

Have we overstated the tropical biodiversity crisis?

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Tropical forests are the most biologically diverse and ecologically complex of terrestrial ecosystems, and are disappearing at alarming rates. It has long been suggested that rapid forest loss and degradation in the tropics, if unabated, could ultimately precipitate a wave of species extinctions, perhaps comparable to mass extinction events in the geological history of the Earth. However, a vigorous debate has erupted following a study by Wright and Muller-Landau that challenges the notion of large-scale tropical extinctions, at least over the next century. Here, I summarize this controversy and describe how the debate is stimulating a serious examination of the causes and biological consequences of future tropical deforestation.

Tropical extinctions

Are we on the verge of a massive die-off of tropical species? Several influential authors have argued so, based on the unassailable observations that most tropical forests are extraordinarily rich in species, remarkably complex ecologically and disappearing at truly alarming rates [1–6]. The clarion call of such declarations has helped to galvanize public interest in the fate of tropical rainforests and their natural denizens, which, in turn, has led to a marked increase in the number of tropical protected areas over the past two decades [7].

However, a recent study by Wright and Muller-Landau challenges the idea of a mega-extinction crisis in the tropics [8]. Under some circumstances, a highly iconoclastic analysis such as this might simply be dismissed out of hand, but several factors make the present study difficult to ignore. First, the lead author, S. Joseph Wright, is a highly experienced tropical ecologist, with an eminent research record. Second, the paper is empirically based and elegantly analyzed. Third, it was initially presented, and ultimately published, as Wright's presidential address to the Association for Tropical Biology and Conservation (<http://www.atbio.org>). Finally, the main conclusions of the paper, 'that [future] deforestation will slow, regeneration will accelerate, and mass extinction of tropical forest species will be avoided', were detailed in a widely distributed press release [9] that failed to identify the sometimes-heroic assumptions and extrapolations of the study.

As one might expect, a study of this nature, with its crucial and far-ranging implications, has precipitated a vigorous scientific debate. Here, I summarize this dispute,

critically evaluate the Wright and Muller-Landau study and its assumptions, and highlight some implications of the rising controversy for future research priorities.

Projecting future deforestation and extinctions

Whereas several studies have estimated past deforestation rates in the tropics [10–12], fewer have attempted to project future deforestation and its implications for species losses. The study by Wright and Muller-Landau does so by (i) demonstrating a strong, linear relationship between the logarithm of human population density (especially rural population density) and the estimated net loss of original forest cover for 45 developing nations in Asia, Africa and the Americas (Figure 1) that collectively contain nearly 90% of all surviving tropical forests; (ii) projecting the future growth of rural and urban populations in those 45 nations by the year 2030 (Figure 2); (iii) using the population projections to predict future changes in deforestation rates and forest cover for each nation; and (iv) invoking the well established species–area relationship (e.g. Ref. [3]) to estimate the magnitude of expected species losses for the Asian, African and American tropics.

Population size and forests

Among its various assumptions (Box 1) and empirical findings, a key element of the Wright and Muller-Landau study is that the density of rural inhabitants, rather than total population density, is most strongly correlated with percent forest cover at a national level (Figure 1). This, the authors assert, is because rural slash-and-burn farmers cause most forest loss [13] and prevent forests from regenerating, and they assume that this trend will continue. The authors also use total population density to predict upper limits for forest-cover losses and extinctions, but their regression models and arguments strongly emphasize the importance of rural populations. A second key element is that UN projections suggest that, whereas the populations of many tropical nations will continue to grow in coming decades, especially in Africa and Asia, there will be a strong trend toward increasing urbanization (Figure 2). As a result, rural populations are expected to increase little in the Asian and American tropics, although they will continue to grow quite rapidly in Africa.

Given the apparently strong link between rural population size and forest cover, and the expected minor growth in rural populations, Wright and Muller-Landau assert that net forest cover will not change dramatically, especially in Asia and the Americas. Hence, they argue, species extinctions will be surprisingly modest, with just 21–24% and

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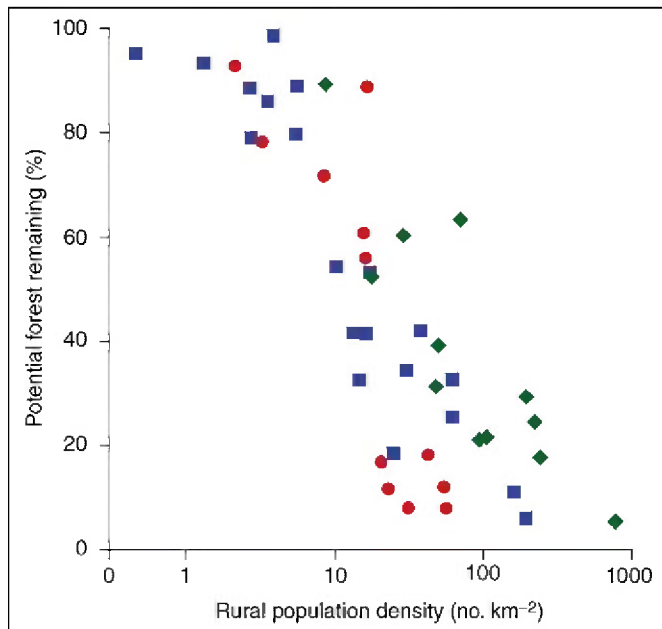


Figure 1. Relationship between rural population density and remaining closed-canopy forest [(current forest area/estimated original forest area) \times 100] for 45 tropical nations in Africa (circles), the Americas (squares) and Asia (diamonds). Adapted with permission from Ref. [8].

16–35% of all species being threatened with possible extinction in the Asian and African tropics, respectively. The American tropics are expected to fare even better, given that a higher proportion of forest is likely to survive, although a continent-wide prediction is precluded by inconsistent definitions of forest cover used in earlier studies. These estimates deviate strongly from potential losses of up to three-quarters of all tropical species suggested by some researchers (e.g. Ref. [5]).

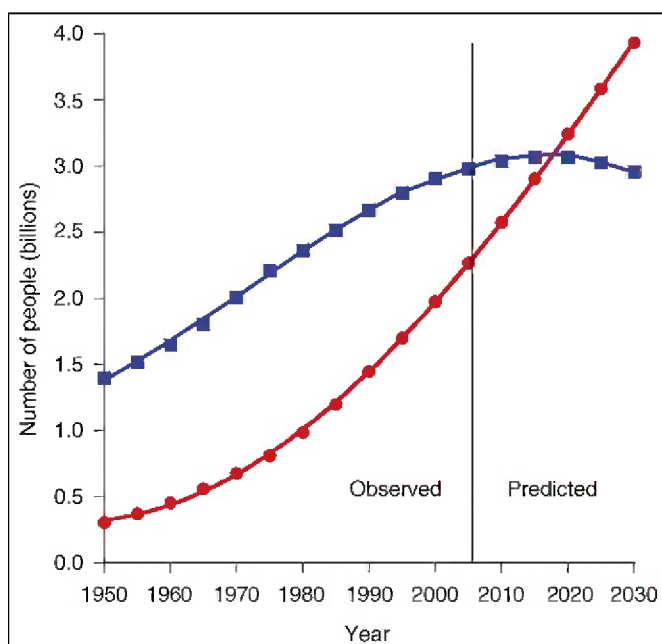


Figure 2. Observed and projected changes in rural (squares) and urban (circles) populations for developing nations, based on data from the UN Population Division [32]. Projected changes are for the median UN scenario.

Box 1. Key assumptions and datasets of Wright and Muller-Landau

Although controversial, the Wright and Muller-Landau study involves an impressive effort in data mining and integration. To conduct their analyses, the authors gleaned or derived estimates of original forest cover based on satellite imagery and ecosystem modeling [56]; net loss of forest cover, produced by the UN Food and Agricultural Organization [10]; and projected growth in rural and urban populations, from the UN Population Division, for 45 tropical countries [32]. Of course, the reliability of these extrapolations relies crucially on the data sets that form the foundation of the analyses.

Wright and Muller-Landau acknowledge that their study involves many assumptions and caveats [8]. Among the most important are: (i) the fact that their model is not mechanistic but 'phenomenological' (i.e. largely based on an observed correlation between human population density and net forest cover for tropical nations, which could arise for a variety of direct and indirect reasons); (ii) that important variations in the proximate and ultimate drivers of deforestation exist among tropical regions [39,40], but are not incorporated into their model; (iii) that the relationship between population density and forest cover could conceivably change; (iv) that their deforestation projections are for net forest cover, which includes not only old-growth forest, but also regenerating, logged and otherwise disturbed forests and plantations; (v) that the median UN projections for population growth and urbanization trends that they used are accurate; and (vi) that their conclusions apply mainly to the major tropical continental biota of Africa, Asia and the Americas, rather than to localized 'hotspots' of species endemism [21].

Despite these important qualifications, Wright and Muller-Landau assert that the various trends that they identify (declining population growth, increasing urbanization, lower-than-expected forest loss, increasing forest regeneration and the mitigating effects of past extinction filters) militate against the idea of an impending mass extinction of tropical species [8].

Time lags and extinction filters

Wright and Muller-Landau go further, arguing that many species imperiled by habitat disruption will not in fact go extinct. They correctly assert that, even when large expanses of habitat are destroyed, most species do not disappear immediately. Rather, there is generally a time lag between habitat loss and extinction [14,15]. The authors believe that substantial areas of agricultural land are likely to be abandoned, because the population growth rates of many developing nations are slowing (at least relative to the breakneck pace of earlier decades) and because of increasing urbanization. This could enable significant forest regeneration, which could help buffer species losses from deforestation.

In addition, Wright and Muller-Landau argue that, in some tropical regions, especially Equatorial Africa, forests repeatedly contracted into small refugia during cooling and drying phases of the Pleistocene, from 2 million to 12 000 years ago. Furthermore, Central America and certain other areas, such as parts of the Amazon, Congo Basin and New Guinea, sustained sizeable indigenous populations that cleared expanses of primary forest and hunted extensively (e.g. Ref. [16]). The net effect, the authors assert, is that such areas would have already lost many of their extinction-prone species, rendering them less vulnerable to future species losses from deforestation.

Mounting criticisms

To date, the Wright and Muller-Landau study has provoked a rebuttal by Brook *et al.* [17], to which Wright and Muller-Landau quickly responded [18], as well as critical commentaries by Gardner *et al.* [19] and Sloan [20]. Here, I critique key assumptions of the original analysis, while highlighting major disagreements between the authors and their detractors.

Vulnerable hotspots

At the outset, it is important to emphasize that the conclusions of Wright and Muller-Landau apply principally to the major continental tropical regions of Asia, Africa and the Americas. As the authors acknowledge, extinction rates are likely to be higher in biodiversity hotspots [21], such as Madagascar, the Philippines and the Brazilian Atlantic forests, which are geographically restricted areas with high species endemism, heavy habitat loss and rapidly increasing human populations [22]. The 25 biodiversity hotspots identified by Myers *et al.* [21] include the entire known ranges of nearly half (44%) of all known vascular plants and over a third (35%) of all vertebrates, and the 16 hotspots that sustain tropical forest have already lost, on average, 90% of their forest cover [23]. Because many local endemics in these hotspots are outside of protected areas [23,24], species extinctions are likely to be substantially higher than those projected by Wright and Muller-Landau for the major continental regions.

Local endemics

Wright and Muller-Landau believe that extinctions will be limited in large forest tracts such as the Amazon, Congo Basin and New Guinea, in part because many species in these regions have relatively large geographical ranges. However, these areas also sustain numerous local endemics [25–28]. A recent biogeographical model suggests, remarkably, that Amazonia could contain 30 000–100 000 locally endemic species of seed plants*. Even within seemingly monotonous expanses of forest, current and historical barriers, such as rivers, mountains and past forest refugia, have created complex patterns of species endemism [25–28]. Hence, even the largest tropical forest tracts currently in existence contain many restricted endemics that are inherently vulnerable to habitat disruption.

Declining old-growth forest

Another key consideration is that Wright and Muller-Landau focus on changes in net forest cover, rather than on old-growth forest. As the authors emphasize, in coming decades, vast areas of old-growth tropical forest will be cleared, logged, fragmented, or otherwise degraded, and some cleared areas will regenerate after land abandonment or be replaced by exotic tree plantations. In their projections, all forest types count equally, but the distinction between old-growth and regenerating or fragmented habitats can be profound for extinction-prone species (Figure 3), as various authors have contended (e.g. Refs [19,29–31]). Based on an extensive literature



Figure 3. Many old-growth specialists, such as this lemuroid ringtail possum *Hemibelideus lemuroides* from tropical Australia, avoid fragmented or secondary forests (photo by William Laurance).

review, Gardner *et al.* [19] conclude that Wright and Muller-Landau's assertions about the high conservation value of regrowth forests are both premature and overly optimistic, at least for forest vertebrates. This, they assert, reflects many uncertainties caused by a paucity of available research, the fact that a third to a half of all old-growth species avoid younger (<30-year-old) regrowth, and the reality that secondary forests are ephemeral components of landscapes that are frequently reclaimed, reducing their utility for wildlife conservation [19].

Uncertain population trends

The UN population projections such as those used by Wright and Muller-Landau also contain large uncertainties. For example, global population projections for the year 2100 vary enormously, from ~7 to 15 billion people (e.g. Refs [6,32]). Such projections are sensitive to a range of assumptions about future human behavior, some of which are merely informed speculation [33]. The median projection used by Wright and Muller-Landau, for instance, assumes that dramatic population growth in Equatorial Africa will soon decline, despite the fact that the usual antecedents of such a demographic transition (e.g. increasing industrialization, urbanization and

* Hopkins, M.J.G. (2005) Amazonian Plant Biodiversity, Oral presentation, Annual Meeting of the Association for Tropical Biology and Conservation, Uberlândia, Brazil.

women's education) are still weak in the region [34]. There is also much uncertainty in urban and rural population trends in developing countries, especially when examined at a subnational level [35,36]. In the words of a leading population researcher, 'no professional demographer takes the UN median projection as seriously as non-demographers such as Wright are doing.' (R. Engelman, pers. commun.)

Growing industrialization and globalization

Wright and Muller-Landau also assume that population density and forest cover will remain strongly correlated (Box 1), but this relationship is changing as both industrialization and per-capita consumption increase rapidly in developing nations [6,37,38]. Industrial drivers of tropical deforestation, such as large-scale cattle ranching, soy farming, oil-palm plantations, timber extraction, oil and gas development (Figure 4), and major highways and infrastructure projects, have risen markedly in importance during the past two decades [39,40]. This trend will surely continue, with global industrial activity expected to expand three–sixfold by 2050 [6], and with potentially dramatic increases in land demands for biofuel production (Box 2). Hence, in many tropical regions, future pressures on forests will be determined more strongly by industrial drivers, globalization and macroeconomic forces than by local population density [40].

Rural populations and forests

Another hotly disputed point is whether future pressures on forests will decline as a result of slowing rural population growth. Wright and Muller-Landau conclude that



Figure 4. Expanding road networks for timber, oil and mineral extraction, such as this oil-project road in Gabon, promote sharp increases in tropical deforestation (photo by William Laurance).

Box 2. Environmental impacts of burgeoning biofuels

As oil prices climb, the competitiveness of alternative energy sources increases. Much attention is now focused on biofuels, such as ethanol, which can easily be used to fuel automobiles. A variety of crops grown in the tropics, such as sugarcane, palm oil, corn and grains, are being used for ethanol production.

In the coming decades, large-scale biofuel production, along with rising food demands in developing nations, could create acute economic pressures to expand agricultural yields. Brazil, the largest producer of sugar in the world, already devotes half of its annual crop to produce ethanol for fueling cars. As a result of such rising demand, global prices for sugar have reached a 25-year high [57].

Unfortunately, large-scale biofuel production requires vast expanses of arable land. For example, even if the entire grain crop in the USA were devoted to ethanol production, it would satisfy less than one-sixth of current US demand for automobile fuel [58]. In concert with food production and other land uses, escalating needs for biofuels could dramatically increase the pace of tropical forest conversion.

urban population density did not improve their predictions of current forest cover (Figure 1), and used this to bolster their argument that rural people are the principal driver of deforestation. However, Brook *et al.* [17] contend that, even where rural populations stabilize, rapidly expanding cities will have major impacts on forests, by increasing demand and markets for timber, food, biofuel and other resources [40,41]. They further argue that statistically disentangling the effects of rural versus urban populations is difficult, given that the two have been tightly correlated historically in developing countries (Figure 2); only in the coming decades are the two expected to diverge, as urbanization increases.

A related tenet of the Wright and Muller-Landau argument is that future species extinctions will be buffered by expanding forest regeneration. As discussed earlier, however, many vulnerable species do not use secondary forests. There is, moreover, little compelling evidence that most tropical nations will experience substantial forest recovery, because of escalating demands for arable land [37,38], and because their rural populations are not so much expected to fall as to plateau or grow less rapidly than will urban populations (Figure 2). Drawing on examples from the Neotropics, Sloan [20] further argues that even sparse or declining rural populations can still cause heavy and sustained deforestation, contrary to the views of Wright and Muller-Landau. Indeed, a recent study demonstrates that the poorest and most poorly governed nations, which unfortunately include many tropical countries, are less likely than other nations to make the transition from deforestation to afforestation [42].

Magnitude of extinctions

Perhaps the deepest disagreement in this debate concerns the magnitude of expected extinctions following a massive reduction of old-growth forests. Wright and Muller-Landau believe that only those species that undergo the most dramatic and historically unprecedented population declines will disappear [8,18]. Brook *et al.*, however, perceive a far different reality [17]. They believe that many species are already committed to extinction by virtue of major declines and fragmentation of their populations

(see also Refs [1–6,23,43,44]). They further argue that the species–area relationships used by Wright and Muller-Landau will underestimate extinctions because they assume that surviving forests are merely shrinking in area, when in fact they are also being extensively fragmented. Lastly, they assert that the dramatic pace of contemporary habitat loss, combined with the synergistic effects of future climatic change, overhunting, emerging pathogens and many forms of habitat degradation [7,44–48], could sharply increase the rate of species extinctions (Wright and Muller-Landau agree that chronically overhunted species could vanish [8] and that major climate change could severely disrupt tropical forests [18]).

The precautionary principle

Finally, the Wright and Muller-Landau study seems to violate the precautionary principle, which maintains that one should err on the side of caution in conservation matters. Concerns about potentially massive species losses have provided the political impetus for substantially expanding protected areas and conservation programs in the tropics [7]. Even if future extinctions should be lower than many anticipate (partly because of these new conservation initiatives), the population sizes, geographical ranges and genetic variation of innumerable species are collapsing under the weight of burgeoning anthropogenic threats [49]. Many predators and megafaunal species, for example, have already vanished or are clinging to survival in small parts of their original geographical ranges [50,51]. Such species are becoming functionally, if not actually, extinct, and these losses are likely to have pervasive, long-term impacts on ecosystem structure and functioning [52,53]. Hence, it seems too early to put an optimistic spin on the impending loss of tropical biodiversity; far better for our great-great grandchildren to make such a propitious finding, than to celebrate now and potentially leave our descendents to discover precisely the opposite.

Concluding remarks

Wright and Muller-Landau's analysis challenges the common view that forest conversion is driving a massive loss of tropical biodiversity. They carefully identify the main assumptions of their models (Box 1), although, as I and others [17,19,20] have argued, the limited species losses that they predict are likely to be overly optimistic. Most notably, their projections include neither the expected extinctions in crucial hotspots of species endemism nor the effects of global climate change, and they maintain (despite much scientific uncertainty) that the bulk of tropical species will persist in degraded and secondary habitats. Moreover, although there are important links between human population size and environmental degradation [6,7,37], the impact of local populations on forest cover (Figure 1) is changing as industrialization, per-capita consumption and economic globalization rapidly increase in developing nations.

Despite these concerns, the Wright and Muller-Landau study provides a clear rationale for projecting future species losses and highlights pressing research priorities. Among these is the need to evaluate critically the degree

to which regenerating and degraded habitats, which are increasing dramatically at the expense of old-growth forests, can sustain tropical biodiversity [8]. Another priority is to advance our understanding of the proximate and ultimate drivers of forest loss, especially at regional and sub-regional scales, and how those drivers change in importance over time [39,40]. Improving basic estimates of forest cover, loss and regeneration for tropical nations is another key aim.

Tropical forests and their biota are facing an enormous array of anthropogenic threats [7]. As scientists, we are obliged to evaluate even pressing environmental issues objectively. But, as realists, we must also appreciate that certain political interests and authors actively embrace scientific uncertainty (e.g. Refs [54,55]) in an effort to advance their particular agendas. It is because of such concerns that I have critiqued the thought-provoking Wright and Muller-Landau study, for I believe it seriously understates the tropical biodiversity crisis.

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