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Forest recovery in post-pasture Amazonia: Testing a conceptual model of space use by insectivorous understory birds

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ABSTRACT

Understanding how animals move in a complex habitat mosaic is critical to biodiversity conservation as deforested lands and secondary rainforests accumulate in landscapes previously dominated by primary forests. To visualize the spatiotemporal dynamics of secondary forest recovery after pasture abandonment, we formed a conceptual model predicting avian space use during a temporal sequence beginning with deforestation and continuing through regrowth of old secondary forest. We tested five predictions of the model at the Biological Dynamics of Forest Fragments Project near Manaus, Brazil, using 73 radio-tagged understory insectivores of three species: two woodcreepers (*Glyphorynchus spirurus*, *Xiphorhynchus pardalotus*) and a terrestrial antthrush (*Formicarius colma*). Both woodcreepers provided evidence to support all predictions except that of greater path tortuosity in primary forest. Woodcreepers using secondary forest had larger home ranges, larger core areas, and faster movement rates than in primary forest. Further, the proportion of all species' core areas in primary forest exceeded the proportion of home ranges in primary forest. *Formicarius colma* showed a fundamentally different pattern than the woodcreepers: it essentially avoided secondary forest until 27–31 years after pasture abandonment, at which point movements were indistinguishable from those in primary forest. *Formicarius colma* and other terrestrial insectivores show implastic spatiotemporal responses to recovering secondary growth, which we suspect contributes to the sensitivity of this guild to forest disturbance. Quantifying the value of marginal (and economically inconsequential) habitats such as secondary forest will be essential as land managers strive to maintain species persistence and connectivity in increasingly heterogeneous tropical landscapes.

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1. Introduction

Understanding movement patterns of individual animals is particularly important in heterogeneous landscapes because the accumulation of individuals' movements ultimately drives source–sink and metapopulation dynamics (Brawn and Robinson, 1996), gene flow and genetic structuring (Bates et al., 2004; Coulon et al., 2004; Riley et al., 2006), and species' persistence in isolated forest fragments (Ferraz et al., 2007; Lens et al., 2002). Detailed studies of individual movement can reveal mechanisms behind the spatiotemporal dynamics of how animals return to recovering landscapes. Specifically, both theoretical and empirical work from temperate ecosystems demonstrate that animals in high-quality habitats rich in resources (e.g., food, cover etc.) have small home ranges and core areas, use areas of high resource availability within home ranges, and move slowly in curvy paths relative to animals able to tolerate lower quality habitats (Arditi and Dacorogna, 1988; Caldwell and Nams, 2006; Fryxell et al., 2008; Vásquez et al., 2002; Ward and Saltz, 1994); however, those patterns are poorly understood for most organisms—particularly in the tropics. On the other hand, in cases where habitat is lost completely and practically no resources remain (e.g., when forest is cut and burned), individuals may disappear entirely. As animals gradually begin to return as the vegetation recovers after a major disturbance, the spatial patterns revealed by metrics of space use should reflect the gradual recovery of the vegetation and associated resources, with those patterns of space use eventually being indistinguishable from those of the original habitat at the point of "recovery" from the perspective of animal space use. The better we can develop a mechanistic understanding of spatiotemporal dynamics of how animals return to habitat after disturbance events, the better our ability to manage these lands for biodiversity conservation in this era of rapid anthropogenic change.

One region suffering egregious anthropogenic change recently is the Amazon Rainforest. Over the last 20 years, the Brazilian Amazon, comprising about 60% of the entire Amazon, has had more than 300,000 km^2 of rainforest cut and abandoned or converted to anthropogenic land uses, representing an area larger than Poland (Brazilian National Space Research Institute (INPE), 2010). Although deforestation

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rates in the Brazilian Amazon have slowed since 2005, in large part because of moratoriums on forest clearing for soy (in 2006; Rudorff et al., 2011) and beef (in 2009; Boucher, 2011), it continues to lose 7000 km^2 per year (Brazilian National Space Research Institute (INPE), 2010). However, not all deforested lands remain as such; in the eastern and central Brazilian Amazon, the typical post-deforestation pattern has been abandonment either immediately, or about five years after conversion to cattle pastures, whereupon the transition from pasture to secondary forest begins (Fearnside, 2005). In the Brazilian Amazon alone the area of secondary forest increased from 29,000 to 161,000 km^2 from 1978 to 2002 alone (Neeff et al., 2006). These vast expanses of secondary forests in Amazonia present an opportunity for conservation, yet our understanding of their value for wildlife is poor and their conservation value is still debated, in part because there are few empirical studies in secondary growth (Brook et al., 2006; Wright and Muller-Landau, 2006a, 2006b).

Space use by insectivorous understory birds should be a particularly useful indicator of intact ecological processes within primary and secondary rainforests because this community is diverse, relatively easy to sample, sensitive to forest fragmentation and often specialized on high-quality forest (Barlow et al., 2007; Sekercioglu et al., 2002; Stouffer and Bierregaard, 1995). A mechanistic understanding of when and how insectivorous birds return to regenerating secondary forests is in its infancy; however, two recent studies from our study site at the Biological Dynamics of Forest Fragments Project (BDFFP) revealed that Amazonian birds do eventually return to rainforest following

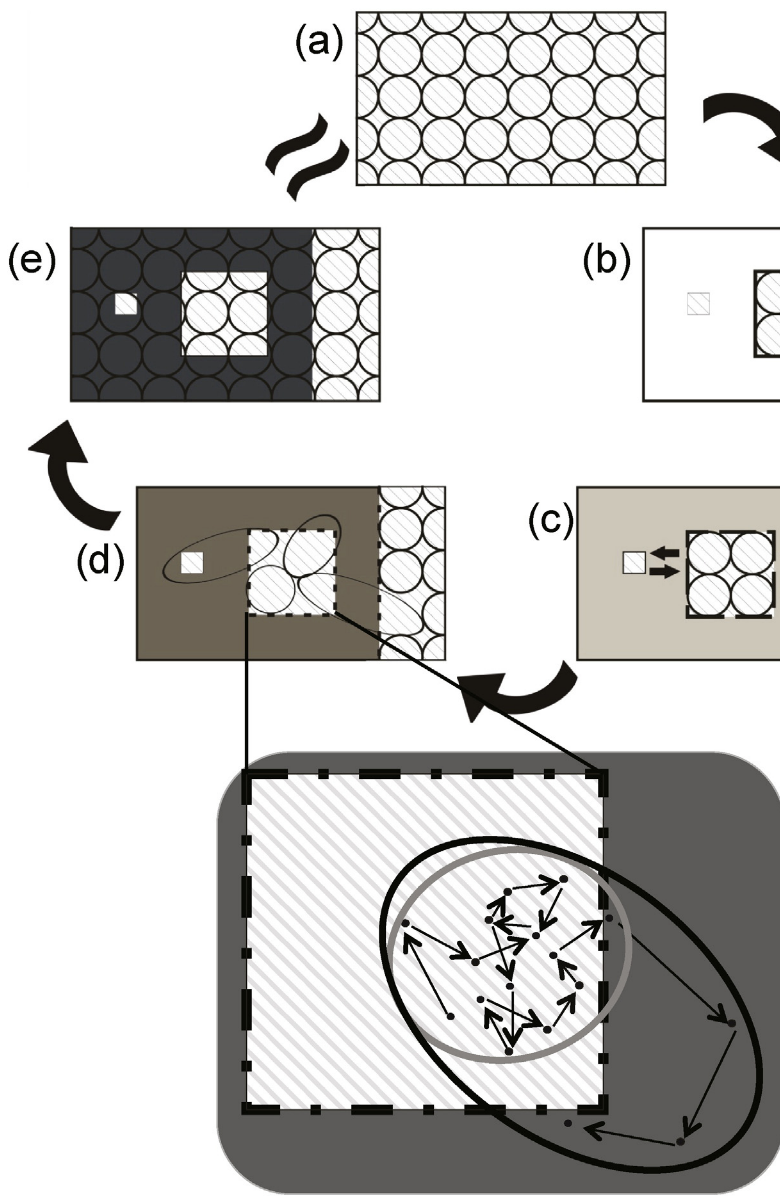

Fig. 1. Conceptual model illustrating dynamics of avian territories and movement during recovery of secondary forest following deforestation and fragmentation. Ellipses represent resident bird territories for a hypothetical species ubiquitous in primary forest, diagonally hatched fill represents primary forest and increasingly dark solid shading (white to dark gray) represents increasingly old secondary forest. Thick black lines representing the edges of primary forest are dashed relative to permeability of the edge. As continuous forest (a) is initially cut (b), birds are entirely excluded from the recently cut area and entirely restricted to forest fragments. At this point, home range boundaries are aligned along the interface and birds are excluded from fragments too small to sustain their home ranges. During early regrowth (c), increased vertical structuring of the young secondary forest permits some movement (e.g., dispersal) across secondary forest—some individuals may occasionally use small fragments. As secondary forest matures and begins to recover resources (d), birds begin to expand their territories into secondary forest and small fragments, showing increased rates of movement across the interface. At the point of recovery (e), bird territory boundaries and cross-interface movements are indistinguishable from those in primary forest, regardless of fragment size. In the close-up of (d), a higher proportion of the animal's core area (gray ellipse) is within primary forest, whereas the overall home range (black ellipse) contains a higher proportion of secondary forest. Here individual bird movements (thin arrows) show that birds in primary forest move in short, curvy (i.e. high tortuosity) paths; conversely, movements in secondary forest are straighter (i.e. low tortuosity) and longer, so movement rate is relatively high.