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
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, 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]).

**Time lags and extinction filters**

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.

**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) mitigate against the idea of an impending mass extinction of tropical species [8].
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 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 reclared, 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
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 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...
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.

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

References

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