

RESPONSE

Using occupancy estimates to fine-tune conservation concerns

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Our study (Sberze *et al.*, 2010) combined three personal contributions: a professor's (M. C.-H.) experience in neotropical ornithology, a post-doc's (G. F.) practice with occupancy estimation, and a graduate student's (M. S.) interest in nocturnal birds. The work was developed in the Biological Dynamics of Forest Fragments Project (BDFFP), a 30-year landscape manipulation experiment focused on biological change in artificially isolated forest patches created by forest clearing in the early 1980s (Laurance *et al.*, 2002). Circumstances beyond control of the BDFFP led to gradual abandonment of cleared land and subsequent growth of *c.* 30 km² of secondary forest (SF) surrounded by old growth (OG) and embedding the experimental patches. Our occupancy study of nocturnal birds was at once an effort to take advantage of unplanned secondary growth (as accurately pointed out in Sekercioglu's commentary) and a contribution to the ongoing debate about the conservation value of SF (Laurance & Wright, 2009). We are grateful to the editors of *Animal Conservation* for featuring our paper and to Ken Feeley, Çagan Sekercioglu and Daisy Dent for their kind and insightful commentaries. We aim this reply at clarifying some of our methodological choices and identifying two avenues for future progress.

We believe that our study convincingly illustrates the potential conservation relevance of SF thanks to a set of simple methodological choices. Both abundance and occupancy estimates provide biologically meaningful quantifications of population state. Abundance estimates, however, require mark–recapture or counts of individuals at measurable distances from the observer (Williams, Nichols & Conroy, 2002). Our focus on occupancy was in part due to the difficulties of counting nocturnal birds mentioned by Sekercioglu (2010). At the same time, the occupancy approach provided a sound conceptual basis for comparing different types of land cover and allowed us to replicate sampling at a large and reasonably representative spatial extent. While attempting to cover as much ground as possible on foot, MS had to limit the time per sampling point. This temporal constraint reduced the probability of detecting species at each visit, increasing the importance of explicitly accounting for detection failure in the analyses, which we did. Also due to walking constraints, sampling points had to be relatively close to each other. We addressed this problem by quantifying the influence of occupancy in neighboring points upon occupancy at each focal point (spatial autocorrelation). Since we did not find strong evidence of spatial autocorrelation, the procedure gave us confidence that our sampling

points are not pseudo-replicates. The spatial analysis was our strongest reason to use a Bayesian framework, although Feeley (2010) correctly suggests that we could have further explored the framework by using informative priors. We chose not to do this because we were interested in finding out whether our data revealed *a priori* expectations despite the use of priors that did not convey those expectations.

Although most of our predictions were supported by the data, we were surprised by the general preference for SF over OG among owl species. We suspect that relatively high abundance of rodents in SF may attract owls, but we have no data to back up this explanation. We agree with Feeley (2010) that birds in SF may be in a demographic sink, that is a place where reproduction fails to keep pace with local mortality (Pulliam, 1988). This should inspire caution in the interpretation of results and motivate further investment in life-history study, a need that all commentaries have identified. Dent (2010) is particularly clear about this point, emphasizing how life-history information will help generalizations about what types of species are more or less vulnerable to landscape change. We believe that multi-taxon occupancy studies backed with detailed life-history information should be a major avenue of future progress (Gardner *et al.*, 2009). The challenge resides in how much rigor will be required of life-history assessments. Life history studies are field-intensive and must be conducted one species at a time: more rigor will mean smaller sets of species and more limited contribution to generalization. Progress on this front requires a combination of smart data-mining, conceptual simplicity, and analytical sophistication. Ideally, this should be done without forgetting phylogenies, because species often share more than the life-history traits that we decide to measure (Harvey, 1996; Owens & Bennett, 2000).

Relentless effort in life-history study should be complemented with further development of occupancy studies. This second avenue of progress presents analytical challenges but relatively little additional fieldwork. Recent work by Zipkin, DeWan & Royle (2009) illustrates how multi-taxon models of occupancy developed in a Bayesian framework make it possible to borrow information across species and thus produce inferences about species for which there are relatively few data. Perhaps even more important for the SF–OG comparisons is the infusion of a dynamic perspective in occupancy studies (MacKenzie *et al.*, 2003). Our nocturnal bird study treats OG and SF as static environments for which we estimate average site-occupancy values. It would be desirable to estimate not only the occupancy at a

given point in time but the rate at which occupancy changes – through local extinction and colonization – from time to time in different environments. This is important not only because natural disturbance in OG may lead to short-term changes in occupancy but also because SF is an inherently transient environment. Furthermore, occupancy dynamics may depend not only on the characteristics of a sampling site but also of its surroundings, making it important to understand the spatial context and distribution of SF and OG around a study site (Chazdon *et al.*, 2009).

There is much to learn about the ability of OG species to colonize disturbed habitats, not only in SF but also in urban environments. Throughout over 20 years of observations in the city of Manaus, some 50 km south of our study area, MCH has witnessed the establishment of two nocturnal species typical of open country (*Athene cucularia* and *Rhinoptynx clamator*) and the continued presence of SF species (*Megascops choliba*, *Nyctidromus albicollis*), while several OG species can still be found in increasingly degraded urban fragments (*Pulsatrix perspicillata*, *Nyctibius grandis*, *Lurocalis semitorquatus*, *Caprimulgus nigrescens*). As in the SF, we do not know if this last group sustains populations that will survive without immigration from OG. We hope that our focus on occupancy – the probability that a site is occupied by a species – has contributed some biological substance to the important and already rich debate about the value of SF habitats. We also hope that the future will bring more multi-taxon occupancy studies with strong life-history information, as well as further development of occupancy dynamic studies. The latter point cannot be understated, because SF is by definition a transient type of land cover that, if left alone (or properly managed), may ultimately turn into OG. There is no doubt that continued habitat destruction and degradation will compromise the persistence of many OG species; thus, the sensible management of SF will make a crucial difference.

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