



Integrating species life-history traits and patterns of deforestation in amphibian conservation planning

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ABSTRACT

Aim To identify priority areas for amphibian conservation in southeastern Brazil, by integrating species life-history traits and patterns of deforestation.

Location State of São Paulo, Brazil.

Methods We used the software MARXAN to evaluate different scenarios of amphibian conservation planning. Our approach differs from previous methods by explicitly including two different landscape metrics; habitat split for species with aquatic larvae, and habitat loss for species with terrestrial development. We evaluated the effect of habitat requirements by classifying species breeding habitats in five categories (flowing water, still water permanent, still water temporary, bromeliad or bamboo, and terrestrial). We performed analyses using two scales, grid cells and watersheds and also considered nature preserves as protected areas.

Results We found contrasting patterns of deforestation between coastal and inland regions. Seventy-six grid cells and 14 watersheds are capable of representing each species at least once. When accounting for grid cells already protected in state and national parks and considering species habitat requirements we found 16 high-priority grid cells for species with one or two reproductive habitats, and only one cell representing species with four habitat requirements. Key areas for the conservation of species breeding in flowing and permanent still waters are concentrated in southern state, while those for amphibians breeding in temporary ponds are concentrated in central to eastern zones. Eastern highland zones are key areas for preserving species breeding terrestrially by direct or indirect development. Species breeding in bromeliads and bamboos are already well represented in protected areas.

Main conclusions Our results emphasize the need to integrate information on landscape configuration and species life-history traits to produce more ecologically relevant conservation strategies.

Keywords

Amphibian declines, area prioritization, Brazil, habitat fragmentation, habitat split, protected areas, systematic conservation planning.

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INTRODUCTION

Deforestation does not progress randomly throughout landscapes (Viana *et al.*, 1997; Ezard & Travis, 2006; Silva *et al.*, 2007) because of the non-random spatial distribution of land suitable for specific human activities and laws that often protect particular habitats or vegetation types. Riparian

vegetation, for example, is protected by law in many countries (Gregory *et al.*, 1991). Thus, if enforcement is effective, deforestation should be biased to areas other than riparian zones. In contrast, humans tend to concentrate their activities in valleys where water is readily available for agriculture, industry and human consumption, resulting in deforestation and disconnection of riparian zones from upland vegetation

(Viana *et al.*, 1997; Silva *et al.*, 2007). Wetter parts of the landscape, which encompass a large proportion of amphibian breeding sites, are frequently converted for agricultural or urban development (Viana *et al.*, 1997).

Amphibian species with different developmental modes vary in their responses to habitat change (Gascon *et al.*, 1999; Tocher *et al.*, 2001; Bell & Donnelly, 2006; Urbina-Cardona *et al.*, 2006; Becker *et al.*, 2007). Species with aquatic larvae often need landscape complementation, relying on the integrity of and connection between terrestrial and aquatic habitats to complete their biphasic life cycles (Werner & Gilliam, 1984; Pope *et al.*, 2000; Becker *et al.*, 2009). Discontinuity between suitable aquatic and terrestrial habitats forces many species with aquatic larvae to perform risky breeding migrations through disturbed environments, potentially contributing to population declines (Becker *et al.*, 2009). This habitat split is the strongest factor determining richness of amphibians with aquatic larvae in the Brazilian Atlantic Forest (Becker *et al.*, 2007). Conversely, most species with terrestrial development can complete their life cycle in the absence of water bodies (Haddad & Prado, 2005) and thus suffer primarily with the loss of terrestrial vegetation. Therefore, distinct patterns of deforestation have different effects on the spatial configuration of terrestrial and aquatic habitats, and these, in turn, can affect amphibian species with distinct life-history traits in different ways (Becker *et al.*, 2007).

The Brazilian Atlantic Forest is a biodiversity hotspot, harbouring a large number of endemic frogs (Morellato & Haddad, 2000; Mittermeier *et al.*, 2005). This biome is threatened because of severe habitat destruction, and the spatial distribution of upland forests and lowland riparian vegetation varies across regions. Therefore, areas with the same overall deforestation rate can have very different degrees of natural riparian vegetation remaining, as well as varying connectivity with terrestrial environments (Rodrigues *et al.*, 2009). This variation makes this region an ideal place to investigate how species life-history traits interact with deforestation patterns, and the implications for amphibian conservation planning. In addition, the conflict between conservation of water resources and destruction of terrestrial vegetation in riparian zones is a key factor in amphibian conservation planning, yet its effects on amphibian communities have not yet been fully explored (Becker *et al.*, 2009).

Here, we apply conservation planning analyses to south-eastern Brazil to identify sets of priority areas for amphibian conservation, considering the current network of protected areas in the State of São Paulo, Brazil. Our ultimate goal is to pinpoint areas for habitat protection and inventory work before we lose a considerable portion of amphibian diversity. Our approach differs from previous methods by explicitly including different landscape metrics – habitat split, for species with aquatic larvae, and habitat loss, for species with terrestrial development – to develop conservation planning scenarios. We tested the effect of habitat requirements classifying species breeding habitats in five categories [flowing water, still water permanent, still water temporary, bromeliad and bamboo, and

terrestrial (e.g., leaf litter, soil)]. We suggest alternative habitat restoration plans according to species life-history requirements.

METHODS

Study regions

Originally extending for 1,300,000 km² along the Brazilian coast and into parts of Paraguay and Argentina, the Brazilian Atlantic Forest has been reduced to *c.* 10% of its historical range (Morellato & Haddad, 2000; Rodrigues *et al.*, 2009). Fragments currently remaining harbour a fauna and flora with one of the highest levels of endemism in the world, with many species of vertebrates still being described (Alves *et al.*, 2009; Pimenta *et al.*, 2009). For amphibians in particular, the Atlantic Forest harbours *c.* 300 endemic species, many of which have suffered population declines and local extinctions attributed primarily to habitat change (Heyer *et al.*, 1988; Weygoldt, 1989; Eterovick *et al.*, 2005; Becker *et al.*, 2007). Moreover, in some regions, patterns of human economic development have resulted in landscapes with a large number of upland 'dry fragments', disconnected from streams and other water sources at lower elevations. Other regions, however, still have intact riparian buffers despite substantial deforestation (Viana *et al.*, 1997; Silva *et al.*, 2007).

We focused on the State of São Paulo, which was historically dominated by Atlantic Forest with some remnants of Cerrado in the central and westernmost parts of the state (Ribeiro *et al.*, 2009). São Paulo is the most populated state in Brazil, with *c.* 40 million inhabitants. Over the last century, massive deforestation for agriculture, cattle-raising and urbanization (Viana *et al.*, 1997; Morellato & Haddad, 2000) has confined many remnants of natural vegetation to steep slopes and hilltops (Viana *et al.*, 1997; Silva *et al.*, 2007). Currently, the remaining fragments of natural vegetation are concentrated in the coastal zones (Instituto Florestal, 2004; Ribeiro *et al.*, 2009).

Data

We gathered a database of 220 anuran species known from the State of São Paulo (Araújo *et al.*, 2009) and compiled their respective geographic ranges (IUCN *et al.*, 2009). Using GIS procedures in Arc View 9.3 (ESRI, 2008), we divided the region into (1) a regular equal-area grid of 220 cells (hexagons of 1200 km²) and (2) 22 watersheds (mean watershed size: 11273.9 km² ± 5451.1 SD). Species geographic ranges were overlaid to extract data on species richness for each grid cell and/or watershed. We chose these two different spatial approaches to explore how the choice of uniform or topographically relevant spatial limits affects the outcome of conservation planning. In particular, grid cells are spatially consistent, but random relative to the environment, and each identifies diversity at a small spatial scale. In contrast, watersheds are regionally bound due to topography, and thus

may better reflect biogeographical assemblages of species but also usually encompass a much larger area.

We obtained a GIS database (1:50,000) with information on land cover, watershed and protected areas (IUCN categories I–IV: ecological stations, state and national parks) from the Programa Biota and Instituto Florestal, an initiative of the Fundação de Amparo à Pesquisa do Estado de São Paulo – FAPESP (Instituto Florestal, 2004). We obtained the state hydrological database (1:50,000) from the Instituto Brasileiro de Geografia e Estatística – IBGE (IBGE, 1985).

Analyses

To identify priority areas for amphibian conservation, we grouped species by their developmental mode: species with aquatic larvae (176 species) or species with terrestrial development (44 species). The determination of developmental mode followed previously defined categories of reproductive types identified for Neotropical anurans (Haddad & Prado, 2005). Species with developmental modes requiring aquatic habitats (running and still surface waters) were classified as species with aquatic larvae, whereas species completing their development in terrestrial vegetation (leaf litter, soil, bromeliad tanks and bamboo stems) were classified as species with terrestrial development (see also Loyola *et al.*, 2008a). We classified species breeding habitats in five categories: flowing water (FW), still water/permanent (SP) and still water/temporary (ST) for species with aquatic larvae; and bromeliad or bamboo (BB), and terrestrial (DI) (e.g., direct and indirect terrestrial developers) for species with terrestrial development. The reason we considered species breeding in bromeliad tanks or bamboo stems as terrestrial developers is because these species rely on terrestrial vegetation independent of the presence of surface waters (Haddad & Prado, 2005).

We used the software MARXAN (v. 1.8.2) to evaluate and compare different conservation planning scenarios (Possingham *et al.*, 2000). Using an optimization procedure, based on a simulated annealing algorithm, we identified priority sets of areas (grid cells or watersheds) that represent, as a set, all species at least once, based on the complementarity concept (Kirkpatrick, 1983; Pressey *et al.*, 1996). This algorithm begins with a random set of grid cells/watersheds, and at each iteration, swaps units in and out of that set, measuring the change in cost according to a cost function. The procedure was repeated 100 times, and final conservation planning scenarios (i.e. sets of grid cells or watersheds) were obtained after 10 million iterations. MARXAN allows users to set a penalty value for losing a species. We set a high penalty value to ensure that all species were represented with a minimum number of grid cells or watersheds. As each MARXAN run provides a somewhat different solution, we used the metric ‘selection frequency’ to compare scenarios. Selection frequency represents the number of times each planning unit is selected in the solutions to the overall problem (Leslie *et al.*, 2003). Planning units (here grid cells and watersheds) that are selected above a certain

threshold-percentage (>90%) of runs are considered as high-priority conservation areas.

Several spatial prioritization studies aim to meet predefined conservation objectives for the minimum total ‘cost’. Conventionally, the cost of a site for conservation is simply proportional to its area. Here, we examined the cost of the grid cells or watersheds selected by the optimization algorithm based on two ‘cost’ metrics: habitat split and habitat loss. Thus, each grid cell and watershed received a ‘cost’ value based on current values of these landscapes metrics. Habitat split was calculated as the percentage of total stream length and permanent pond perimeter that did not overlap with natural forest cover within each grid cell or watershed. Habitat loss was the percentage of non-natural vegetation cover occurring within each grid cell or watershed. Because amphibians with aquatic larvae are expected to have a stronger response to habitat split, and species with terrestrial development to habitat loss (Becker *et al.*, 2007), we used these costs as constraints on the analyses. Sets of priority areas capable of representing species with aquatic larvae (including FW and SP reproductive habitats) should, whenever possible, favour the inclusion of grid cells or watersheds with lower values of habitat split. Conversely, key areas for representing species with terrestrial development (including BB and DI reproductive habitats) should favour the inclusion of grid cells or watersheds with the lowest values of habitat loss. Because temporary ponds (ST) are not identifiable in the hydrology maps, and can also be associated with upland habitats, we set equal constraints of habitat split and habitat loss for species using this breeding habitat.

Areas with high selection frequency in our analyses were designated as the highest priority set. Sets of grid cells or watersheds obtained from these analyses were drawn on grid or watershed maps using ArcView GIS 9.3 (ESRI, 2008). We combined maps to reveal complementary sets of areas with distinct values of selection frequency that should be included in a reserve system to represent all species with aquatic larvae and those with terrestrial development.

The State of São Paulo already has several protected natural areas. To evaluate their effectiveness and quantify how much additional area needs to be preserved to safeguard the state’s amphibian diversity, we ran additional analyses considering grid cells including protected areas (IUCN categories I–IV and larger than 300 ha). These cells ($n = 56$) were fixed in the analyses because they are already protected. This procedure, often referred to as a ‘gap analysis’ (Margules & Pressey, 2000), allowed us to identify new grid cells that best complement the current reserve network established in the state. Values of habitat split and habitat loss were also used as constraints in these analyses, according to species reproductive habitats, as described above. We used UTM WGS 1984 projection for maps resulting for all analyses.

Finally, we tested whether including amphibian life-history traits into conservation planning actually changes or improves the selection process. Recently, we demonstrated that the ideal choice of priority areas for amphibian conservation depends on their developmental modes (Loyola *et al.*, 2008a), but that

study did not include both cost metrics (habitat split and habitat loss). Here, we selected priority areas based on both cost metrics and also, without considering differences in such life-history trait. For this last analysis we pooled species with aquatic larvae and terrestrial development into other MARXAN runs (performed in the same way as described above). We then compared the total cost of conservation planning scenarios, based on total habitat split and habitat loss found across the selected grid cells. We tested differences of mean habitat split and habitat loss among conservation scenarios that separated species by developmental mode and considering all species together. In this analysis, we used grid cells with high selection frequency (>90%) and applied arcsine-square root data transformation to perform this test.

RESULTS

Patterns of deforestation and species richness

We found contrasting patterns of deforestation in the coastal and inland regions of São Paulo State (Fig. 1). Deforestation in coastal and more densely populated regions is less severe than that observed in inland agricultural zones; however, deforestation in coastal regions is biased to riparian vegetation, leading to high habitat split at the landscape level, and affecting primarily amphibians with aquatic larvae. Inland agricultural zones, despite having higher rates of habitat loss than coastal areas, harbour more riparian vegetation than expected by chance. This result holds for grid cell (Fig. 1a) and watershed-based analyses (Fig. 1b).

We found a gradient in species richness increasing toward eastern São Paulo both for species with aquatic larvae (Fig. 2a,

b) and terrestrial development (Fig. 2c, d). This gradient is consistent across grid cell and watershed analyses. A single grid cell showed higher richness for both amphibians with aquatic larvae (91 species; 52% of the total) and terrestrial development (24 species; 55% of the total); this cell is located in the eastern coastal region of the state (highlands of Serra da Bocaina, Vale do Paraíba watershed) (Fig. 2).

Priority areas for amphibian conservation

When amphibian developmental modes were not taken into account (all species pooled), the mean habitat split and habitat loss found across priority grid cells was higher (Fig. 3). Priority areas inferred from independent analyses considering species with aquatic larvae and terrestrial development yielded lower levels of habitat split (t -test, $t = -2.417$, d.f. = 27, $P = 0.023$) and habitat loss ($t = 2.150$, d.f. = 17, $P = 0.046$) respectively. Hence, conservation planning scenarios that ignore amphibian reproductive modes did not reduce habitat split and habitat loss in the inferred protected areas compared with independent analysis including life-history traits (Fig. 3).

When amphibian reproductive habitats were included as ecological constraints into spatial prioritization analyses we found 76 grid cells and 14 watersheds capable of representing each species at least once (Fig. 4). Grid cells and watersheds with high selection frequency for preserving species that breed in flowing waters were concentrated in coastal areas and northeastern São Paulo state (Fig. 4a, b). Grid cells crucial to preserving species that breed in still permanent (Fig. 4c, d) and temporary water bodies (Fig. 4e, f) were scattered across the entire state. Species breeding in bromeliad tanks and bamboo stems can be safeguarded by protecting central to northern

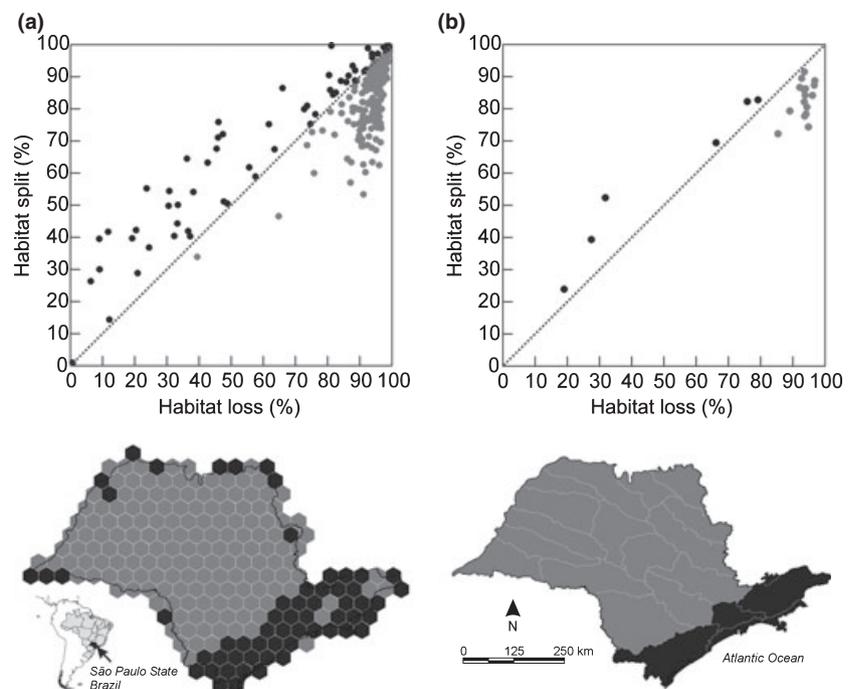


Figure 1 Relationship between habitat loss and habitat split for grid cells (a) and watersheds (b). Dotted line represents expected values if deforestation occurred randomly throughout the landscape. Black represents deforestation biased towards riparian buffers. Grey represents deforestation biased to non-riparian parts of the landscape.

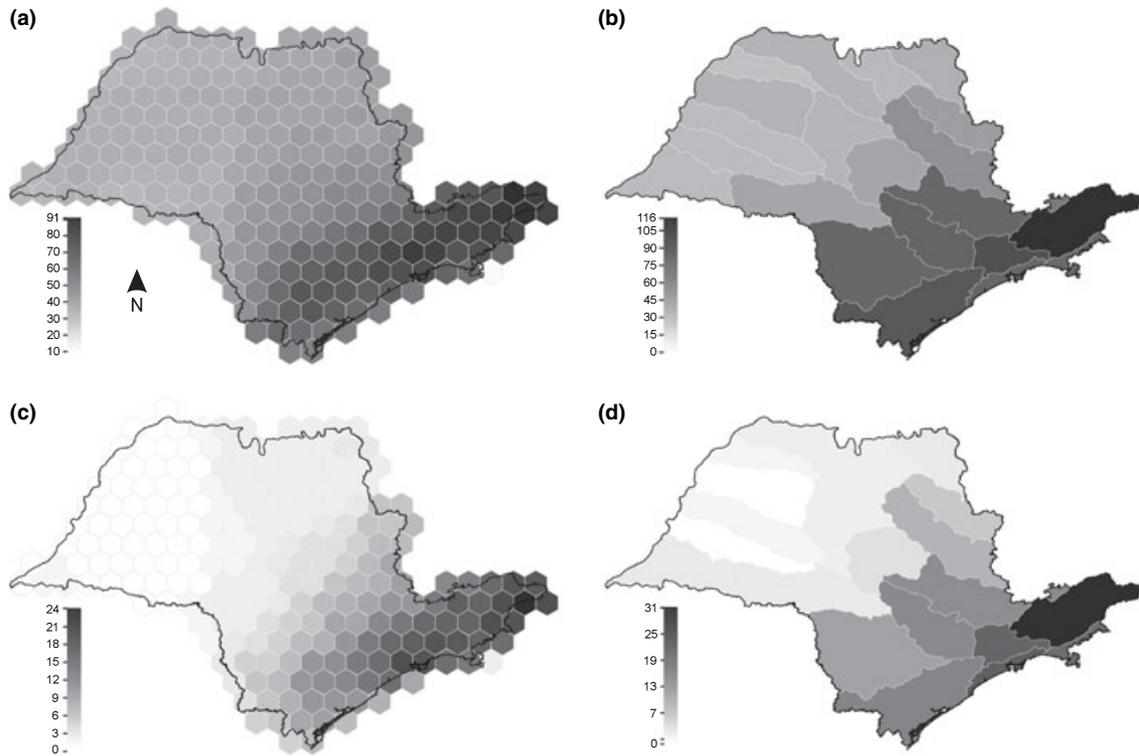


Figure 2 Patterns of species richness for species with aquatic larvae (a, b) and terrestrial development (c, d). Scale represents number of species.

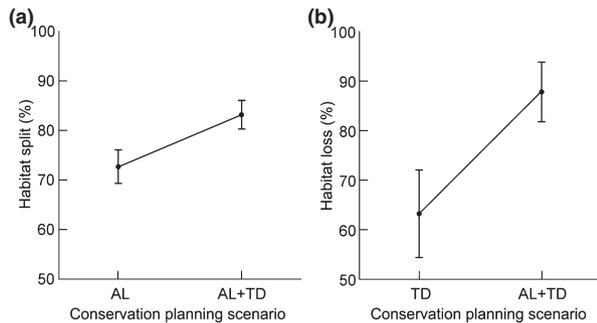


Figure 3 (a) Mean habitat split found within high-priority grid cells (>90% selection frequency) under two conservation planning scenarios; AL considered only species with aquatic larvae; AL + TD considered all species at the same time. All conservation planning scenarios aimed at minimizing habitat split within the landscape. (b) Mean habitat loss found within high-priority grid cells under two conservation planning scenarios; TD considered only species with terrestrial development; AL + TD considered all species at the same time. All conservation planning scenarios aimed at minimizing habitat loss within the landscape.

coastal region (Fig. 4g, h). Species with direct or indirect terrestrial development will be most protected by preserving grids in eastern parts of the state and some isolated areas in the northeast (Fig. 4i, j). These results were independent of the scale of analyses.

After taking into consideration the grid cells already protected in state and national parks, we found that a substantially smaller number of grid cells is required to complement the original network of protected areas and protect all amphibian species. We detected 17 priority grid cells necessary to represent all species at least once (Fig. 5). Most of the cells protect species with only one (six cells) or two (10 cells) reproductive habitats. We found only one cell representing species with four habitat requirements, thus emphasizing the importance of considering life-history traits in amphibian conservation planning. The highest priority areas for preserving species that breed in flowing and permanent still water were concentrated in the southern regions of the state, while those crucial for species breeding in temporary ponds were concentrated in central and eastern regions (Fig. 5). The highland regions of Serra da Mantiqueira and Serra da Bocaina are key areas for preserving species with a variety of reproductive habitats, including those breeding in flowing and still water as well as breeding by direct and indirect terrestrial development. Species breeding in bromeliads and bamboos were already well represented in protected areas (Fig. 5).

DISCUSSION

One of the largest challenges for tropical conservation biology is to develop methods to accurately prioritize conservation efforts. Our results emphasize that linking information about

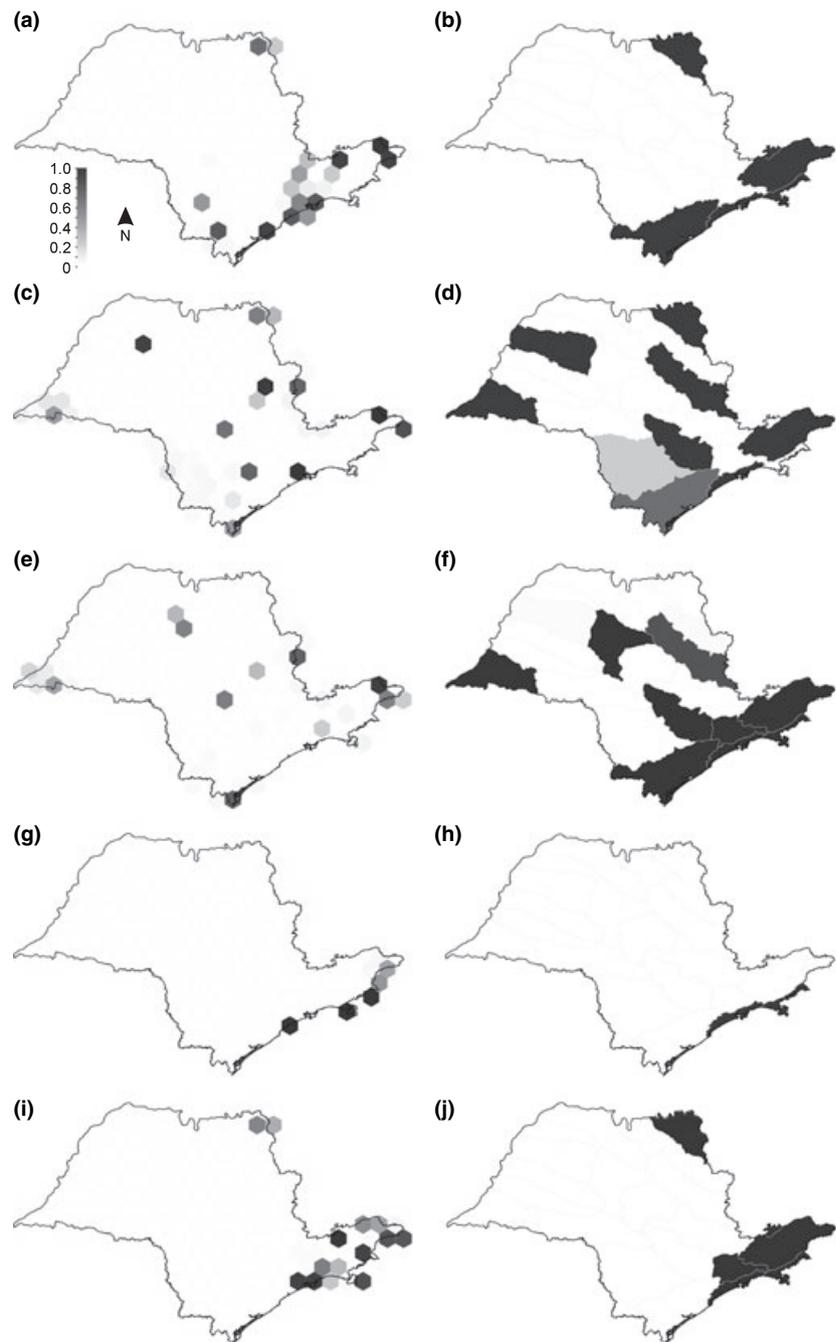


Figure 4 Spatial distribution of grid cells or watersheds revealed by their selection frequency in the 100 solutions obtained for frog species breeding in flowing water – FW (a, b); still water/permanent – SP (c, d); still water/temporary – ST (e, f); Bromeliad or bamboo – BB (g, h) and breeding terrestrially by direct or indirect development – DI (i, j). Scale represents selection frequency.

landscape configuration and species life-history can produce more ecologically relevant amphibian conservation strategies, because developmental mode dictates how species respond to given patterns of deforestation (Becker *et al.*, 2007). Integrating life-history and patterns of deforestation can therefore guide the location and types of habitats to be restored for most efficient biodiversity conservation.

In the state of São Paulo, we found different patterns of distribution of high-priority areas to protect species requiring distinct reproductive habitats, underscoring the importance of considering species-landscape interactions in prioritization efforts (Loyola *et al.*, 2008a). Our results indicate that different

regions will be favoured by distinct restoration plans. Conservation efforts in regions aiming to protect species breeding in flowing and permanent still waters should focus on restoration of riparian buffers, especially in southern coastal regions. These regions are needed to protect species requiring connectivity between aquatic and terrestrial habitats to complete their life cycles. In regions with high habitat split, such as coastal areas of São Paulo (see Fig. 1), amphibians with aquatic larvae often migrate during the wet season from upland forest fragments to streams and permanent ponds in the disturbed valley (Becker *et al.*, 2009). In the dry season, most species seek shelter in the natural terrestrial habitat, forcing species to move to upland

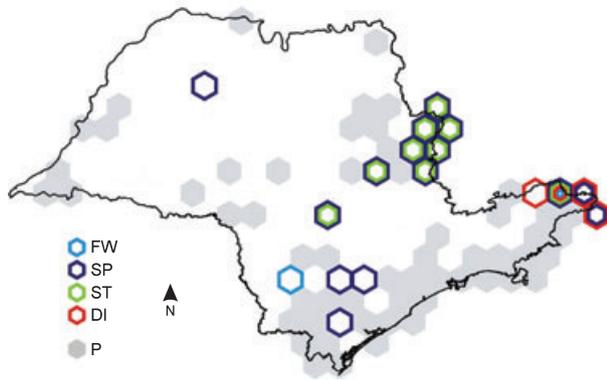


Figure 5 Spatial distribution of priority area sets revealed incorporating grid cells with protected areas (IUCN I–IV categories) higher than 300 ha – P (grey). Reproductive habitats as follows: flowing water – FW (light blue), still water/permanent – SP (dark blue), still water/temporary – ST (green), terrestrial by direct or indirect development – DI (red).

forest fragments and exposing them to the multiple hazards of unnatural migrations (Becker *et al.*, 2009). In contrast, priority areas aiming to protect species with terrestrial development should focus on restoration of forested habitats. In the Brazilian Atlantic Forest, many species with terrestrial development can avoid crossing disturbed open habitats because they have lower dependence on surface waters for reproduction (Haddad & Prado, 2005). However, this reduced migration along fragmented landscape can result in isolated and patchy populations that will be more prone to the negative effects of inbreeding and bottlenecks (Peakall & Lindenmayer, 2006; Dixo *et al.*, 2009). For species with direct and indirect terrestrial development, corridors among large forest fragments and safeguarding large forest preserves will be the most effective conservation strategy. In addition, the fact that all species breeding in bromeliads and bamboo stems are represented in forests inside protected parks underscores the need for strict enforcement of laws protecting these northern coastal reserves (see Fig. 4g, h).

Our results corroborate previous studies showing the importance of explicitly accounting for the existing protected-area networks in defining priorities for future conservation efforts. Once we considered protected areas in our analyses, fewer additional grid cells were required to complement the established reserve network in the state of São Paulo. The hottest ‘hotspot’ for amphibian conservation in the state includes segments of the Serra da Mantiqueira and Serra da Bocaina mountain ranges in southeastern São Paulo. In this region, we found four priority grid cells for conserving species with a variety of reproductive habitats (see Fig. 4). Our results show that amphibians of São Paulo would benefit from new protected areas along Serra da Mantiqueira, where continuous natural habitat is needed to safeguard endemic species with a variety of habitat requirements.

Not surprisingly, most grid cells and watersheds with high selection frequency cluster in regions with high species

richness that also coincide with historical habitat stability (Carnaval & Moritz, 2008; Carnaval *et al.*, 2009), underscoring how unique patterns of diversification in this area also impact prioritization decisions. Prioritization studies at different spatial scales and using alternative biogeographical units of analysis can sometimes produce contrasting outcomes (Larsen & Rahbek, 2003), yet our results revealed the same patterns and priorities based on grid cells and watersheds. Much of the debate on the biases due to spatial scale has focused on the accuracy of predicting biodiversity patterns (Rahbek & Graves, 2001), whereas less attention has focused on issues of scale in conservation planning (Larsen & Rahbek, 2003). Our results indicate that it should be possible to use larger geographical units, such as watersheds or ecoregions, as a coarse filter for establishing conservation priorities (Loyola *et al.*, 2008b) in other regions of the Atlantic Forest. Because the priority areas obtained using different geographical units were spatially congruent, larger units could be identified first using landscape features that naturally delimit regions of biodiversity, and then scaled-up to higher resolution to produce targeted conservation proposals.

Prioritization analyses should be considered indicative of the potential efficacy of future conservation efforts, rather than prescriptive (Valenzuela-Galvan & Vazquez, 2008). These analyses will be most useful to conservation planners as a means of assessing potential costs in achieving particular conservation goals. The identification of a comprehensive set of natural areas is only the first step toward an *in situ* biodiversity conservation strategy, which requires a more complex process of policy negotiation and implementation (Loyola *et al.*, 2008a). Final decisions should be based on comparing alternatives and considering the interests of all stakeholders (Pressey *et al.*, 1997). Our scenarios are no substitute for this integrated negotiation process, but they are part of a wide-ranging effort (Soutullo *et al.*, 2008) to strengthen the scientific basis for conservation decisions.

Our study is novel in its attempt to assess conservation needs independently for frogs with different life-history traits. In a previous work (Becker *et al.*, 2007) we clearly demonstrated that mechanisms of endangerment are different for aquatic and terrestrial breeding amphibians, and we show here that taking those mechanisms into account influences the optimum prioritization scheme and restoration targets (see also Loyola *et al.*, 2008a). After restoration, continued monitoring of the outcome of conservation efforts should help us identify further specific biological characteristics that provide maximum returns for conservation (Margules & Pressey, 2000). Because species vary in their conservation requirements, evidence-based conservation decisions are necessary to take into account the multiple characteristics that might be ecologically relevant (Svancara *et al.*, 2005).

The coastal region of São Paulo, where deforestation is more prevalent in riparian zones, harbours not only the majority of irreplaceable areas but also the highest species richness. The majority of cells with high selection frequency in this region

protect species with aquatic larvae. This result illustrates why habitat split should be considered in restoration programmes for the Brazilian Atlantic Forest, to curb deforestation that specifically occurs in riparian zones (Fig. 1). If current legislation protecting riparian vegetation were adequately enforced (Brazilian Forest Code 4771/65), the degree of habitat split for amphibians would be low in the State of São Paulo, even under scenarios of substantial habitat loss. Preventing further habitat split may help safeguard the majority of amphibian species in this diverse region because most (80%) anurans recorded in the state have aquatic larvae.

Preservation of riparian forests is an important step for biodiversity conservation more generally, and not only for amphibians. Riparian zones mitigate the effects of deforestation on other organisms such as fishes (Lorion & Kennedy, 2009), birds (Smith *et al.*, 2008) and invertebrates (Sweeney *et al.*, 2004). Forested riparian zones provide allochthonous organic matter inputs (e.g., large woody debris, leaf litter, terrestrial insects and vertebrates) that serve as food and habitat for stream organisms (Sweeney, 1993), provide shade that moderates water temperature (Abell *et al.*, 2007) and maintain stream channel features (Sweeney *et al.*, 2004). The fact that forested riparian zones also filter sediments, nutrients and pollutants from agricultural runoff (Osborne & Kovacic, 1993) make the preservation and restoration of these habitats a general priority.

Habitat loss figures prominently in global conservation assessments (see Brooks *et al.*, 2006), but additional attention to the spatial configuration of both terrestrial and aquatic habitats will improve the design of reserve networks for amphibian conservation at the regional scale (Crawford & Semlitsch, 2007; Gardner *et al.*, 2007). Legal requirements to maintain forest cover within riparian zones combined with the need to maintain access to sources of clean water present a good opportunity to work with landowners to enhance amphibian conservation strategies in fragmented landscapes. A lack of careful land-use planning in many countries has led to the disproportionate destruction of riparian vegetation, causing a drastic reduction in the availability and quality of water (Sweeney *et al.*, 2004). As a consequence, water is becoming a scarce resource for a wide range of organisms, including humans (Daily, 1997). Our results highlight the importance of curbing further habitat split, because once it occurs only extensive restoration programmes (Wuethrich, 2007) will reverse its negative impacts. In the Brazilian Atlantic Forest, conserving forested habitats, but also considering connectivity among terrestrial and aquatic habitats will be necessary to design effective conservation strategies to safeguard its megadiverse and imperiled fauna.

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REFERENCES

- Abell, R., Allan, J.D. & Lehner, B. (2007) Unlocking the potential of protected areas for freshwaters. *Biological Conservation*, **134**, 48–63.
- Alves, A.C.R., Sawaya, R.J., dos Reis, S.F. & Haddad, C.F.B. (2009) New species of *Brachycephalus* (Anura: Brachycephalidae) from the Atlantic Rain Forest in Sao Paulo State, Southeastern Brazil. *Journal of Herpetology*, **43**, 212–219.
- Araújo, O.G.S., Toledo, L.F., Garcia, P.C.A. & Haddad, C.F.B. (2009) The amphibian assemblage of São Paulo State, Brazil. *Biota Neotropica*, in press.
- Becker, C.G., Fonseca, C.R., Haddad, C.F.B., Batista, R.F. & Prado, P.I. (2007) Habitat split and the global decline of amphibians. *Science*, **318**, 1775–1777.
- Becker, C.G., Fonseca, C.R., Haddad, C.F.B. & Prado, P.I. (2009) Habitat split as a mechanism for local population declines of amphibians with aquatic larvae. *Conservation Biology*, DOI: 10.1111/j.1523-1739.2009.01324.x
- Bell, K.E. & Donnelly, M.A. (2006) Influence of forest fragmentation on community structure of frogs and lizards in northeastern Costa Rica. *Conservation Biology*, **20**, 1750–1760.
- Brooks, T.M., Mittermeier, R.A., Fonseca, G.A.B., Gerlach, J., Hoffman, M., Lamoreaux, J.F., Mittermeier, C.G., Pilgrim, J.D. & Rodrigues, S.L. (2006) Global biodiversity conservation priorities. *Science*, **313**, 58–61.
- Carnaval, A.C. & Moritz, C. (2008) Historical climate modelling predicts patterns of current biodiversity in the Brazilian Atlantic forest. *Journal of Biogeography*, **35**, 1187–1201.
- Carnaval, A.C., Hickerson, M.J., Haddad, C.F.B., Rodrigues, M.T. & Moritz, C. (2009) Stability predicts genetic diversity in the Brazilian Atlantic Forest hotspot. *Science*, **323**, 785–789.
- Crawford, J.A. & Semlitsch, R.D. (2007) Estimation of core terrestrial habitat for stream-breeding salamanders and delineation of riparian buffers for protection of biodiversity. *Conservation Biology*, **21**, 152–158.
- Daily, G.C. (1997) *Nature's services: societal dependence on natural ecosystems*. Island, Washington, DC.
- Dixo, M., Metzger, J.P., Morgante, J.S. & Zamudio, K.R. (2009) Habitat fragmentation reduces genetic diversity and connectivity among toad populations in the Brazilian Atlantic Coastal Forest. *Biological Conservation*, **142**, 1560–1569.
- ESRI. (2008) *ArcView 9.3*. Redlands, CA.
- Eterovick, P.C., Carnaval, A., Borges-Nojosa, D.M., Silvano, D.L., Segalla, M.V. & Sazima, I. (2005) Amphibian declines in Brazil: an overview. *Biotropica*, **37**, 166–179.
- Ezard, T.H.G. & Travis, J.M.J. (2006) The impact of habitat loss and fragmentation on genetic drift and fixation time. *Oikos*, **114**, 367–375.

- Gardner, T.A., Barlow, J. & Peres, C.A. (2007) Paradox, presumption and pitfalls in conservation biology: the importance of habitat change for amphibians and reptiles. *Biological Conservation*, **138**, 166–179.
- Gascon, C., Lovejoy, T.E., Bierregaard, R.O., Malcolm, J.R., Stouffer, P.C., Vasconcelos, H.L., Laurance, W.F., Zimmerman, B., Tocher, M. & Borges, S. (1999) Matrix habitat and species richness in tropical forest remnants. *Biological Conservation*, **91**, 223–229.
- Gregory, S.V., Swanson, F.J., Mckee, W.A. & Cummings, K.W. (1991) An ecosystem perspective of riparian zones. *BioScience*, **41**, 540–551.
- Haddad, C.F.B. & Prado, C.P.A. (2005) Reproductive modes in frogs and their unexpected diversity in the Atlantic Forest of Brazil. *BioScience*, **55**, 207–217.
- Heyer, W.R., Rand, A.S., Cruz, C.A. & Peixoto, O.L. (1988) Decimations, extinctions, and colonizations of frog populations in southeast Brazil and their evolutionary implications. *Biotropica*, **20**, 230–235.
- IBGE (1985) *Topographic maps 1:50,000*. Instituto Brasileiro de Geografia e Estatística, Brasília, Brazil.
- Instituto Florestal/Secretaria do Meio Ambiente, Programa Biota/FAPESP, Centro de Referência em Informação Ambiental (2004) Mapa de Vegetação Remanescente do Estado de São Paulo.
- IUCN, Conservation International & NatureServe. (2009) Global Amphibian Assessment. Cambridge, UK. Available at: <http://www.iucnredlist.org/amphibians> (accessed 1 May 2009).
- Kirkpatrick, J.B. (1983) An iterative method for establishing priorities for the selection of nature reserves – an example from Tasmania. *Biological Conservation*, **25**, 127–134.
- Larsen, F.W. & Rahbek, C. (2003) Influence of scale on conservation priority setting – a test on African mammals. *Biodiversity and Conservation*, **12**, 599–614.
- Leslie, H., Ruckelshaus, M., Ball, I.R., Andelman, S. & Possingham, H.P. (2003) Using siting algorithms in the design of marine reserve networks. *Ecological Applications*, **13**, 185–198.
- Lorion, C.M. & Kennedy, B.P. (2009) Riparian forest buffers mitigate the effects of deforestation on fish assemblages in tropical headwater streams. *Ecological Applications*, **19**, 468–479.
- Loyola, R.D., Becker, C.G., Kubota, U., Haddad, C.F.B., Fonseca, C.R. & Lewinsohn, T.M. (2008a) Hung out to dry: choice of priority ecoregions for conserving threatened Neotropical anurans depends on life-history traits. *PLoS ONE*, **3**, e2120.
- Loyola, R.D., Oliveira, G., Diniz-Filho, J.A.F. & Lewinsohn, T.M. (2008b) Conservation of neotropical carnivores under different prioritization scenarios: mapping species traits to minimize conservation conflicts. *Diversity and Distributions*, **14**, 949–960.
- Margules, C.R. & Pressey, R.L. (2000) Systematic conservation planning. *Nature*, **405**, 243–253.
- Mittermeier, R.A., Gil, P.R., Hoffman, M. et al. (2005) *Hotspots revisited: Earth's biologically richest and most endangered terrestrial ecoregions*. University of Chicago Press, Chicago.
- Morellato, P. & Haddad, C.F.B. (2000) Introduction: the Brazilian Atlantic Forest. *Biotropica*, **32**, 786–792.
- Osborne, L.L. & Kovacic, D.A. (1993) Riparian vegetated buffer strips in water-quality restoration and stream management. *Freshwater Biology*, **29**, 243–258.
- Peakall, R. & Lindenmayer, D. (2006) Genetic insights into population recovery following experimental perturbation in a fragmented landscape. *Biological Conservation*, **132**, 520–532.
- Pimenta, B.V.S., Napoli, M.F. & Haddad, C.F.B. (2009) A new species of casque-headed tree frog, genus *Aparasphenodon* Miranda-Ribeiro (Amphibia: Anura: Hylidae), from the Atlantic Rainforest of southern Bahia, Brazil. *Zootaxa*, **2123**, 46–54.
- Pope, S.E., Fahrig, L. & Merriam, N.G. (2000) Landscape complementation and metapopulation effects on leopard frog populations. *Ecology*, **81**, 2498–2508.
- Possingham, H., Ball, I. & Andelman, S. (2000) Mathematical methods for identifying representative reserve networks. *Quantitative methods for conservation biology* (ed. by S. Ferson and M. Burgman), pp. 291–306. Springer-Verlag, New York.
- Pressey, R.L., Possingham, H.P. & Margules, C.R. (1996) Optimality in reserve selection algorithms: when does it matter and how much? *Biological Conservation*, **76**, 259–267.
- Pressey, R.L., Possingham, H.P. & Day, J.R. (1997) Effectiveness of alternative heuristic algorithms for identifying indicative minimum requirements for conservation reserves. *Biological Conservation*, **80**, 207–219.
- Rahbek, C. & Graves, G.R. (2001) Multiscale assessment of patterns of avian species richness. *Proceedings of the National Academy of Sciences of the United States of America*, **98**, 4534–4539.
- Ribeiro, M.C., Metzger, J.P., Martensen, A.C., Ponzoni, F. & Hirota, M. (2009) Brazilian Atlantic Forest: how much is left and how is the remaining forest distributed? Implications for conservation. *Biological Conservation*, **142**, 1141–1153.
- Rodrigues, R.R., Lima, R.A.F., Gandolfi, S. & Nave, A.G. (2009) On the restoration of high diversity forests: 30 years of experience in the Brazilian Atlantic Forest. *Biological Conservation*, **142**, 1242–1251.
- Silva, W.G., Simões, J.P.S. & Simonetti, C. (2007) Relief influence on the spatial distribution of the Atlantic Forest cover on the Ibiúna Plateau, SP. *Brazilian Journal of Biology*, **67**, 403–411.
- Smith, T.A., Osmond, D.L., Moorman, C.E., Stucky, J.M. & Gilliam, J.W. (2008) Effect of vegetation management on bird habitat in riparian buffer zones. *Southeastern Naturalist*, **7**, 277–288.
- Soutullo, A., De Castro, M. & Urios, V. (2008) Linking political and scientifically derived targets for global biodiversity conservation: implications for the expansion of the global network of protected areas. *Diversity and Distributions*, **14**, 604–613.
- Svancara, L.K., Brannon, R., Scott, J.M., Grooves, C.R., Noss, R.F. & Pressey, R.L. (2005) Policy-driven versus evidence-

- based conservation: a review of political targets and biological needs. *BioScience*, **55**, 989–995.
- Sweeney, B.W. (1993) Effects of streamside vegetation on macroinvertebrate communities of white clay creek in eastern north-america. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **144**, 291–340.
- Sweeney, B.W., Bott, T.L., Jackson, J.K., Kaplan, J.D., Newbold, J.D., Standley, W.C., Hession, W.C. & Horwitz, R.J. (2004) Riparian deforestation, stream narrowing, and loss of stream ecosystem services. *Proceedings of the National Academy of Sciences*, **101**, 14132–14137.
- Tocher, M.D., Gascon, C. & Meyer, J. (2001) Community composition and breeding success of Amazonian frogs in continuous forest and matrix habitat aquatic sites. *Lessons from Amazonia: the ecology and conservation of a fragmented forest* (ed. by R.O. Bierregaard Jr, C. Gascon, T.E. Lovejoy and R.C.G. Mesquita), pp. 235–247. Yale University Press, New Haven.
- Urbina-Cardona, J.N., Olivares-Perez, M. & Reynoso, V.H. (2006) Herpetofauna diversity and microenvironment correlates across a pasture-edge-interior ecotone in tropical rainforest fragments in the Los Tuxtlas Biosphere Reserve of Veracruz, Mexico. *Biological Conservation*, **132**, 61–75.
- Valenzuela-Galvan, D. & Vazquez, L.-B. (2008) Prioritizing areas for conservation of Mexican carnivores considering natural protected areas and human population density. *Animal Conservation*, **11**, 215–223.
- Viana, V.M., Tabanez, A.A.J. & Batista, J.L. (1997) Restoration and management of fragmented landscapes. *Tropical forest remnants: ecology, management and conservation of fragmented communities* (ed. by W.F. Laurance and R.O. Bierregaard), pp. 347–365. University of Chicago Press, Chicago.
- Werner, E.E. & Gilliam, J.F. (1984) The ontogenetic niche and species interactions in size structured populations. *Annual Review of Ecology Evolution and Systematics*, **15**, 393–425.
- Weygoldt, P. (1989) Changes in the composition of mountain stream frog communities in the Atlantic mountains of Brazil: frogs as indicators of environmental deterioration? *Studies on Neotropical Fauna and Environment*, **243**, 249–255.
- Wuethrich, B. (2007) Biodiversity – reconstructing Brazil's Atlantic rainforest. *Science*, **315**, 1070–1072.

BIOSKETCH

Gui Becker has a background in natural history, landscape ecology and macroecology. His main research is understanding how host–pathogen dynamics respond to anthropogenic habitat disturbances, and uses geographic information system as a tool to investigate how habitat alteration affects disease and population dynamics of wild animals. Gui extends his work to conservation biogeography, especially identifying priority areas for amphibian conservation in the Neotropics.

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