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Research Letters

Time-lags in primate occupancy: a study case using dynamic models



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ABSTRACT

Species response to land-use changes are usually assessed by investigating factors affecting distribution, with a single snapshot in time. However, several processes can lead to a same pattern. Focusing on observed, short-term patterns limits our ability to make inferences about ecological processes and responses to environmental change over time. In this study, we assessed changes in occupancy of two primate species in southeastern Brazil, following a major habitat loss due to implementation of a hydroelectric dam. Occupancy was assessed before dam construction and 11 years after, while explicitly accounting for imperfect detection. We assessed the effect of forest patch size and isolation on occupancy and rates of extinction and colonization, driven by landscape modification. Then we calculated occupancy under metapopulation equilibrium and expected time-lags resulting from non-equilibrium. We compared two primate species inhabiting forest patches, the black penciled marmoset *Callithrix penicillata* and the black-fronted titi monkey *Callicebus nigrifrons*, with markedly different ecological characteristics. Those differences may explain why occupancy dynamics were driven by distinct elements. A fast response to habitat changes was observed only for marmoset, an opportunistic species. However, non-equilibrium states and the possibility of time-lag effects were observed for titi monkey, a species dependent on forest habitat. Our analyses support the need to establish long term monitoring and assess system vital rates over time. A single snapshot in time may lead to erroneous interpretations of a species response to habitat alteration.

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Introduction

Appearances can be deceiving. A site that currently hosts high biodiversity may not provide sufficient conditions for long-term persistence of species. Although habitat loss and land-use changes are the main causes of local extinctions in the tropics, species extinction may not be immediate (Hanski, 2013; Hylander and Ehrlén, 2013). When habitat loss is sudden, there may be a time-lag before extinction and colonization dynamics reach a new equilibrium with current habitat distribution – non-equilibrium dynamics (Krauss et al., 2010; Ovaskainen and Hanski, 2002; Tilman et al., 1994). As consequence, sometime after disturbance some species may be found in fragments where persistence is unlikely, even with no further land use change (the so-called “extinction debt”) (Hanski, 2000; Tilman et al., 1994).

A snapshot in time may therefore be a misleading representation of the capacity of a site to sustain biodiversity in long term (Krauss et al., 2010; Metzger et al., 2009; Vellend et al., 2013). Monitoring over time is therefore required for assessing effects of land use changes on local dynamics (Hanski, 2013). One way to monitor species persistence in fragmented landscapes is modeling extinction and colonization rates of habitat patches, using metapopulation theory. Metapopulation models link the proportion of occupied habitat patches to local extinction and colonization rates (Hanski, 1998, 2000). In a monitoring context, the rate of change in proportion of occupied patches is an important indicator of species viability (Ovaskainen and Hanski, 2002). Furthermore, assessing occupancy trends over time also enables focusing on mechanisms underlying site occupancy dynamics (Hylander and Ehrlén, 2013; Kuussaari et al., 2009; MacKenzie et al., 2003).

In this paper, we assessed the main drivers of changes in occupancy of two primate species, the black penciled marmoset *Callithrix penicillata* and the black-fronted titi monkey *Callicebus nigrifrons*. New World marmosets of genus *Callithrix* are a small-bodied (<500 g) group of monkeys that play a unique role in forests of Central and South America, because they are specialized on tree gouging and feeding on gum exudates (Rylands et al., 2009). Marmosets also have high reproductive rates (usually twins, twice a year), early sexual maturity (around one year old), and are relatively short-lived (up to 10 years in wildlife) (Mittermeier et al., 2013; Mustoe et al., 2012).

Marmoset small body size, rapid reproductive rates and systematic exploitation of plant exudates allow them to occupy several habitat types, even relatively inhospitable environments (Rylands et al., 2009). Indeed, black-penciled marmoset is not only able to tolerate habitat fragmentation, but is usually found in disturbed and secondary forests and also edge habitats (Kinzey, 1997; Vilela and Del-claro, 2011), being listed as “Least Concern (LC)” by IUCN Red List (www.iucn.org).

Titi monkeys of genus *Callicebus* have larger body size (1–2 kg) (Roosmalen et al., 2002), slower reproduction rates and longer generation times, compared to marmosets (Kinzey, 1997). Female first birth happens at around 3.7 ± 1.3 years, breeding females give birth to a single offspring annually

(Valeggia et al., 1999), and they live up to 25 years (Mittermeier et al., 2013).

Black-fronted titi monkey (*C. nigrifrons*) originally had a wide distribution in Brazilian Atlantic forest and Cerrado. However, fragmentation and urbanization of forests within its range caused remaining populations to be isolated and generally small (Roosmalen et al., 2002). Due to 20–25% population declines in past 25 years, black-fronted titi monkey is listed as “Near Threatened (NT)” by IUCN Red List.

We created a sampling scheme that allowed us to infer the effect of a massive land use change in southeastern Brazil – the implementation of a hydroelectric reservoir (Fig. S1) – on primates’ occupancy, extinction and colonization probabilities. The effect of forest patch size and connectivity on extinction and colonization dynamics was also assessed. We tested the following hypothesis: (1st) time-lags can be found if observed occupancy is different from equilibrium expectations; (2nd) the faster a species responds to environmental disturbances, the less we expect it to exhibit time-lags; (3rd) occupancy is determined by patch size and/or connectivity in a positive relation; (4th) reductions in size and/or connectivity increase extinction and reduce colonization rates.

Materials and methods

Sampling design and occupancy models

Single-season occupancy models estimate the probability that a site is occupied by a species during a short time interval, given that species is detected imperfectly (MacKenzie et al., 2002). In a single-season sampling scheme, a number n of sites are repeatedly visited on T sampling occasions. Detection/non-detection of species on each sampling occasion will result in survey histories for each sampled site. For example, ‘110’ indicate that species was detected at first and second occasion, but not at third. A model based on survey histories for each site is performed using probabilistic arguments so that occupancy and detection parameters (ψ and p) are estimated via maximum-likelihood or Bayesian procedures (MacKenzie et al., 2006).

The simplest way to verify whether a population is in equilibrium with current landscape is to compare occupancy fit to present-day vs past landscape (Kuussaari et al., 2009). Time-lags can then be assumed if species distribution is best described by past rather than present landscape features (Kuussaari et al., 2009). That combination of historical and contemporary data sources has been considered a reliable way to infer about long term effects of habitat disturbances (Kuussaari et al., 2009; Vellend et al., 2013). Therefore, to test for existence of time-lag effects, we modeled current occupancy as function of patch size and connectivity before vs after habitat loss (Fig. 1).

However, inferring ecological processes (extinction and colonization dynamics) from patterns (site occupancy) may not be reliable because several processes can produce the same pattern (MacKenzie et al., 2003). Observed patterns of landscape occupancy can result from non-equilibrium dynamics and hide decreasing population trends, for example. Therefore, changes in occupancy can only be assessed when

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