

Predicting the Uncertain Future of Tropical Forest Species in a Data Vacuum

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WHEN SUPPORTED BY SUFFICIENT EVIDENCE, predictive analyses and scenario building can make important contributions towards devising conservation policy strategies. Wright and Muller-Landau (2006a, henceforth termed WMLa) provide a timely analysis that attempts to predict the future of tropical forest species based on human population-driven projections of tropical deforestation. Citing evidence of slowing population growth and rapid urbanization they suggest that deforestation rates are expected to decrease, and natural forest regeneration through secondary succession to accelerate. WMLa use their predictions of an increase in secondary forest area to paint an optimistic picture of the future, going so far as to suggest that the widely anticipated mass extinction of tropical forest species will be avoided (see also Aide & Grau 2004).

Brook *et al.* (2006, henceforth termed BBKS) reject the optimistic predictions of WMLa by reinforcing the importance of a number of original caveats made by WMLa, as well as raising additional objections. BBKS indicate that the relationship between rural and urban population growth and deforestation is too complex to be reliably predicted. They also argue that the negative effects of the heavy momentum set in motion by current patterns of deforestation and population growth (*i.e.*, loss of irreplaceable primary source habitat, *e.g.*, Brooks *et al.* 2002, Brook *et al.* 2003, and extinction debt, Tilman *et al.* 1994) are irreversible before future reductions in deforestation rates are able to rescue committed extinctions.

Despite this criticism Wright and Muller-Landau (2006b, henceforth WMLb) retain confidence in their optimistic projection, arguing that their simulations were robust to variability in the growth of urban versus rural human populations projected by the FAO, which already take into account existing biases in age structure. However, in addition to assumptions regarding human demography and the fate of undisturbed primary forests, the predictions of WMLa rely centrally upon net changes in forest cover and the (explicit) assumption that all types of forest cover can be treated equally—specifically that primary, secondary, and degraded forests can be considered to have *similar ecological value*. Citing a single key

study dealing with faunal recovery following regeneration (Dunn 2004), and three dealing with floristic succession (Turner *et al.* 1997, Chazdon 2003, Lugo & Helmer 2004) WMLa conclude that secondary forests (a) provide a suitable habitat for many species and (b) will provide the necessary haven for species currently restricted to small patches of native habitat. In contrast BBKS argue convincingly that forest quality is more important than total forest area, and that degraded and secondary forests are indisputably depauperate, support significantly fewer old-growth specialists, and provide reduced ecosystem services. WMLb acknowledge the importance of this distinction in stating that “a crucial difference between BBKS and WMLa [in interpreting the implications of WMLa] concerns the conservation value of degraded and secondary forests.”

Secondary forests clearly are an increasingly important component of tropical forest landscapes (Perz & Skole 2003, Wright 2005, FAO 2005), and we welcome the fact that WMLa have highlighted the increasing conservation importance of natural forest regeneration. However, we are concerned that a paper entitled “The Future of Tropical Forest Species” presents very little ecological data on the biodiversity value of naturally regenerating forests in the tropics. In order to evaluate the relative merits of the arguments made by WMLa and WMLb versus BBKS, it is vital that we understand the proportion of species that is completely dependent on old growth forest—a point duly acknowledged by WMLb. Our main purpose in this commentary is to shed some objective light on the strength of the optimistic predictions made by WMLa by assessing our current understanding of the role of secondary forests for the conservation of tropical forest species. To do this we surveyed scientific papers published in international journals which have reported on the value of regenerating lands for four main groups of tropical forest vertebrate: birds, amphibians, reptiles, and primates.

Birds are perhaps the best-known tropical taxa, yet we identified only 15 studies that examined the value of second growth for tropical forest birds. Nine of these 15 studies examined small plots following subsistence agriculture; of these, all were smaller than 5 ha where plot sizes were reported. Only two studies (Borges & Stouffer 1999, Sodhi *et al.* 2005) were in areas of secondary forest larger than 1000 ha. Levels of replication were also very poor, and eight of the

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studies had no replication within treatments. Four studies did not present data from primary forests control. Moreover, comparisons are hindered by differences in methodologies: eight use observations (point counts or transects), four use mist netting, and three combine both methods.

Although existing studies can be used to look at broad response patterns, such as the increase in species richness with forest age (Dunn 2004), they are clearly insufficient to predict the suitability of extensive areas of secondary forest for tropical forest birds. Although most studies of older second growth (*i.e.*, > 8 yr old) record the presence of many species normally associated with primary forest (Bowman *et al.* 1990, Andrade & Rubio-Torgler 1994, Blake & Loiselle 2001, Waltert *et al.* 2004, Borges 2005), the small plot sizes suggest that many of these species recorded in secondary forests may be transients that are routinely subsidized from adjacent primary forest by daily or seasonal movements within a heterogeneous forest mosaic (*e.g.*, Terborgh & Weske 1969, Blake & Loiselle 2001).

We found only 11 studies that examined the value of second growth for amphibians and/or reptiles in the humid tropics. Six of these studies were from the Neotropics, with only one from continental Africa, two from Southeast Asia, and two from elsewhere. The focus of these studies varied widely, with three focusing on abandoned plantation forestry, seven on abandoned agricultural lands, and one on natural regrowth following clear-felling. Only five studies reported the use of an undisturbed primary forest control plot greater than 1000 ha, although all except two had a control greater than 100 ha. All studies failed to report information on the size of the second growth areas sampled, except one where plot size was less than 10 ha (Pawar *et al.* 2004). Six studies had no site-level replication within treatments, and the largest number of independent replicates within a single study was four (Ernst & Rodel 2005). The majority of studies employed active searches to sample herpetofauna, but only three combined data from more than one sampling technique.

As with birds, differences in research focus, sampling design and effort, and sampling methods severely confound our ability to draw firm conclusions from these studies. One general pattern is that between one-half and two-thirds of all species found within primary forest are frequently found in secondary forest younger than 30 yr old (Crump 1971, Lieberman 1986, Tocher *et al.* 2002, Vallan 2002). In addition, studies examining different age-classes of secondary forest indicate that species richness generally increases with age of succession (Bowman *et al.* 1990, Heinen 1992, Pawar *et al.* 2004), although we did not find any studies considering secondary forests older than 35 years. In any case, we currently have no data on the degree to which older secondary forests provide suitable habitat for primary forest specialist species, or whether small plots of second growth can support viable populations and communities in the absence of rescue effects from neighboring primary forest.

In comparison to other vertebrate taxa, primates are well studied and have attracted relatively high conservation attention and investment. However, we found only 11 studies that examined the relative value of secondary growth for primates. Only six studies reported the age of the secondary forest sites, and only four re-

ported size of survey plots. Of these, three were restricted to areas far smaller than the home ranges of many primates (< 50 ha). Only one study surveyed a comparatively large area of secondary forest (> 4000 ha), as well as large undisturbed primary forest control sites (Smith *et al.* 1997). Ten of the 11 studies used line transects to sample primates, while only two of these employed complementary census techniques, including nest detection (García & Mba 1997) and point counts (Green 1978). In six cases, secondary forest plots were embedded within primary forest transects, and provided no indication of transect length or replication. The remaining five studies had between 1 and 13 replicates, of which only three calculated primate densities using habitat and species-specific detection distances (Fimbel 1994, Smith *et al.* 1997, Sorensen & Fedigan 2000).

Even if a given primate species is found in a disturbed habitat, reduced group size can ensure that their local extinction is inevitable (O'Brien *et al.* 2003). Periods of fruit scarcity in primary forest are thought to be crucial in determining primate population densities (Brugiere *et al.* 2002), yet only four of these secondary forest studies captured a full annual cycle (Green 1978, Branch 1983, Estrada *et al.* 1994, Medellín & Equihua 1998), and none of these presented density estimates. In terms of the suitability of secondary forests for primates, all studies found that one or more primate species known from neighboring primary forest was at a lower density or absent from secondary forest sites. In most cases the fraction of primary forest species missing from second growth was between a one-third and one-half, of the overall assemblages (*e.g.*, Branch 1983, Estrada *et al.* 1994, Fimbel 1994, Smith *et al.* 1997, Medellín & Equihua 1998).

In summary, differences in local habitat, management history and landscape context severely limit our ability to generalize the results from studies on faunal recovery in regenerating tropical forests to encompass scenarios beyond those that have been studied to date (Chazdon 2003, Dunn 2004, see Table 1). The extent to which extensive secondary forests on degraded and abandoned lands will provide suitable habitat for the majority forest species remains an open question because of limitations of interstudy comparisons, combined with a paucity of studies, poor sampling effort and weak study design. In particular, flaws in sampling design, as well as data analysis and interpretation, can often result in systematic study biases that serve to underestimate differences between primary and secondary forests for biodiversity conservation—or in other words provide best case scenarios for demonstrating the potential conservation value of secondary forests (Table 1). Unfortunately, practical, logistical and financial constraints frequently prevent field workers from overcoming all of these limitations, especially in areas of the world which are already heavily degraded.

The meta-analysis by Dunn (2004) provides the only quantitative review of the value of secondary forests for tropical forest animal species and is central to the argument of WMLa. However, in focusing on the importance of recovery in species richness WMLa give insufficient attention to the specific emphasis by Dunn (2004) that species composition recovers much more slowly, and the timeline for complete recovery remains uncertain as even for the longest chronosequences available (100 yr), mature-forest species can still

TABLE 1. Sources of bias that can underestimate the importance of differences between primary and secondary forest for biodiversity conservation.

Source of bias	Explanation
Poor quality control sites	Pre or postcolonial disturbance in many tropical countries has created a “shifting-baseline” syndrome such that current control sites frequently fail to reflect true levels of diversity in undisturbed forest.
Limited spatial scale of control sites	Beta-diversity or species turnover is often more strongly influenced by geography (<i>e.g.</i> , differences in topography, edaphic conditions) in primary versus secondary forest (where local conditions and disturbance history can be more important) (<i>e.g.</i> , Ernst & Rodel 2005). Studies limited in spatial scale are therefore unlikely to include truly independent primary forest replicates, and consequently are more likely to be biased toward finding smaller experimental effects.
Limited spatial scale of secondary forest sites	Spill-over and edge effects can often lead to artificially elevated levels of diversity due to the temporary presence of species that are able to move through secondary forest, but require primary habitat for particular resource requirements or breeding (<i>e.g.</i> , Terborgh & Weske 1969, Vallan 2002).
Poor sample representation (through low trapping or capture effort)	Species with specialist resource requirements are often restricted to particular microhabitats or times of the year. Such species are often more likely to occur in heterogeneous environments (<i>i.e.</i> , primary forest), as well as being less susceptible to standardized sampling methods. Inappropriate accounting of such differences in sample representation between primary and secondary forest can bias against revealing the true diversity of undisturbed habitat. Despite being commonly employed, standard-effort sampling often fails to account for such biases (<i>e.g.</i> , Cao <i>et al.</i> 2002).
Failure to realize the limitations of certain methodologies	Certain sampling methods can favor estimates of species richness in disturbed environments when compared to undisturbed environments. An example of this is the use of mist nets to sample birds, where there is a more defined vertical stratification of species in primary forest (<i>e.g.</i> , Blake & Loiselle 2001, Barlow <i>et al.</i> in press)
Interpreting patterns of species abundance as indicators of habitat quality	Patterns of density can often provide a misleading picture of habitat quality (van Horn 1983), and contemporary patterns of diversity and abundance in secondary forest may not be sustainable (but instead rely upon rescue effects from primary habitat).
Failure to recognize ecological guild-specific responses to disturbance	Combining or pooling species with distinct ecological characteristics can easily mask important and contrasting disturbance-response trajectories, leading to spurious conclusions regarding the effects of disturbance (<i>e.g.</i> , Pearman 1997).
Failure to account for differences in species conservation value	Growing evidence indicates that range restricted (regional endemic) species are more likely to occur in primary than secondary forest (Dunn & Romdal 2006, Cleary & Mooers in press). Consequently, although secondary forests may host a large number of primary forest species, they may fail to conserve the species that are most at risk of extinction.

be absent from secondary forests (Shankar Raman *et al.* 1998). If this pattern is generally true, then secondary forests will not provide a reliable and effective safety net for the many tropical forest species, and areas of the world that are undergoing rapid loss of primary habitat will permanently lose many species.

The fact that the same data can be used to support contrasting perspectives on the value of secondary forests for the conservation of tropical forest species (Dunn 2004 vs. WLMa) highlights the importance of an objective evaluation of the current status of our

knowledge. Although the analysis by Dunn (2004) indicates that both species richness and composition exhibit limited recovery over time, the generality of these conclusions is limited as there were fewer than five studies for any taxon other than birds and ants, most of the study plots were small and confounded by edge effects, and over half of all studies were unreplicated. Moreover, Dunn (2004) explicitly recognizes that these studies represent the recovery of faunal taxa under largely optimal conditions, when source populations are nearby and forest clearance is on a small scale and of

low intensity. Existing studies provide an important service in identifying secondary forests as being more favorable for conservation than many other land-use options (*e.g.*, agriculture, plantations), although the fact that they are often undervalued has frequently resulted in over-exploitation or conversion (see FAO 2005). However, in the context of the optimistic picture painted by WMLa, we argue that the current status of understanding is so weak as to invalidate any reliance upon the value of secondary forests for future conservation of tropical forest biodiversity. Whereas the model predictions of WMLa tell us something of the future of tropical forest cover, they tell us very little about the future of tropical forest species.

WMLb defend their optimistic outlook about the conservation value of secondary forests by maintaining that “whatever their value in the short-term, most secondary and degraded forests have the potential to attain a structure and species composition similar to primary forests in the long-term, provided that they are sufficiently connected to sources of primary forest species and protected from further disturbance.” We challenge the validity of this assumption as secondary forests are highly heterogeneous, and their potential biodiversity value can be dramatically reduced because (a) in many areas there is very little, if any, remaining primary habitat that can provide necessary source populations (*e.g.*, Castelletta *et al.* 2000, Brook *et al.* 2003), (b) remaining patches of primary forest are often heavily degraded, isolated by hostile matrix habitat, and poorly connected to regenerating forests (Peres & Michalski 2006), (c) synergistic interactions between different forms of structural and nonstructural disturbance, including forest fragmentation, surface fires, diffusion of alien species and/or pathogens, and hunting, can further erode the biodiversity value of tropical secondary forests (see Laurance & Peres 2006), (d) heavy soil erosion and nutrient depletion may inhibit natural regeneration of degraded lands abandoned following intensive agriculture and urbanization by rural populations (Uhl *et al.* 1988), (e) biotic seed dispersal into abandoned pastures can be severely limited, and restricted to forest edges (da Silva *et al.* 1996), and (f) for many areas of the tropics secondary forests are typically ephemeral components of the landscape (Perz & Skole 2003), and may be returned to alternative land-uses which are independent of rural population densities (*e.g.*, plantation forests) after only a few decades.

Much research effort in tropical conservation is allocated to modeling future deforestation scenarios and conservation threats and WMLa is only one such example (see also Laurance *et al.* 2001, Soares-Filho *et al.* 2006). Whereas these studies are important in unveiling potential large-scale changes in the structure and composition of tropical landscapes, our review shows that very little reliable field data are available to translate the consequences of such changes (current or future) for biodiversity. In the absence of a strong empirical foundation we run the risk of making flawed and potentially misleading predictions, leading to dangerously inappropriate or complacent policy recommendations.

Tropical forests are currently facing an unprecedented level of threat from multiple factors, including land-use change on a massive scale, habitat fragmentation, wildfires and overhunting (Laurance & Peres 2006), exacerbated by endemic corruption (Smith *et al.* 2003) and climate change (*e.g.*, Lewis *et al.* 2004). Such threats, cou-

pled with the poor current status of our knowledge mean that it is highly unlikely that we will fully understand the conservation value of secondary forests before we have already converted most of the remaining primary forest to other land uses. Whereas speculation on the potential biodiversity value of secondary forests is intellectually stimulating, we consider that the urgency of the situation strongly justifies the application of the precautionary principle. We therefore agree with WMLb that although secondary forests may be more favorable than many alternative land uses, the most pragmatic conservation recommendation currently available is to assist tropical forest countries to both maintain existing primary forest reserves and set aside new areas of old growth that remain unprotected (Fagan *et al.* 2006). However, we also believe that the optimistic predictions of WMLa undermine the importance of this goal, and our concern is heightened by the fact that the main predictions of WMLa occur in the absence of any active changes in conservation policy (thereby potentially—but unintentionally—advocating complacency). It is our conviction that we currently lack the data necessary to make robust predictions about the conservation value of secondary forests for most species. Until these data become available, predictions such as those provided by WMLa lack any strong empirical basis, and should not provide grounds for premature optimism.

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