoid or unimodal models (see Fig. S1, Supporting information). If the lower asymptote (Y_{\min}) was found to be higher than 0, we conservatively set the penetration distance at 500 m (i.e. beyond the range of our analysis but assuming infinity was not necessarily a suitable limit). We defined *edge avoidance* as decay in abundance or activity prior to the edge. Quantitatively, a species was considered to exhibit edge avoidance if it showed a sigmoid response and if the distance between the edge (0 m) and the inflection point of the function was > 50 m. We compared the *magnitude* and *extent* of the edge effect and the *penetration* distance between the different ecotone types (open habitat vs. tree plantations) using a *t*-test. In this analysis, each species inside each gradient was considered a replicate.

At the assemblage level, we used a 2×3 chi-square independence analysis to compare the proportion of species that exhibited each of the response functions (mean, sigmoid and unimodal model) with either tree plantations or open habitats. The same analysis was used to compare the proportion of species exhibiting edge avoidance, edge preference and a neutral response to edges between both edge types. To account for proportions equal to zero, we used the *G* statistic instead of the standard chi-square. In a second step, we examined the influence of edge effects on species assembly based on the proportion of forest species that remain unaffected by the edge at each distance point along the interior–exterior gradient for both types of ecotone. The area in which a species was defined to be influenced by edges was calculated from the inflection points of the sigmoid and unimodal models. Species that exhibited no response to edge (mean model) or where the best model was the power or linear one (indicating the incomplete coverage of the edge response by the field data) were excluded from this analysis.

Finally, we compared the capacity of the continuous and the 'classic' approaches to estimate the suitability of anthropogenic habitat for native forest species. In the first case, suitability in the core habitat (beyond the area affected by edges) was calculated from the asymptote of either the sigmoid function or the power function (in cases where the unimodal function produced the best fit); in the second case (classic approach), the abundance was directly calculated as the proportion of records for each species within a given habitat type without considering the distance to the native forest. Then, we fitted a linear function to identify whether one of the approaches tends to under-

overestimate suitability. Here, we separated the comparison according to the type of response identified by the continuous approach (i.e. what type of model fitted best) because the different response curves should be associated with different areas in which the classic approach may over- or underestimate suitability (see Fig. S1, Supporting information). Finally, we used a linear regression to assess whether the magnitude and extent of the edge effect influenced the magnitude of divergence between the classic estimation of abundance and the one calculated based on a continuous approach.

Results

POINT-COUNT SURVEYS

A total of 1124 bird point counts were surveyed in the study area. From these, 655 point counts were located inside native forest, 338 were located on tree plantations and 221 were located in open habitats. A total of 215 species and 8356 individuals were recorded. After excluding species with <30 records per ecotone type (i.e. insufficient data for the regression analysis), we had sufficient data from 46 species and 5112 individuals available for analysis. Exceptions to the 30-record rule were *C. caudata* and *P. leucoptera*, which were included in the analyses (with more than 20 records in both cases) to allow a comparison between the results obtained from the point-count data and those obtained from the telemetry data (see Appendix S1 in Supporting Information).

The majority of species showed a significant response to the interior–exterior gradient within the ecotone with open habitats and tree plantations (see Appendix S1, Supporting information; Figs 2 and 3). The response of a higher proportion of species was best described by the sigmoid function within the ecotone with tree plantations compared with the ecotone with open habitats ($2 \times 3 \chi^2$, 0.74 vs. 0.53), whereas the proportion of species best described by the unimodal function showed the opposite pattern (0.16 within the ecotone with open habitats vs. 0.00 with tree plantations) (χ^2 , $G_2 = 7.1$, $P = 0.02$). The proportion of species having a neutral response was similar between ecotone types (0.31 vs. 0.26 for the open and tree plantations, respectively). The proportion of species avoiding edges was marginally higher within the ecotone with tree plantations compared with open habitats, whereas the proportion of species preferring forest showed the opposite pattern (0.52 vs. 0.22 and 0.00 vs. 0.16, respectively, $2 \times 3 \chi^2$, $G = 5.2$, $P = 0.07$).

Although the *extent* of the edge effect was similar for tree plantations and open habitats (334 vs. 247 m, $t_{42} = 0.8$, $P = 0.40$), the *magnitude* was higher in ecotones with open habitats compared with tree plantations (96% vs. 80%, $t_{31} = 2.6$, $P = 0.01$). In contrast, the *penetration* distance of forest species into tree plantations was markedly greater than into open habitat (305 vs. 33 m, respectively, $t_{39} = -5.6$, $P < 0.01$). The proportion of forest species that remains unaffected by edges (beyond the inflection points on the sigmoid and unimodal functions) along the interior–exterior gradient was best fitted by a sigmoid function, within both the ecotone with tree plantations and with open habitats ($R^2 = 0.99$, $P < 0.001$) (Fig. 4). Edge effects inside the forests were more

pronounced within the ecotone with tree plantations compared with open habitat, but the magnitude of the effect was far lower when penetrating into the plantations as a consequence of the larger numbers of species occurring far deeper within the tree plantations but not in open habitats.

When comparing the suitability of habitats between the continuous (Y_{\min}) and the classic approach (i.e. with and without consideration of distance), we found that the classic approach underestimated the suitability of the preferred habitat compared with the values calculated from the sigmoid function ($R^2 = 0.86$, $P < 0.001$, Slope = 1.1). However, the classic approach overestimated the suitability of the non-preferred habitat compared with the suitability calculated from both the sigmoid and the unimodal functions, in both land-use types ($R^2 = 0.48$, $P < 0.001$, Slope = 0.49) (Fig. 5a). Finally, we found that the divergence in the calculated suitability between the continuous and the classic approaches was correlated with the magnitude of the edge effect (log transformed; $R^2 = 0.37$, $P < 0.001$) but not with the extent of effect ($R^2 = 0.04$, $P = 0.8$; Fig. 5b).

TELEMETRY SURVEYS

The three target species showed a significant response to all ecotone types, with the exception of *P. leucoptera*, which did not exhibit an edge response or a perceptible difference in suitability between old growth forest and young forests (Fig. 6, see Appendix S2, Supporting information). The response of the species to the edges was highly variable, but some general patterns can be described. First, among the three species, the response of *C. caudata* was the most variable between the ecotone types. In some ecotones, the species tended to avoid edges (scrubs, urban areas and young forest) but in others, it showed a preference for edges (plantations and agriculture). The magnitude of the edge response for this species was consistent between the point-count and telemetry data; the species was only present in some anthropogenic habitats and only near edges. However, the extent of the edge effect calculated from the point-count data (233 m) was larger than the extent calculated from the telemetry data (ranging from 64 to 142 m; see Appendix S2, Supporting information).

Pyriglena leucoptera was the only species showing a complete edge response in all of the gradients, indicating that the response of this species to edges occurs only at short distances. In general, this species exhibited a preference for edges (i.e. behaving as an edge species), except within the ecotones with young forest, where it showed no response to the edge and merely penetrated into the young forest. This response to young growth forest (i.e. perceived as equally suitable to the native habitat) was similar to the response identified from our analysis of the point-count data for plantations (see Appendices S1 and S2, Supporting information).

In contrast with *P. leucoptera*, *S. scansor* showed an incomplete edge response within the majority of the ecotones. This result indicates that the species is sensitive to edges but that the response occurs across larger distances than sampled in this

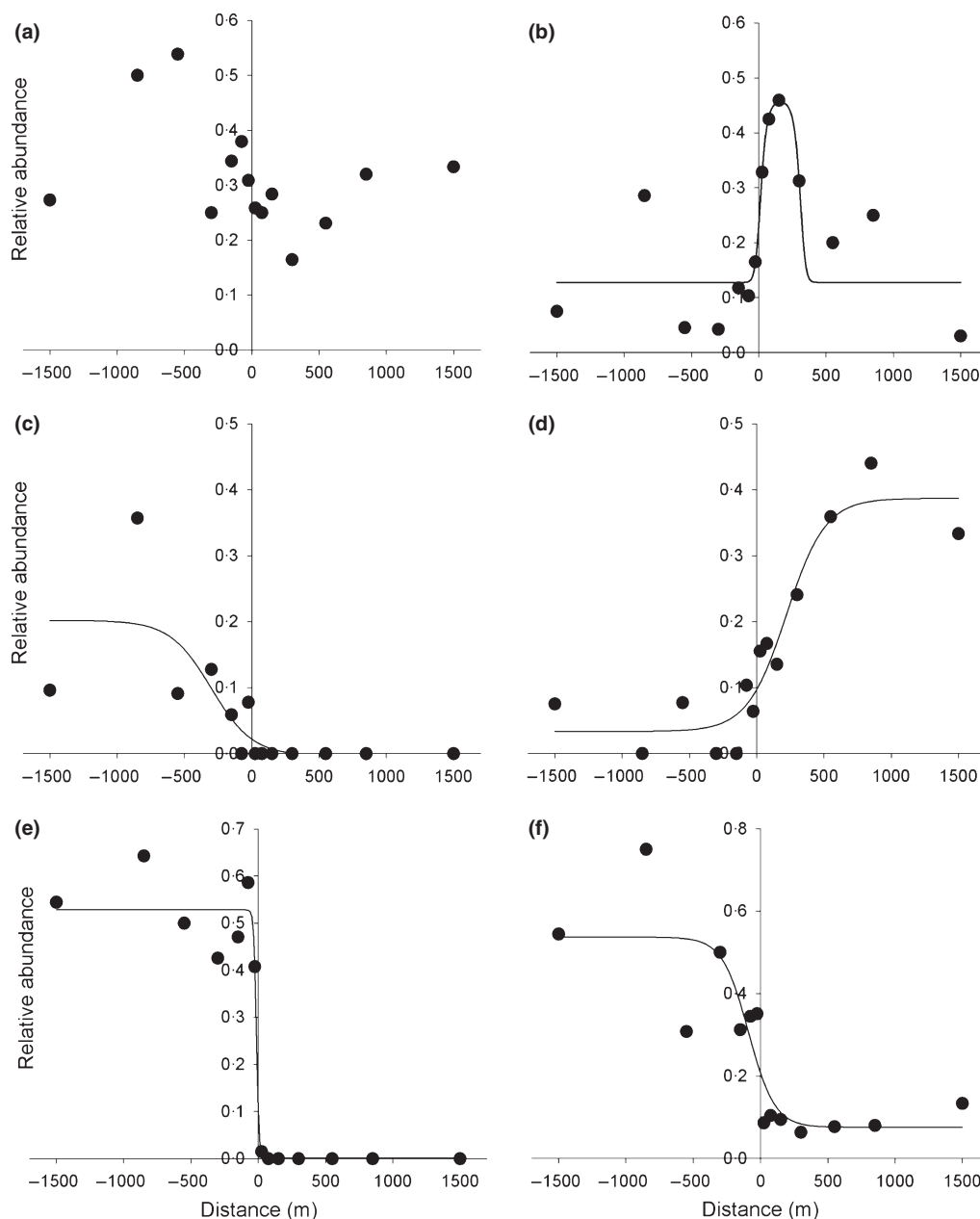


Fig. 2. Examples of the responses of bird species to different ecotones in the Atlantic forest of Argentina and Paraguay based on point-count data. Relative abundances were calculated as the proportion of sampled point counts with the presence of each species. (a) generalist species [*Vireo olivaceus* (Linnaeus)], (b) edge preference [*Troglodytes aedon* (Vieillot)], (c) edge avoidance for a forest species [*Bayiphtengus ruficapillus* (Vieillot)] and (d) non-forest species [*Zonotrichia capensis* (Müller)], and two different edge responses and penetration capacities of the same species [*Basileuterus culicivorus* (Deppe)] on the ecotone with (e) open habitat and (f) tree plantations.

study. However, in the ecotones between forest and settlements and between forest and young forest, the species was found to behave as an edge species (see Appendix S2, Supporting information).

Discussion

EDGE EFFECT: THE CONTINUOUS APPROACH

The continuous analysis methodology presented by Ewers & Didham (2006) allows the identification of a different pattern

of response to edges and the quantification of the extent and magnitude of the edge effect in a standardized and objective form. Our study demonstrates that this approach can be extended (i) to provide a standardized tool for calculating a corrected estimate of habitat suitability for a species; (ii) to improve understanding of the impacts of edges on species and assemblages; and (iii) to analyse field data across different methodologies for data collection, study areas and geographic scales. A slight adjustment of the methodology was necessary to calculate the habitat suitability when edge preference was identified. The symmetrical nature of a unimodal function

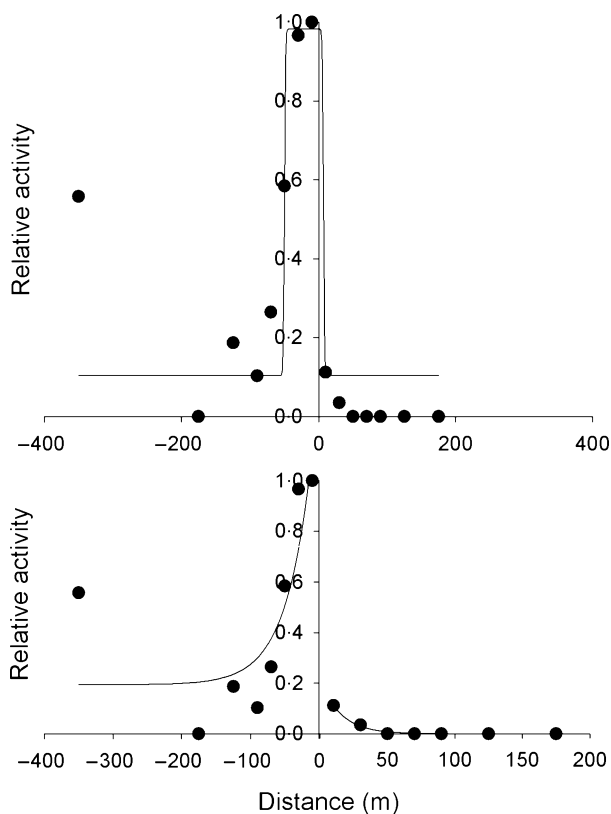


Fig. 3. Separation of a single unimodal function (upper figure) (e.g. *Leptotila verreauxi*) into two power functions (lower figure) to estimate different asymptotes on both sides of the ecotone.

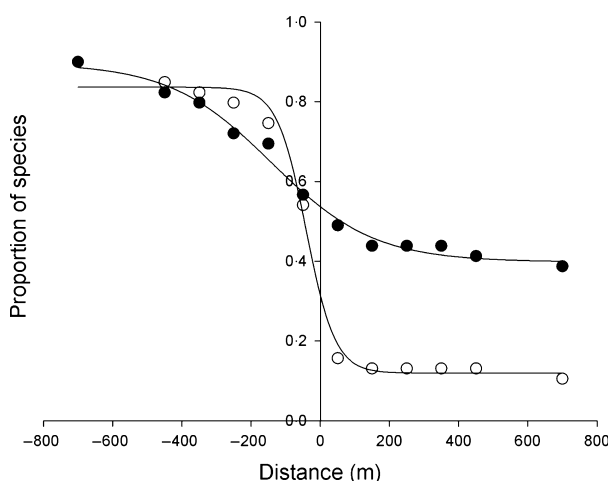


Fig. 4. Proportion of forest species remaining within a distance-belt (without showing an edge effect) within the ecotone between native forest and either tree plantations (filled circles) or open habitats (open circles).

forces the underestimation of the species abundance with a preferred habitat and overestimation within a less-preferred habitat. This limitation is particularly important for species like *P. leucoptera*: although this species commonly occurs along edges in fragmented landscapes, it also clearly occurs within core areas of the forest and should therefore still be considered a forest species (Hansbauer *et al.* 2008).

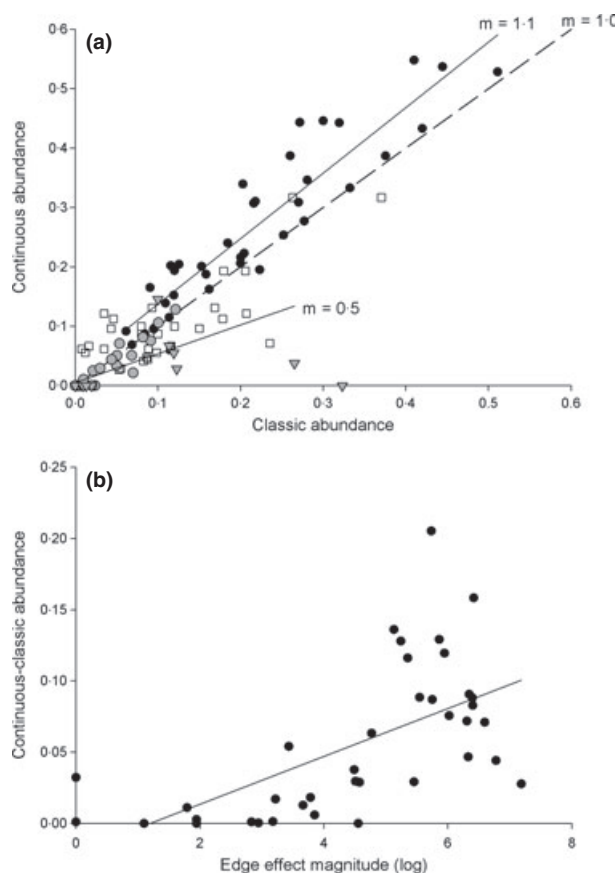


Fig. 5. Influence of edge effects on the calculated habitat suitability: continuous vs. classic approach (with and without considering the distance to the preferred habitat). Symbols in the upper figure represent the different response types to edges: (i) circles indicate habitat suitability calculated from the sigmoid function for the preferred habitat (black circles) and non-preferred habitat (grey circles); (ii) triangles indicate species having a unimodal response (edge preference); and (iii) empty squares indicate species that are insensitive to edges.

The analyses performed within this study assume that all forest patches are equally suitable habitat. However, forest patches may differ in quality not only because of edges but also as a result of their overall area and history (Banks-Leite, Ewers & Metzger 2010). This may be of particular importance in fragmented landscapes. However, Argentina and some parts of Paraguay still maintain relatively pristine forests with high connectivity (including many corridors); therefore, the effects of patch area and history can be considered to be substantially reduced (Zurita & Bellocq 2010). In addition, because many fragments of different sizes were sampled in Argentina and Paraguay, the variability arising from the area effect may occur without introducing a directional bias. The Ibiuna landscape in Brazil, in contrast, experienced both clear-cutting and forest recovery and is far more heterogeneous (Hansbauer *et al.* 2010). This effect was reduced by selecting study sites in patches of equal size and quality, but it still suggests that greater caution should be taken when preparing, analysing and interpreting data originating from local scale studies, and especially data from fragmented landscapes and the influence of the edge effect magnitude.

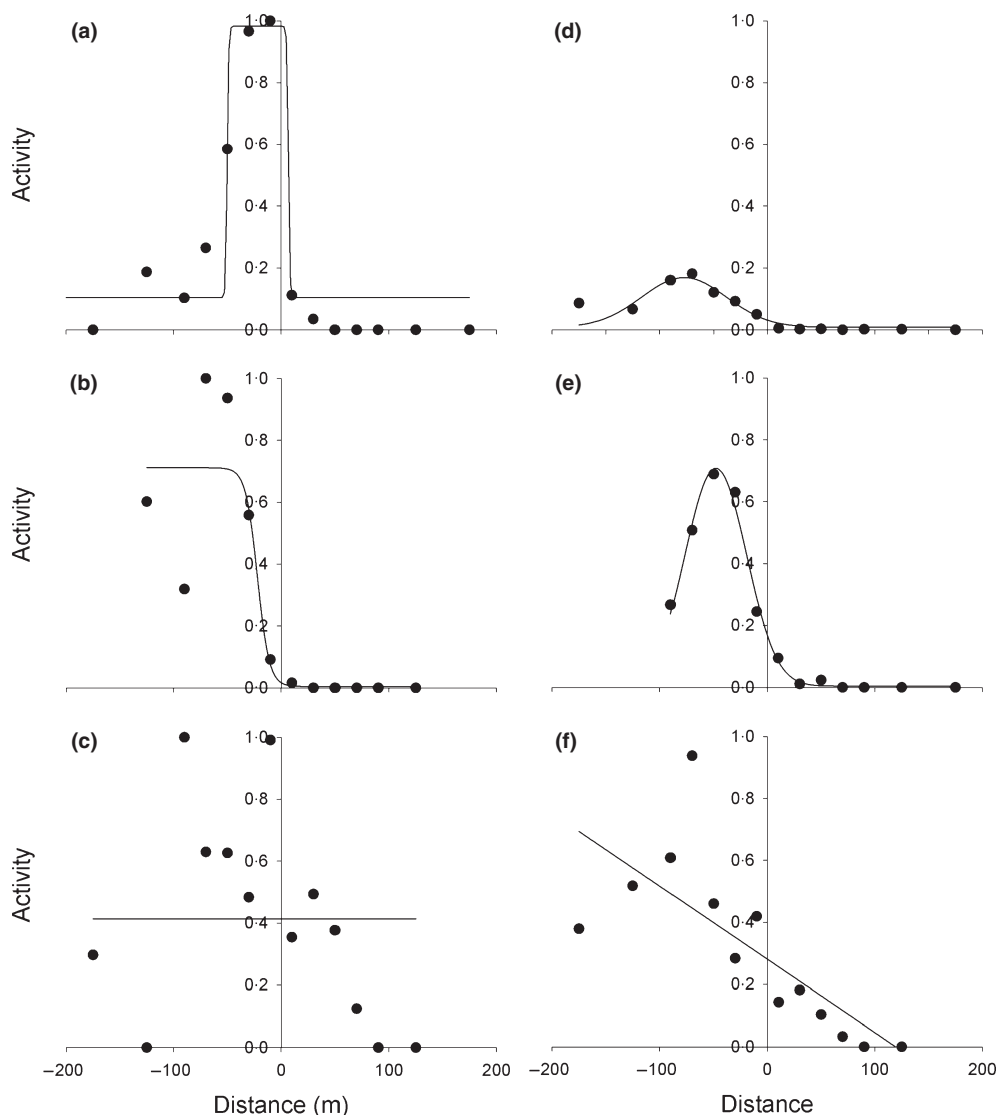


Fig. 6. Examples of the responses of *Poryglena leucoptera* (a, b and c) and *Chiroxiphia caudata* (d, e and f) to the ecotone with agricultural areas (a and d), tree plantations (b and e) and young secondary forest (c and f) in the Atlantic forest of Brazil, based on telemetry data (activity–density). Negative values indicate distances inside the forest and positive values indicate distances inside the anthropogenic matrices.

Having corrected for some of these effects, it is likely that the differences in the edge effect between the point-count and the telemetry data did not result from an inconsistency in our methodology but reflect a real effect of the differences in landscape structure and habitat quality. The tendency of species to exhibit edge preference (46% in Brazil compared with 10% in Argentina and Paraguay) may result from these differences in habitat quality and fragmentation pattern. Species in the fragmented landscape in Brazil may be forced to use suboptimal habitats and move closer to edges or even into anthropogenic environments to fulfil their needs, whereas in Argentina and Paraguay, larger fragments and higher habitat quality may allow species to behave as forest-interior species (Zurita & Bellocq 2010). This interpretation is also supported by the higher magnitude of the edge effect in Brazil compared with Argentina and Paraguay (89% vs. 65% on average).

EDGE RESPONSE

In accordance with previous studies, we found that a significant proportion of birds (37% on average) avoid edges (Laurence 2000; Banks-Leite, Ewers & Metzger 2010), with a large range of edge-avoidance values of up to several hundreds of metres into the forest (Laurence 2000). Overall, this represents a high proportion of species, because we only included ‘common’ species with a sufficient number of records. Despite this general pattern, the response of the forest species to the edges was strongly influenced by the contrast between the natural and anthropogenic habitats. Several species have been shown to avoid edges in response to one edge type but not another; moreover, species such as *C. caudata* behave as edge species in some situations and as forest-interior species in others.

The result at the assemblage level may appear to contradict the conclusions that tree plantations are more suitable for

native forest species in the Atlantic forest than open habitats (Zurita *et al.* 2006; Zurita & Bellocq in press and our results for Y_{\min}) and that the contrast in the environmental conditions between the preferred and non-preferred habitats determine the degree of edge effect (Prevedello & Vieira 2010). However, this may be related to the mechanism behind the edge effect in forest habitats. First, predation risks, which are known to cause strong edge avoidance, may be more important in ecotones with tree plantations because they allow access to potential predators (Batáry & Báldi 2004). Secondly, the ecotone between the forest and open habitat is usually dominated by light-demanding vegetation species (such as shrubs and pioneer trees), which provide a diversity of flowers and fleshy fruits, usually consumed by forest birds (Oosterhoorn & Kappelle 2000). Finally, landscapes dominated by agriculture and open pasture are often also more fragmented; consequently, species in such landscapes are forced to utilize suboptimal habitats and move closer to edges (Zurita & Bellocq 2010). Depending on the biology of the species, the underlying mechanisms and the confining effects of the landscape, the same ecotone could actually result in a strong edge response for some species and a neutral edge response for others (Reino *et al.* 2009; Prevedello & Vieira 2010; Pe'er *et al.* 2011a).

FUNCTIONAL CONNECTIVITY: THE IMPORTANCE OF USING A CONTINUOUS APPROACH

Both edge effects and ease of movement in anthropogenic habitats will influence functional connectivity (Laurence 2000; Antongiovanni & Metzger 2005; Hansbauer *et al.* 2010; Pe'er *et al.* 2011b). Measures of connectivity based exclusively on suitability are likely to underestimate forest fragmentation effects (Tischendorf & Fahrig 2000). Individuals may carry out exploratory visits, disperse through the matrix or even utilize resources within anthropogenic habitats, but often such movements extend only a limited distance into the 'matrix' and do not indicate that the habitat is 'suitable' at greater distances (Hansbauer *et al.* 2008; Reino *et al.* 2009).

Our results emphasize that the classic approach for estimating the suitability of habitats tends to bias the estimated use of the habitats by species. However, whether the bias is positive or negative depends on the nature of response of the species to the edges and whether the habitat is preferred or non-preferred. More importantly, because overestimation is likely to occur for the non-preferred habitat, this may yield an over-optimistic perception of the conservation value of the human matrices. Both the classic and continuous approaches have their merits and limitations because positive and negative biases occur under different circumstances. Therefore, an important outcome of our study is the identification of situations where the use of a classic approach is most likely to yield biases: namely in hyper-fragmented landscapes and among species that exhibit a sigmoid function of edge avoidance; that is, those situations that demand most attention from conservation managers.

Patches of native habitat separated by more than 300 m of tree plantations or 50 m of open habitat are essentially isolated

for the majority of forest birds included in this study. If we consider that the average distance between fragments is more than 1000 m (Ribeiro *et al.* 2009), then functional connectivity between the fragments is close to zero in the majority of the Atlantic forest. Argentina is an exception because of the large area of native forest still remaining (45%) (Galindo-Leal & Câmara 2003) and the low average distance between fragments: only 110 m (calculated from Zurita & Bellocq 2010). Moreover, in many cases, the matrix separating the patches is primarily tree plantations (Zurita & Bellocq 2010). Overall, it appears that forest fragments in the Atlantic forest of Argentina are, in general, functionally well connected. This may explain, at least in part, the maintenance of the native bird community in this region even in fragmented landscapes of only 40% forest cover (Zurita & Bellocq 2010).

In the longer term, better estimation of both edge effects and habitat suitability will improve our understanding of both functional connectivity and the mechanisms that affect populations and communities in fragmented landscapes. Consideration of edge effects and matrix permeability is particularly important when using simulation models to predict connectivity in fragmented landscapes, as otherwise connectivity can be easily over- or underestimated (Pe'er *et al.* 2011b). Our approach offers a simple way of parameterizing such models, to strengthen their capacity to inform decision-makers and landscape planners on potential threats and solutions in terms of landscape connectivity and permeability.

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Supporting Information

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

Fig. S1. Definition of the edge effect.

Appendix S1. Edge effect response based on point count data.

Appendix S2. Edge effect response based on telemetry data.

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