

REVIEW AND
SYNTHESISProspects for tropical forest biodiversity in a
human-modified world

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Abstract

The future of tropical forest biodiversity depends more than ever on the effective management of human-modified landscapes, presenting a daunting challenge to conservation practitioners and land use managers. We provide a critical synthesis of the scientific insights that guide our understanding of patterns and processes underpinning forest biodiversity in the human-modified tropics, and present a conceptual framework that integrates a broad range of social and ecological factors that define and contextualize the possible future of tropical forest species. A growing body of research demonstrates that spatial and temporal patterns of biodiversity are the dynamic product of interacting historical and contemporary human and ecological processes. These processes vary radically in their relative importance within and among regions, and have effects that may take years to become fully manifest. Interpreting biodiversity research findings is frequently made difficult by constrained study designs, low congruence in species responses to disturbance, shifting baselines and an over-dependence on comparative inferences from a small number of well studied localities. Spatial and temporal heterogeneity in the potential prospects for biodiversity conservation can be explained by regional differences in biotic vulnerability and anthropogenic legacies, an ever-tighter coupling of human-ecological systems and the influence of global environmental change. These differences provide both challenges and opportunities for biodiversity conservation. Building upon our synthesis we outline a simple adaptive-landscape planning framework that can help guide a new research agenda to enhance biodiversity conservation prospects in the human-modified tropics.

Keywords

Agriculture, biodiversity, conservation, disturbance, forestry, landscapes, modified lands, species losses, species persistence, tropical forests.

Ecology Letters (2009) 12: 561–582

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INTRODUCTION

Tropical forest ecosystems host at least two-thirds of the Earth's terrestrial biodiversity and provide significant local, regional and global human benefits through the provision of economic goods and ecosystem services. Yet the future of tropical forest species has never been more uncertain. Few areas of the tropics have escaped some form of human impact (Kareiva *et al.* 2007) and the combined influence of persistently high rates of deforestation and forest degradation (FAO 2006), over-harvesting, invasive species and global environmental change threatens to make tropical forests the epicentre of current and future extinctions (Bradshaw *et al.* 2009).

Protected areas are an essential element of any strategy to conserve tropical forest biodiversity, and the only means of safeguarding obligate forest species, such as some large-ranging predators or invertebrates that only live within the decaying remains of ancient logs. However, only 9.8% of the entire tropical forest biome lies within strictly protected areas (Schmitt *et al.* 2008), and the long-term viability of existing reserves is strongly affected by patterns of human activity in adjacent areas (Wittemyer *et al.* 2008). It is therefore clear that the future of much of tropical forest biodiversity depends more than ever on the effective management of human actors and their impacts on landscapes (Harvey *et al.* 2008; Perfecto & Vandermeer 2008). Ecological and conservation science has begun to adapt to this new reality by moving away from a piecemeal approach centred on the protection of isolated reserves and towards a recognition of the coupled social–ecological dynamics that characterize modified lands (Liu *et al.* 2007). Indeed, the very concept of ‘natural ecosystems’ is obsolete in some tropical regions where landscapes have been significantly modified by human activity (Ellis & Ramankutty 2008). Nevertheless the empirical and conceptual scientific framework required to underpin progressive and sustainable conservation strategies in human-modified areas of the tropics is nascent and highly fragmented at best. Ecologists are only just starting to grapple with fundamental questions such as the degree to which tropical forest biotas can persist in human-modified landscapes, or which management strategies will be most effective at enhancing the persistence of forest species for a given spatial and temporal scale, and against a backdrop of rapid global change. Achieving practical answers to these deceptively simple questions is hampered by the fact that existing biodiversity patterns are the result of a myriad of interacting dynamic processes that vary markedly across landscapes, regions and time.

Our goal in this review is to provide a critical synthesis of the scientific insights that guide our understanding of the prospects for forest biodiversity in the human-modified

tropics. What is the nature of the problem and challenge that faces the future of tropical forest species, and how does this constrain and guide the opportunities for conservation in a human-modified world? Within tropical forest ecosystems, obligate forest species (i.e. those that are only found in large remnants of native forest) take natural conservation priority as they are intrinsically more vulnerable to eventual extinction from forest loss than species that are only partly dependent on forest habitat (e.g. taxa that occur naturally at forest edges), and their functional roles (e.g. seed dispersal) may not be easily replaced. However, we do not focus exclusively on these most vulnerable species as such a constrained definition of conservation priority ignores the myriad of opportunities that exist for the conservation of other, less sensitive, elements of forest biodiversity along the gradient of human impacts; from complete protection to intensive agriculture. It is often the species that are on the more vulnerable end of the spectrum yet are not the *most* vulnerable for which we can make the most effective contribution to biodiversity conservation in areas outside large reserves. This approach is particularly relevant for the parts of the world that no longer contain large areas of old-growth forest under protection, as well as for many other regions where rapid rates of agricultural intensification and expansion threaten the long-term viability of isolated reserves.

We structure our review around a comprehensive conceptual framework that integrates the broad range of human and ecological factors that define and contextualize our understanding of the future of tropical forest biodiversity (Fig. 1). In the first section we examine the highly constrained perspective that dominates much of biodiversity research, address the influence of human activities on tropical forest biodiversity, and demonstrate how direct and indirect impacts from landscape change and the cascading effects of biodiversity loss combine in complex ways to generate increasingly modified tropical ecosystems. Second, we examine how a highly variable ecological and human context determines real-world patterns of spatial and temporal heterogeneity in biodiversity prospects across different regions of the world and into the future. Finally, we draw upon these insights to synthesize what we have learnt about the spectrum of conservation opportunity facing tropical forest biodiversity, and the key elements of a new research agenda that is urgently needed if science is to make an effective contribution towards exploiting such opportunities. Throughout the review we endeavour to draw a line under persistent yet outdated debates that are stifling future progress, while emphasizing areas of real uncertainty that require urgent empirical and theoretical attention. This synthesis is not intended as a roadmap for conservation practice. Instead we provide a critical analysis of the ecological factors that underpin urgently needed

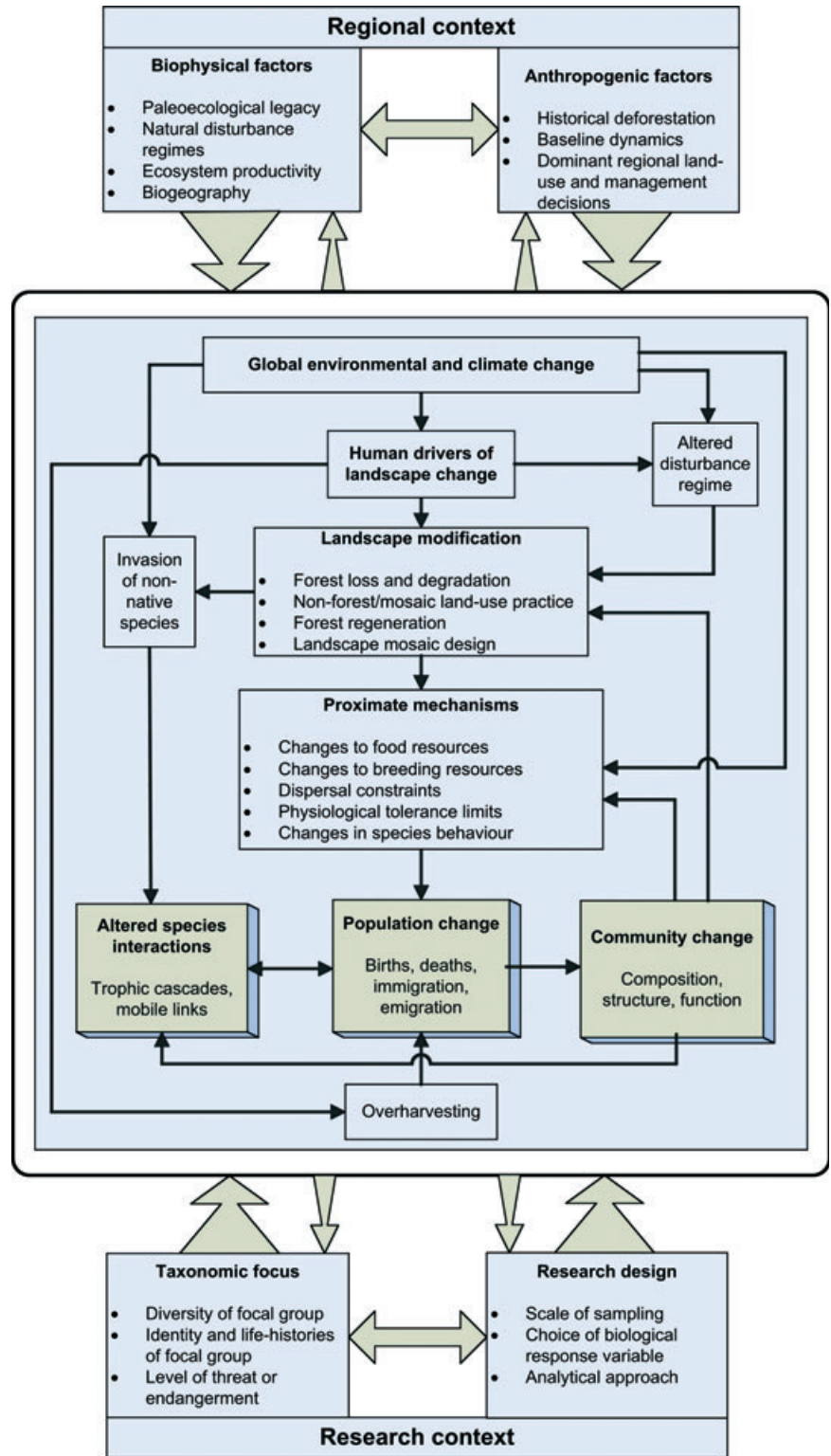


Figure 1 A broad conceptual framework of the threats, processes and feedbacks that determine patterns and trends of biodiversity in human-modified tropical forest landscapes. At present, far more is understood about the first-order human impacts of landscape change (correlative factors) than the causative mechanisms and second-order, cascading effects. Inferences from biodiversity studies are constrained by differences in regional context as well as the context imposed by study-specific differences in research design and focus. Changes to the landscape over time (e.g. agricultural intensification, agricultural expansion, land abandonment, land-use zoning, conservation actions and internal cascading effects of altered biodiversity processes) can lead to feedbacks which alter the relative importance of context-dependent factors and different research approaches. This model is not a closed system, and the background influence of human population and development pressure on drivers of landscape change and over-harvesting is not shown.

multi-disciplinary efforts to implement viable conservation strategies in human-modified systems. We present an ecologically informed template for understanding the

potential for biodiversity conservation in human-modified tropical forests, which in turn requires a more detailed and context-dependent understanding of the social factors that

ultimately determine the success or failure of conservation action on the ground.

UNDERSTANDING THE PROBLEM: THE INFLUENCE OF HUMAN ACTIVITIES ON TROPICAL FOREST BIODIVERSITY

Tropical forest biodiversity is influenced by a myriad of human-associated processes that operate over different temporal and spatial scales (Fig. 1). Our understanding of these dynamics is frequently constrained by the highly context-dependent nature of most ecological research. Agriculture (both traditional and modern), forestry, urbanization and infrastructure development variously combine to drive patterns of deforestation, forest fragmentation and land-use intensification, and are often accompanied by an array of secondary impacts including the over-harvesting of timber and non-timber resources (including game), altered disturbance dynamics (especially fire), altered hydrological flows and the invasion of exotic species. These primary drivers of biodiversity change are often exacerbated by global climate and environmental change. The proximate mechanisms that drive population changes in native forest species operate not only through the direct effects of the loss of breeding or food resources, changes in microclimate, dispersal limitations, and altered species biology and behaviour, but also through the indirect cascading effects of altered biotic interactions following the decline or loss of functionally linked species (Fig. 1).

Biased perspectives: research constraints on perceiving biodiversity prospects in human-modified tropical forests

Logistical and financial constraints severely limit the amount and quality of information we are able to collect about the natural world. Less well appreciated by ecologists are the epistemological constraints imposed on our understanding by biased theoretical constructs, reductionist analytical approaches and semantic devices that are often implicit in biodiversity data interpretation. Here we outline three key considerations that have attracted increasing attention from ecologists working in modified tropical forest systems.

Our understanding of conservation values is derived from a very limited subset of species

Species survival in modified systems depends on maintaining the natural features and functional processes upon which individual species depend (Ewers & Didham 2006; Fischer & Lindenmayer 2007). Extrapolations of generic patterns of biodiversity persistence from data on focal species groups are common despite the fact that most multi-taxa biodiversity studies in modified tropical forest

landscapes have reported low levels of cross-taxon congruency in disturbance response patterns (Table 1). Such discrepancies are due in part to the fact that different species experience landscape change at different spatial and temporal scales, use different habitats and resources within these landscapes, and differ in their sensitivity to landscape change and fragmentation. While some taxa exhibit consistent responses to human activities (e.g. understorey insectivorous birds; Sekercioglu *et al.* 2002), idiosyncrasies are more often the norm and considerable caution is needed when extrapolating the results of individual studies.

Few studies assess the conservation priorities associated with individual species

Compiling information on extinction proneness and species-specific conservation priorities can greatly enhance our understanding of the biodiversity consequences of human activities. To accurately estimate the value of modified landscapes for conserving regional forest biodiversity we need to know the proportion of species that inhabit human-modified systems that were also inhabitants of the original forest landscape. Yet despite the natural priority of these species as a focus of conservation efforts, few studies have been able to identify the extent to which individual species depend on old-growth forest. Those studies that have had access to independently collected natural-history information have, somewhat unsurprisingly, reported consistent and marked losses of species with known associations with old-growth forest following land conversion (Beukema *et al.* 2007; Pardini *et al.* in press). Other work has also shown that it is often those taxa that are of the highest priority for conservation, such as regional forest endemics, that are the most extinction prone in modified tropical landscapes (e.g. Posa & Sodhi 2006; Scales & Marsden 2008). However, simply identifying which species comprised part of the original native forest biota can often be very challenging, and is critically dependent on access to suitable adjacent control sites or historical species records. It is often impossible to recover this kind of information in poorly studied regions that have little forest cover remaining, while the level of forest specialization exhibited by different species is even harder to ascertain with any certainty. Old-growth species represent a broad continuum of resource and habitat requirements and life-history strategies, including both high specialized taxa that are especially vulnerable to forest loss, and disturbance-tolerant species that thrive in more open areas (e.g. edge environments) (Chazdon *et al.* in press). Understanding the extent to which human-modified systems can support this full range of species requires a more detailed understanding of the individual species habitat requirements and dispersal limitations.

Table 1 The level of multi-taxon congruency in response patterns to landscape change in tropical forests

Study	Taxonomic groups	Land-use types and landscape features	Multi-taxon congruency*	
			Species richness†	Community structure‡
Lawton <i>et al.</i> (1998)	Birds, butterflies, flying beetles, canopy beetles, canopy ants, leaf-litter ants, termites and soil nematodes	Old-growth, secondary forest, plantations forest, clear-cut	11%	
Schulze <i>et al.</i> (2004)	Trees, understory plants, birds, butterflies and dung beetles	Old-growth, secondary forests, agroforestry systems and annual crops	48%	
Harvey <i>et al.</i> (2006)	Birds, bats, butterflies and dung beetles	Riparian and secondary forest, forest fallows, live fences and pastures	20% (birds – 38%)	
Faria <i>et al.</i> (2007)	Ferns, frogs, lizards, birds and bats	Old-growth, shade cacao plantations		25% (birds – 37%)
Barlow <i>et al.</i> (2007)	Bats, birds, dung beetles, epigeic arachnids, fruit flies, fruit-feeding butterflies, grasshoppers, large mammals, leaf-litter amphibians, lizards, moths, orchid bees, scavenger flies, small mammals, trees and lianas	Old-growth forest, secondary forest, Eucalyptus plantations	22% (lizards – 44%)	39% (butterflies – 56%)
Basset <i>et al.</i> (2008)	21 focal taxa from across seven orders of arthropod: Coleoptera; Diptera; Hemiptera; Hymenoptera; Mantodea; Neuroptera; Orthoptera	Old and young secondary forest, savannah clearances and garden cropland	3%	35%
Kessler <i>et al.</i> (in press)	Trees, lianas and herbs, epiphytic liverworts, birds, butterflies, lower canopy ants and beetles, dung beetles, bees and wasps and their parasitoids	Old-growth forests and three types of cacao agroforests	0–17%	12–18%
Uehara-Prado <i>et al.</i> (in press)	Fruit-feeding butterflies and five other orders/families of arthropod (Araneae, Carabidae, Scarabaeidae, Staphylinidae and epigeic Coleoptera excluding aforementioned families)	Undisturbed old growth and 'disturbed' forest	13%	66%
Pardini <i>et al.</i> (in press)	Ferns, trees, frugivorous butterflies, leaf-litter frogs and lizards, bats, small mammals and birds	Second-growth forests, shade cacao plantations and interiors and edges of large and small mature forest remnants	0.18	

*Mean correlation coefficient of species richness responses.

†Mean correlation coefficient of community structure responses (based on Mantel tests of similarity matrices).

‡Number and taxon in brackets denotes the level of cross-taxon response congruency for the highest performing single taxon.

Measurement errors and researcher bias frequently result in imprecise estimates of the conservation value of disturbed land

Findings from ecological field research are often highly uncertain due to the fact that studies are frequently small in scale, deal with weak effect sizes, involve multiple competing hypotheses, and exhibit great flexibility in research design and analytical modes. Understanding the reliability of inferences from field data is particularly challenging for a variety of reasons. First, the effects of land-use change on tropical forest diversity are highly scale dependent. This is partly attributable to local spill-over effects across forest boundaries, the fact that different taxa perceive environmental perturbations at fundamentally different scales, and the more rapid increase in alpha and beta-diversity with spatial scale in undisturbed compared with disturbed forest (Dumbrell *et al.* in press). Second, species-occupancy data are uncertain proxies of actual population viabilities, yet very few studies have collected long-term evidence of breeding success, or population dynamics more broadly, in modified tropical forest habitats (e.g. Sekercioglu *et al.* 2007). Translating species occupancy into species viability is further confounded by the fact that most tropical forest species are rare in field samples. Third, common reductionist approaches to studying biodiversity patterns can attribute change to the wrong factor, or result in a failure to fully understand situations where seemingly distinct drivers of change are intrinsically linked or highly interdependent; e.g. in the case of habitat loss and fragmentation (Koper *et al.* 2007), fragmentation and logging impacts (Hillers *et al.* 2008), and area and edge effects (Ewers *et al.* 2007). Such shortcomings are particularly problematic in situations where critical interactions and synergistic effects may represent the ultimate drivers of population loss (Tabarelli *et al.* 2004). Perhaps the most compelling case of synergistic effects that threaten tropical forest biodiversity is the exacerbation of wildfires by logging and fragmentation (e.g. Barlow & Peres 2004). Disentangling the importance of interaction effects in driving biodiversity change across both intact and modified landscapes represents a major frontier in applied ecology (Lindenmayer *et al.* 2008).

Biodiversity responses to landscape change: insights from landscape ecology and fragmentation research

Although we are aware of the constraints under which reliable inferences can be drawn, we identify four broad and inter-related insights that help structure our broad framework for understanding patterns of biodiversity change in modified forest landscapes (Fig. 1).

Old-growth forest habitat is irreplaceable for the maintenance of native species diversity

Work on the effects of clearing old-growth forest has identified a core set of specialist forest species that are

highly vulnerable to land-use change (e.g. Schulze *et al.* 2004; Barlow *et al.* 2007; Faria *et al.* 2007; Basset *et al.* 2008; Philpott *et al.* 2008). J. Barlow & T. A. Gardner (2007, unpublished data) estimated a lower-bound of this core set for a *Eucalyptus* plantation-secondary forest landscape in Brazilian Amazonia to be 34% of the total number of landscape species (1441, comprising 15 species groups), yet this value rose to 47% when accounting for occasional species (i.e. singletons) only that may be transient, or persist as 'living dead' in converted lands. However, understanding which native forest species can maintain viable populations in modified landscapes, and under what management regimes, continues to pose a major challenge for landscape ecologists (Chazdon *et al.* in press). In areas which no longer host large tracts of old-growth forest the maintenance of original tree cover of any form, including small fragments, riparian strips, living fences and isolated trees can be critically important in providing complementary habitats and resources for a significant portion of the original biota (Harvey *et al.* 2006; Sekercioglu *et al.* 2007). The spatial arrangement of this remnant tree cover can be just as important as its total amount, as demonstrated by the importance of pre-existing spatial environmental heterogeneities in driving the high conservation value of scattered forest remnants (e.g. Raheem *et al.* 2008).

Structural complexity provides a crude proxy of biodiversity value across land-use intensification gradients

Species do not perceive human-modified landscapes as black and white mosaics of habitat and non-habitat (Fischer & Lindenmayer 2007). Despite taxon-specific differences in response patterns, forest biodiversity generally declines along a coarse gradient from old-growth forest to secondary forest, agroforestry, plantations, arable crops and pasture (Schulze *et al.* 2004; Harvey *et al.* 2006; Basset *et al.* 2008; Philpott *et al.* 2008), broadly reflecting the decline in floristic and structural diversity. Consequently the retention or management of structurally and floristically complex habitats like agroforests and secondary forests can often ensure the persistence of some forest species in managed landscapes (Lamb *et al.* 2005; Scales & Marsden 2008; Pardini *et al.* in press). Nevertheless, chronosequence studies of regenerating forests demonstrate that biotic recovery occurs over considerably longer time scales than structural recovery, and that reestablishment of certain species and functional group composition can take centuries or millennia (DeWalt *et al.* 2003; Liebsch *et al.* 2008). Spatial heterogeneities and the landscape configuration of a particular land-use type can be critical in determining the total number of species it can support, as shown by the high species turnover among agroforest plots in Sumatra (Beukema *et al.* 2007). A major impediment to our understanding of biodiversity prospects in tropical forest

production landscapes is the lack of species data from some of the world's dominant and rapidly expanding monoculture systems (e.g. corn, sugarcane, rice, soybean and palm oil; e.g. Fitzherbert *et al.* 2008).

Biodiversity persistence in human-modified tropical forests is determined by biological fluxes across the entire landscape mosaic

A landscape perspective is essential for understanding modified tropical forest ecosystems because at some point in their life cycle most species experience their surroundings at spatial scales beyond the plot level, and biological fluxes (e.g. dispersal and foraging) within and between areas of forest and the managed matrix are common (Kupfer *et al.* 2006; Laurance 2008; Perfecto & Vandermeer 2008; Tscharntke *et al.* 2008). The extremely rapid proliferation of forest edges in areas of high deforestation and logging activity gives support to the suggestion that altered ecological processes and the spill-over of species across habitat boundaries are among the dominant factors structuring biodiversity patterns in modified landscapes (Ewers & Didham 2006). Although landscape-wide data are few, a growing body of detailed observational and experimental work has demonstrated that while area effects can be important (e.g. Ferraz *et al.* 2007), the persistence of forest species in remnants of modified tree cover frequently depends upon the need for species to access critical food or breeding habitat elsewhere (e.g. in the case of frogs Becker *et al.* 2007), and the interaction between the habitat quality of the matrix and species-specific differences in dispersal or 'gap-crossing' ability (e.g. Sekercioglu *et al.* 2002; Lees and Peres in press). There is mounting evidence to show that careful design and management of the matrix can help maintain not only species fluxes but also key ecological processes, such as through the establishment of live fences to enhance the movement of seed-dispersing birds and bats across agricultural landscapes (e.g. Medina *et al.* 2007).

Landscape context can have a profound influence on the prospects for biodiversity conservation in human-modified landscapes

Although much of landscape ecology has been conducted at the patch scale, differences in whole landscape mosaic properties, such as the amount and spatial configuration of native forest cover, are vital in understanding the value of modified forest landscapes for biodiversity conservation (Tscharntke *et al.* 2005; Bennett *et al.* 2006). Differences in topography and soil fertility ensure that the spatial extent and pattern of historical deforestation within individual landscapes is rarely random or consistent, and this can have a marked impact on levels of biodiversity retention (Kupfer *et al.* 2006). Arroyo-Rodríguez *et al.* (2009) found that forest patch size was only important for explaining species density–area relationships of plants in landscapes where historical deforestation was highest (Fig. 2) – an effect that

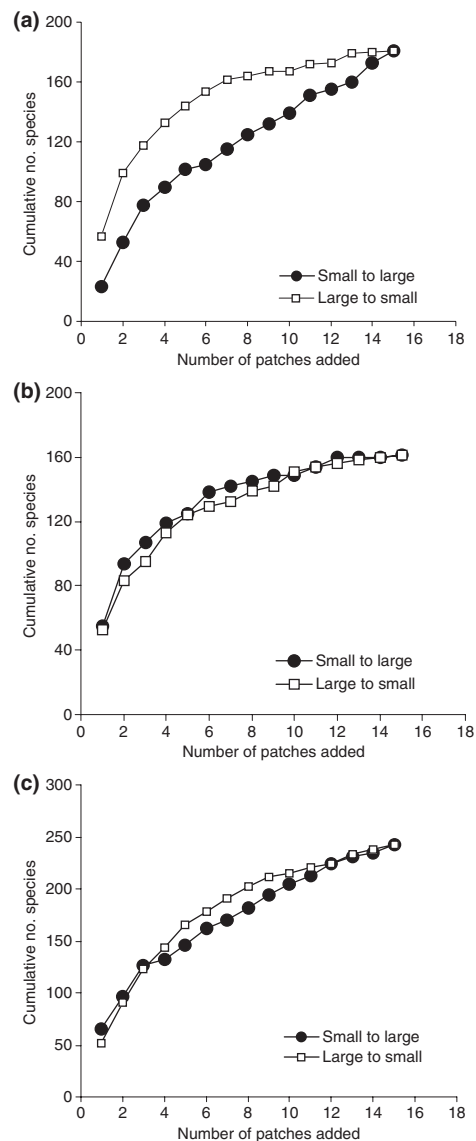


Figure 2 Threshold effect of landscape forest retention on species–density relationships. Data show the cumulative number of plant species against number of patches of remnant rainforest sampled in Los Tuxtlas, Mexico, in landscapes with different degrees of deforestation: (a) highest – 4% forest remaining, (b) intermediate – 11% remaining and (c) lowest – 24% forest remaining. The landscape with the highest level of deforestation is the only case that clearly shows a species–area effect, with species accumulating more rapidly when large patches of forest are added first. Data re-drawn with permission from Arroyo-Rodríguez *et al.* (2009).

may be due to a landscape fragmentation threshold, and/or severe defaunation of primary seed dispersers. However, it should be noted that landscape context encompasses much more than differences in the amount of forest cover. Sampling across limited environmental and geographical gradients can generate unreliable extrapolations of

biodiversity responses to land-use gradients elsewhere (Gillison & Liswanti 2004). Even when different landscapes are defined by similar environmental characteristics, small initial differences in disturbance regimes and human impacts can precipitate marked and cumulative divergences in species composition and ecosystem functioning through time (Laurance *et al.* 2007).

Ecological cascades and the indirect consequences of biodiversity change

Despite the difficulties inherent in untangling indirect drivers of biodiversity change, understanding the consequences of altered species interactions and the potential for co-extinction is fundamental to determining the future of biodiversity in modified terrestrial ecosystems (Koh *et al.* 2004; Laurance 2008; Tylianakis *et al.* 2008), and extending our perception of how biotic communities respond to landscape modification (Fig. 1). Salient insights from work on three qualitatively distinct drivers of ecological cascades in modified forest landscapes readily illustrate the need for more research in this area.

Trophic cascades

While the exact balance of top-down and bottom-up forces in the regulation of terrestrial ecosystems remains controversial, there is growing evidence that food web dynamics may play a critical role in the maintenance of tropical forest ecosystems. Terborgh *et al.* (2001) showed how the cascading effect of vertebrate predator removal from small land-bridge islands in Lago Guri, Venezuela, resulted in highly elevated densities of herbivores (including rodents, howler monkeys, iguanas and leaf-cutter ants), contributing to declines in seedling and sapling recruitment of nearly every plant species present (Terborgh *et al.* 2006), and the loss of some bird species (Feeley & Terborgh 2008). Although the artificial nature of the study conditions at Lago Guri limits our ability to extrapolate these findings to other landscapes, recent experimental work from other systems provides convincing evidence that the disruption of top-down trophic interactions may have severe consequences for tropical forest biodiversity. By excluding insectivorous birds and mammals from the forest floor Dunham (2008) observed a complex top-down cascade where elevated leaf-litter invertebrate densities were linked not only to increased seedling herbivory rates but also to reduced levels of microbivores and inorganic phosphorus in the soil. Similarly Koh (2008) showed that excluding birds from patches of oil palm resulted in a significant increase in insect damage to crop plants. These examples demonstrate that human-induced trophic cascades may be more prevalent than previously thought, and that their cryptic and complex nature often confounds the

ability of researchers to reveal either their mechanistic pathways or overall importance in structuring modified systems.

Cascading effects of changes to mobile-link species

Mobile-link organisms are those that actively move around landscapes and connect habitats across time and space through functional processes, including seed dispersal, pollination and nutrient recycling (Gilbert 1980). Within tropical forests particular attention has been paid to the indirect effects of over-hunting and habitat modification on vegetation communities following the demise of the large vertebrates on which so many plant species depend for primary seed dispersal (Wright 2003). Although declines in mammal populations are widespread across the tropics (Peres & Palacios 2007), non-random patterns of species loss and the mediating effects of changes in seed predation make it difficult to predict the longer-term consequences of vertebrate defaunation on the resilience of tropical forests. However, recent work by Terborgh *et al.* (2008) in Peru suggests that more attention is justified after they found evidence for a marked shift in tree composition in over-hunted tropical forests towards those species that are dispersed abiotically, and by smaller, non-game species. Casting the net more widely it is easy to find other examples where links between tropical forest species and the maintenance of key functional processes have been dislocated in human-modified systems, including the projected regional extinction of tree species which depend on fragmentation-sensitive birds for seed dispersal (da Silva & Tabarelli 2000), and the potential cascading effects of dung beetle declines on key functions such as seed burial, fly control and nutrient recycling following the loss of mammalian resource providers (Nichols *et al.* in press). Given the significant impact of landscape change on tropical forest invertebrates (Barlow *et al.* 2007; Basset *et al.* 2008; Tscharnkte *et al.* 2008) and our poor understanding of the functional roles performed by the vast majority of these species, it is very likely that these examples are only the tip of the iceberg.

Invasive species

For many tropical forest ecologists the threat of invasive species is barely on the radar. However, the changes precipitated by invasive species can often be highly cryptic and occur in areas that otherwise appear reasonably intact. Perhaps the starkest lesson of the potential ecological consequences of a single, successful invasive species is that of the brown treesnake (*Boiga irregularis*) on Guam (Mortensen *et al.* 2008). Since the introduction of the brown treesnake around 1950 most of the native forest birds, nearly half of the native lizards and two of Guam's three bat species have disappeared. These losses have also led to

reduced recruitment of plants that depend on flower-visiting birds for pollination. Examples of island systems that have become dominated by alien plant species abound in the literature, with Puerto Rico (Lugo & Helmer 2004) and Hawaii (Asner *et al.* 2008) representing particularly stark cases. While island systems are known to have a low resilience to the cascading effects of species declines following invasion, land-use intensification in human-modified tropical forest landscapes is also likely to enhance the spread and impact of exotic species on the mainland (Kupfer *et al.* 2006) – such as the case of the yellow crazy-ant *Anoplolepis gracilipes* in oil palm plantations (Fitzherbert *et al.* 2008) and agroforests (Bos *et al.* 2008) in South-East Asia.

Lag effects, thresholds and the emergence of novel tropical forest ecosystems

The key to understanding the resilience of today's modified tropical forest systems lies in both looking back at the past and peering into the future. The biophysical legacy of past human impacts provides the stage on which complex interactions between ongoing human activities, natural disturbance regimes and ecological processes play out to determine the future of tropical forest species (Fig. 1). Nonlinear dynamics, threshold effects and surprise are likely to be the norm rather than the exception in modified systems, and there is mounting evidence to suggest that accumulating human impacts, cascading biological processes and stochastic effects frequently conspire to generate ecological conditions that likely have no evolutionary precedents.

Lag effects

Legacies of human impacts on natural systems are remarkably persistent, and the constraints imposed by differences in site history are varyingly embedded in the structure and function of all forest ecosystems. However, long-term ecological data are rarely available, and it is difficult to deduce the extent to which human impacts in modified landscapes have yet to appear (Ewers & Didham 2006). Indeed, a major challenge in understanding the future of tropical forest species lies in reconciling the mismatch in temporal scale over which human impacts and ecological processes have acted out. Time-lags occur with respect to both biodiversity loss (extinction processes, Brooks *et al.* 1999) and gain (e.g. natural regeneration; Liebsch *et al.* 2008), and the level of inertia depends on species life-history traits such as dispersal and reproductive rates. Despite some success in matching observed and expected faunal declines to past forest loss (e.g. dung beetles in Madagascar; Hanski *et al.* 2007), the apparent persistence of some entire faunas in the face of widespread landscape change illustrates the

tremendous difficulty in making accurate predictions (e.g. butterflies in West Africa; Larsen 2008).

Threshold effects and regime shifts

Although many of the classical examples of threshold effects are from relatively simple, contained systems, such as lakes, there is growing empirical evidence to suggest that human modifications may frequently induce nonlinear effects on the structure, composition and function of complex tropical forests with potentially irreversible consequences. Support for this statement is given by three qualitatively very different examples that illustrate changes in the structure, composition and function respectively of tropical forest ecosystems. First, although difficulties in sampling across multiple landscapes mean that strong empirical support for a landscape threshold (where fragmentation effects act to compound the impact of habitat loss) is lacking, recent work indicates that severe deforestation can lead to marked changes in the distribution and flux of species across modified landscapes (Arroyo-Rodríguez *et al.* 2009; Fig. 2). Second, in studying the positive feedback loop between vegetation structure and fire Barlow & Peres (2008) recently reported that forest species composition in the central Amazon can almost completely turn-over following recurrent fire events, leaving behind a suppressed and biotically impoverished early successional stand (Fig. 3). Third, positive feedbacks between vegetation change and limiting nutrient resources can result in abrupt shifts in biogeochemical cycles, as shown by Lawrence *et al.* (2007) who reported that soil phosphorus declined by 44% after only three cultivation–fallow cycles in tropical Mexico.

Undesirable shifts between ecosystem states are caused by the combined influence of external forces and the internal resilience of the system (Folke *et al.* 2004). System resilience can be destabilized by positive feedback loops capable of driving regime change and high background levels of environmental adversity (e.g. drought cycles; Didham *et al.* 2005), or a correlation between response and effect traits in functionally important species groups (e.g. the loss of large dung beetles that are both sensitive to disturbance and play key functional roles in forest ecosystems; Nichols *et al.* in press).

Novel tropical forest ecosystems

The juxtaposition of many inter-connected structural, compositional and functional changes to tropical forest ecosystems has led to the recognition that human-modified landscapes host increasingly novel species assemblages, and patterns of species interactions that are unlikely to have evolutionary precedents (Hobbs *et al.* 2006; Tylianakis *et al.* 2008). Moreover, there is growing evidence to suggest that the rate of many ecological processes may be both magnified and accelerated in modified tropical forest

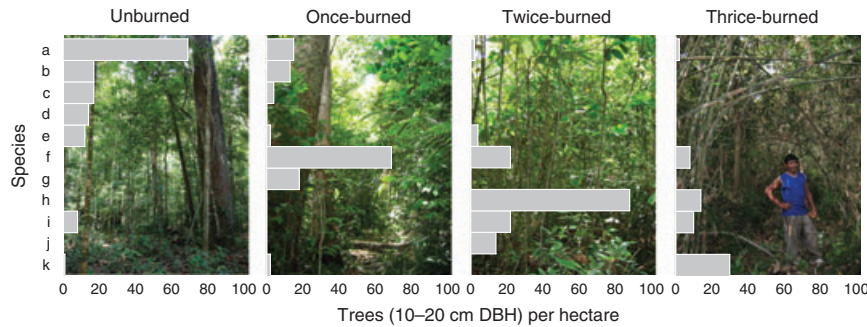


Figure 3 Compositional cascade of tree species composition and forest structure in unburned, once, twice and thrice-burned forest in the Brazilian Amazon. Bars show tree species and genera from the 10 to 20 cm DBH size class that had a density > 10 trees per hectare in at least one burn treatment. Background photographs show the understorey vegetation characteristic of each forest treatment. Tree species are (a) *Protium* and *Tetragastris* spp., (b) *Pouteria* spp., (c) *Sclerobium* spp., (d) *Rimorea* spp., (e) not identified, (f) *Cecropia* spp., (g) *Jacaranda copaia*, (h) *Bombax* sp., (i) *Inga* spp., (j) *Tapirira* sp. and (k) *Cordia* sp. Redrawn with permission from Barlow & Peres (2008).

landscapes, with unpredictable implications for the maintenance of biodiversity (Laurance 2002). Novel systems may foster new patterns of species loss as extinction is most likely to occur when new threats or combinations of threats emerge that are outside the evolutionary experience of species, or threats occur at a rate that outpaces adaptation (Brook *et al.* 2008). However, novel systems can also provide important refuges for recovering forest biodiversity in areas that have been subject to intense historical impacts. For example, in Puerto Rico the invasion of alien tree species to abandoned agricultural lands is thought to have played an important role in the recovery of native species (Lugo & Helmer 2004). Within agroforestry systems, the deliberate enrichment of degraded forest land with native species of subsistence or commercial value can significantly enhance levels of forest biodiversity at landscape and regional scales (Perfecto & Vandermeer 2008).

Although the definition of what constitutes a 'novel ecosystem' remains somewhat arbitrary, their emergence follows the selective loss and gain of key taxa, the creation of dispersal barriers or changes in system productivity that fundamentally alters the relative abundance structure of resident biota (Hobbs *et al.* 2006). Two compelling examples are the creation of 'new forests' in Puerto Rico that are composed of species assemblage structures that have not previously been recorded from the island (Lugo & Helmer 2004), and the fundamental alteration in the 3D structure of native Hawaiian rainforests following the establishment of alien plant species (Asner *et al.* 2008). Understanding the structure and function of novel ecosystems is of fundamental importance in evaluating patterns of biodiversity change, and the sustainability of conservation strategies within modified tropical forest landscapes (Chazdon 2008). Lessons learnt from natural disturbance and recovery dynamics may be of limited application in the management

of novel systems, which are structured by a novel combination of processes. Adjusting to this challenge, and ensuring that these novel ecosystems are managed to deliver lasting conservation benefits, represents a major priority for ecologists in the coming decades, especially when set against the backdrop of rapid climate change.

UNDERSTANDING THE CHALLENGE: THE SHIFTING SPATIAL AND TEMPORAL CONTEXT OF TROPICAL FOREST BIODIVERSITY IN A COMPLEX HUMAN-MODIFIED WORLD

Modified tropical forest landscapes in different regions of the world are distinguished by their evolutionary, biophysical, historical and present-day socio-economic context. These differences provide both challenges and opportunities for biodiversity conservation (Harvey *et al.* 2008). At the same time, tropical forests worldwide are facing an increasingly uncertain future due to the ever tighter coupling of human-ecological systems and the overarching influence of global environmental change. To be effective conservation management strategies for human-modified systems must take this context dependent and highly dynamic operational framework into account (Fig. 1).

The biogeographic and regional context of species vulnerability to anthropogenic disturbance

The conservation challenges facing practitioners in a given region can be strongly influenced by the underlying resilience of tropical forest biota and regional variability in the historical legacy of anthropogenic disturbance. Interpreting the importance of these factors is exacerbated by the difficulties in extrapolating from sparse research findings to poorly studied areas of the world.

Biophysical context

Hypotheses regarding biogeographic-scale variability in the vulnerability of forest biota to human activities are difficult to test empirically. Nevertheless, we identified seven such hypotheses, each with varying levels of support, which deserve further study.

1. Regional differences in the contraction and expansion of tropical forest areas during the Pleistocene may have rendered some biota more resilient to anthropogenic disturbance (as proposed for tropical Africa; Danielsen 1997).
2. Biogeographic variability and differences in the interconnectedness of adjacent biomes can have a strong influence on disturbance responses – as shown by the higher levels of diversity and species turnover in dung beetle assemblages within West African plantation forests in areas where rainforest is naturally interdigitated with extensive areas of savannah (Davis & Philips 2009), compared to similar yet species-poor plantations that are embedded within continuous rainforest of lowland Amazonia (Gardner *et al.* 2008a).
3. Differences in ecosystem productivity can determine underlying differences in ecological resilience, as shown in the variable response of large mammal assemblages to hunting pressure across the Amazon basin (Peres 2000).
4. Species at the edge of their geographical distribution or at the upper limit of their altitudinal range are likely to be particularly prone to extinction in the face of landscape change (either due to physiological or dispersal constraints), as demonstrated by the fact that 37% of the birds that have gone extinct from San Antonio, Colombia, in the last century were at the limit of their altitudinal range (Kattan *et al.* 1994).
5. Historical exposure to natural disturbance regimes such as fire and wind damage may increase the resilience of some tropical forest biota to human activities. Robust tests of this hypothesis are lacking, but abnormally severe disturbances (such as frequent wildfires in areas that rarely burn) have been shown to precipitate disproportionate species losses (e.g. high levels of large tree mortality following wildfire in the Amazon; Barlow *et al.* 2003).
6. Island systems may be more prone to the cascading effects of species loss on mutualistic interactions (e.g. pollination) than mainland tropical forests due to lower levels of functional redundancy (Cox & Elmqvist 2000).
7. Regional differences in levels of endemism, driven partly by geological legacies, can have a significant influence on the global consequences of local human impacts. For example some tropical forest regions exhibit much higher background levels of beta-diversity

than others (e.g. Panama vs. western Amazonia; Condit *et al.* 2002).

Legacies of anthropogenic disturbance

High levels of inter-regional variability in both historical (FAO 2006) and ongoing rates of deforestation (Hansen *et al.* 2008) have important implications for biodiversity conservation prospects in different areas of the tropics. For example, some regions have already lost most old-growth forests and the dominant near-forest vegetation is often either secondary forest (Neeff *et al.* 2006), or some form of agroforestry (e.g. shade-coffee and cacao, jungle-rubber and home-gardens; Scales & Marsden 2008). These past human impacts have imposed species filters on regional biota, and have led not only to reductions in both alpha and beta-diversity through species loss and biotic homogenization, but also to localized increases in diversity following colonization (assisted or otherwise) by species from non-forest ecosystems. Consequently, the vulnerability of existing biotic communities to contemporary anthropogenic disturbance is conditioned by the extent to which past human impacts have selectively driven more vulnerable species to local or regional extinction (Balmford 1996), and facilitated the arrival of non-native species. Species that have survived such extinction filters are inherently more resilient to many present-day perturbations, which may explain the failure of species–area models to accurately predict species loss in regions that have already experienced widespread deforestation (e.g. Brazilian Atlantic Forest; Brown & Brown 1992).

Shifting baselines

One important consequence of large-scale regional deforestation and forest degradation is that ecologists are limited to measuring contemporary human impacts against a continuously shifting baseline. Few long-term species time-series data exist for tropical forest sites, but a compilation of available studies questions the accuracy of baseline data from areas of forest that are presumed to be undisturbed by revealing a persistent and marked pattern of species loss over the last century in different locations across the world (Table 2). Species data from un-manipulated sites are critically important for informing conservation assessments and restoration targets, and the fact that so many human-modified tropical forest sites exhibit such dynamic baselines poses a serious challenge to ecologists who need to readjust to continuously shifting goalposts across both space and time.

Research transfer

It is impossible to know everything about everywhere. As such ecologists consistently depend upon a process of

Table 2 Shifting biodiversity baselines in long-term tropical forest study sites

Study	Region	Species group	Time period	Observed biodiversity loss at local scale	Suggested cause of biodiversity loss
Castalletta <i>et al.</i> (2000)	Singapore	Birds	1923–1998	31% of total original species (203) and 67% loss of original forest species (91)	Forest loss (only 5% cover remains)
Trainor (2007)	Damar island, Indonesia	Birds	1890–2001	17% loss of original forest species (38)	Forest loss and degradation (75% forest cover remains)
Kattan <i>et al.</i> (1994)	Colombian Andes	Birds	1911–1990	31% loss of original forest species (128)	Forest loss and fragmentation
Sodhi <i>et al.</i> (2006)	Bogor Botanical Garden, Indonesia	Birds	1931–2004	59% loss of original species (97)	Forest loss, isolation and disturbance
Robinson (1999)	Barro Colorado Island Panama	Birds	1923–1996	36% loss of original forest and edge species (193)	Isolation effects
Sigel <i>et al.</i> (2006)	La Selva, Costa Rica	Birds	1960–1999	Approximately 20% species increased (open habitat generalists) and 20% species decreased (understorey specialists) in abundance	Area and isolation effects
Hanski <i>et al.</i> (2007)	Madagascar	Dung beetles	1953–2006	43% loss of original species (51)	Forest loss (only 10% cover remains)
Escobar <i>et al.</i> (2008)	La Selva, Costa Rica	Dung beetles	1969–2004	Decreased species richness and community evenness	Isolation and habitat loss in neighbouring landscape
Mortensen <i>et al.</i> (2008)	Guam, Pacific Ocean	Birds, lizards, bats	1960–2003	81% loss of original forest birds (11), 50% loss of native lizards (12) and 66% loss of native bats (3)	Introduced brown treesnake (<i>Boiga irregularis</i>)
Whitfield <i>et al.</i> (2007)	La Selva, Costa Rica	Amphibians and lizards	1970–2005	75% decline in total densities of leaf-litter amphibians and lizards	Reduction in leaf-litter due to climate change

knowledge transfer between places and across time to provide the theoretical and empirical context necessary to interpret biodiversity patterns and inform management strategies. Understanding the validity of this transfer process is a research priority in its own right. Severe geographical biases in the distribution of research effort across the tropical forest biome clearly highlight the problem facing conservation scientists and practitioners working in poorly studied landscapes and regions (Fig. 4). The extent of the problem is further evidenced by the fact that a significant proportion of biodiversity studies from across the tropics make some level of comparison with research findings that are derived from a small number of well studied human-modified landscapes (e.g. the Biological Dynamics of Forest Fragmentation Project in Brazil, and Las Cruces research station in Costa Rica; Fig. 5). In the search for expediency there is a real danger that false ecological narratives can be propagated from a limited set of context-specific studies or localities, leading to inappropriate knowledge transfers and misleading paradigms that could hamper the development

of effective conservation strategies in less well studied areas of the world. Specific examples of the inappropriate generalization of research findings across regions and systems are commonplace and include the lumping of human-modified forest systems into single ecological categories (e.g. 'secondary forests', 'plantations' and 'agroforestry') despite high levels of internal heterogeneity in biophysical properties and management regimes, the assumption that rankings of relative biodiversity value across these land-uses are regionally consistent irrespective of fundamental inter-study differences in landscape context and research design, and the incorrect assumption that all small forest fragments slowly implode over time due to edge effects (e.g. Schedlbauer *et al.* 2007).

Uncertain futures

Human-modified tropical forest landscapes are the product of highly dynamic and interdependent human–ecological systems. The uncertainty that is derived from this close

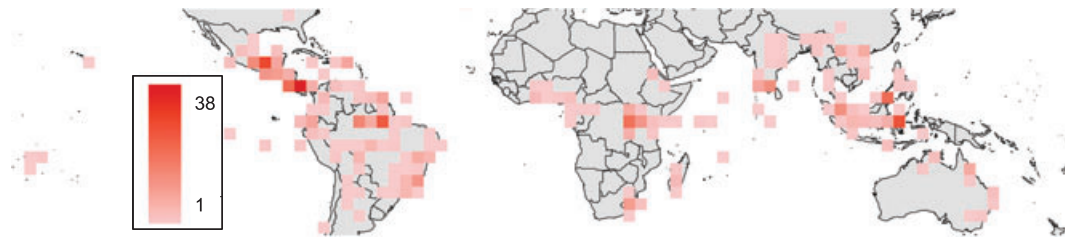


Figure 4 Summary of research effort on biodiversity in human-modified tropical forest landscapes. Colour scale is linear and illustrates the number of single species group biodiversity studies in modified tropical forest landscapes in each 4-degree grid cell. The global distribution of individual studies clearly shows that some areas of the tropics have received significant researcher attention (Central America, Atlantic Forest of Brazil) compared with others (western Amazon, West Africa, Papua New Guinea). The majority of studies are concentrated in a few places, with 16% of the total number of study sites accounting for 50% of the total research effort. Analysis is based on a database selected from a global keyword search on Thompson ISI, Biosis and Zoological Records from 1975 to 2008 that included the terms: (bird* OR mammal* OR reptile* OR amphibia* OR arthropod* OR plants* OR lepidoptera* OR hymenoptera* OR arachnid* OR coleoptera* OR diptera* OR homoptera* OR isoptera*) AND (Tropical forest* OR tropics) AND (clear-cutting* OR log* OR deforestation* OR fire* OR agriculture conversion* OR disturbance* OR degradation* OR secondary forest* OR plantation* OR fragment*). Selecting only those studies that reported data on the change in biodiversity for at least one taxon between a control and disturbed area, the final database included 591 comparative studies (including multiple entries for multi-taxa studies) from across the world.

coupling, together with the likely pervasive impacts of climate change through a wide array of synergistic and feedback effects, adds a layer of complexity to applied ecological research that has only started to gain appreciation within the scientific community.

Coupled human–ecological systems

Increasing globalization of human activities and rapid movements of people, goods and services suggest that mankind is now in an era of novel coevolution of ecological and socio-economic systems at regional and global scales (Liu *et al.* 2007). Untangling the complexities of these couplings, such as legacy and feedback effects, thresholds, cross-scale processes and emergent properties could play a critical role in developing ecologically sustainable management strategies for tropical forest systems. One consequence of the dynamic nature of the socio-economic systems that govern tropical forests is the fact that many modified landscapes exist as highly unstable spatio-temporal mosaics (Bennett *et al.* 2006; Neeff *et al.* 2006; Pressey *et al.* 2007) which are often governed by complex, multi-scale market and regulatory pressures. Understanding the dynamics of landscape mosaics is vital to understanding the long-term persistence of biodiversity in human-modified systems.

The spectre of climate change

Global climate change is certain to influence the challenges and opportunities facing tropical forest conservation in profound and complex ways. In many circumstances the threat imposed by climate change is superimposed on a system whose resilience is already weakened by past and

ongoing human activities. There are a number of ways in which tropical forest species may suffer from climate change impacts. Tropical forest ectothermic species may be inherently vulnerable to climate warming, because many of them live in constant shade and are not generally adapted to the high operative temperatures found in warmer, open habitats (Tewksbury *et al.* 2008). Moreover, much of the tropics lack a source pool of species adapted to higher temperatures that can replace those that will be driven up altitudinal gradients by warming, raising the threat of ‘biotic attrition’ in species diversity within lowland forests (Colwell *et al.* 2008). Even where species source pools exist, the constraints imposed on climate-induced range expansion by landscape change may mean that many forest species are reshuffled into non-analogue communities with unpredictable effects on biotic interactions and functional processes (see Tylanakis *et al.* 2008). The effects of climate change on the stability of tropical forests can be particularly severe when mediated through the exacerbation of disturbance regimes, as seen following the devastating spread of wildfire in the Amazon after severe droughts in 2005 (Aragão *et al.* 2007). Finally, novel climate systems may increase the likelihood of single, yet potentially catastrophic ecological changes such as the introduction, establishment and spread of non-native species (Brook *et al.* 2008).

Most of these possible interaction effects are tentative hypotheses that lie at the frontiers of our current scientific understanding and require urgent research attention. For example, suggestions that global environmental change, including climate change, may be driving increases in the rate of vegetation dynamics in the Amazon basin (Phillips

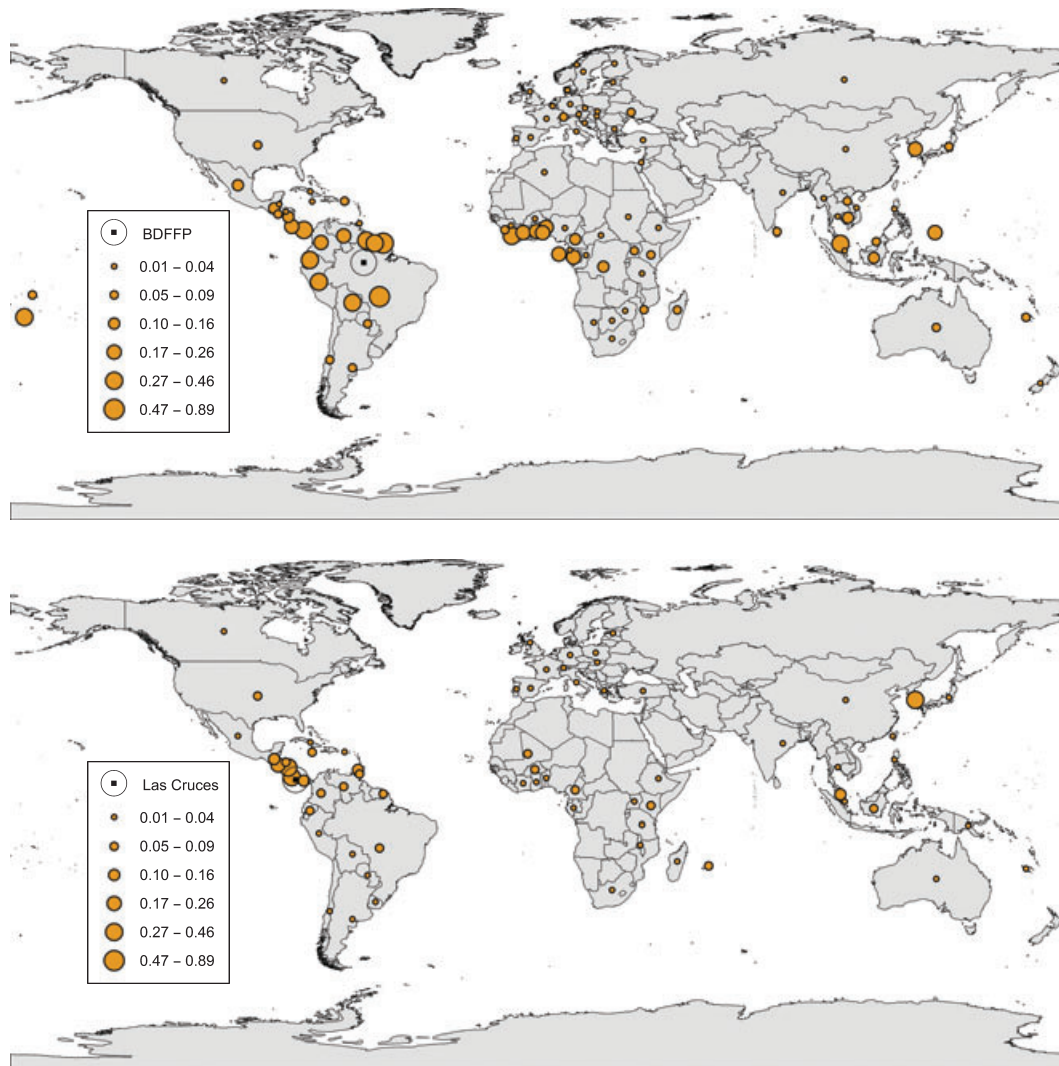


Figure 5 Transfer of research findings from two very well-studied human-modified tropical forest landscapes (Biological Dynamics of Forest Fragmentation Project, Manaus, Brazil, and Las Cruces, Costa Rica) to other countries in the world. These two landscapes have been host to two pioneering projects on fragmentation effects and the conservation value of human-modified landscapes respectively. Points on map represent centroids for each country, where the size of each point is determined by the number of times a study published from either Manaus (a) or Las Cruces (b) between 1998 and 2003 was cited by work from that country divided by the total volume of relevant research produced in the country (estimated using the keywords: conservation *OR* biodiversity *OR* ecology). For a significant number of countries more than half the research papers on biodiversity conservation, on average, cited work from Manaus and Las Cruces, with the effect being even stronger for the Manaus project.

et al. 2004) have been contested by subsequent analyses from other tropical forest sites which instead suggest that many forests are still recovering from previous anthropogenic disturbances (Chave *et al.* 2008). It should also be recognized that climate change may precipitate nonlinear dynamics in coupled human–ecological tropical systems, e.g. through the migration of human populations from drought-stricken or flooded regions, and accelerating rates of land-use change such as the rapid expansion of biofuels into

native forests and areas formerly dedicated to food crops, and the displacement of agriculture into existing protected areas.

Unknown unknowns

Predictions of the future of tropical forest species need to acknowledge the possibility of truly unpredictable and surprising events. The more interconnected tropical forest systems become through dynamic changes in coupled

human–ecological systems and the impacts of climate change, the greater the chance of real surprise. Turner *et al.* (2003) demonstrate one such unpredictable event in the Yucatan peninsular – where a hurricane impact coupled with drought led to particularly severe dry season fires, precipitating the spread of the invasive bracken fern (*Pteridium aquilinum*), which in turn led to the migration of farmers away from affected areas and increased forest clearance in undisturbed land.

UNDERSTANDING THE OPPORTUNITY: STRUCTURING A NEW RESEARCH AGENDA FOR BIODIVERSITY CONSERVATION SCIENCE IN THE HUMAN-MODIFIED TROPICS

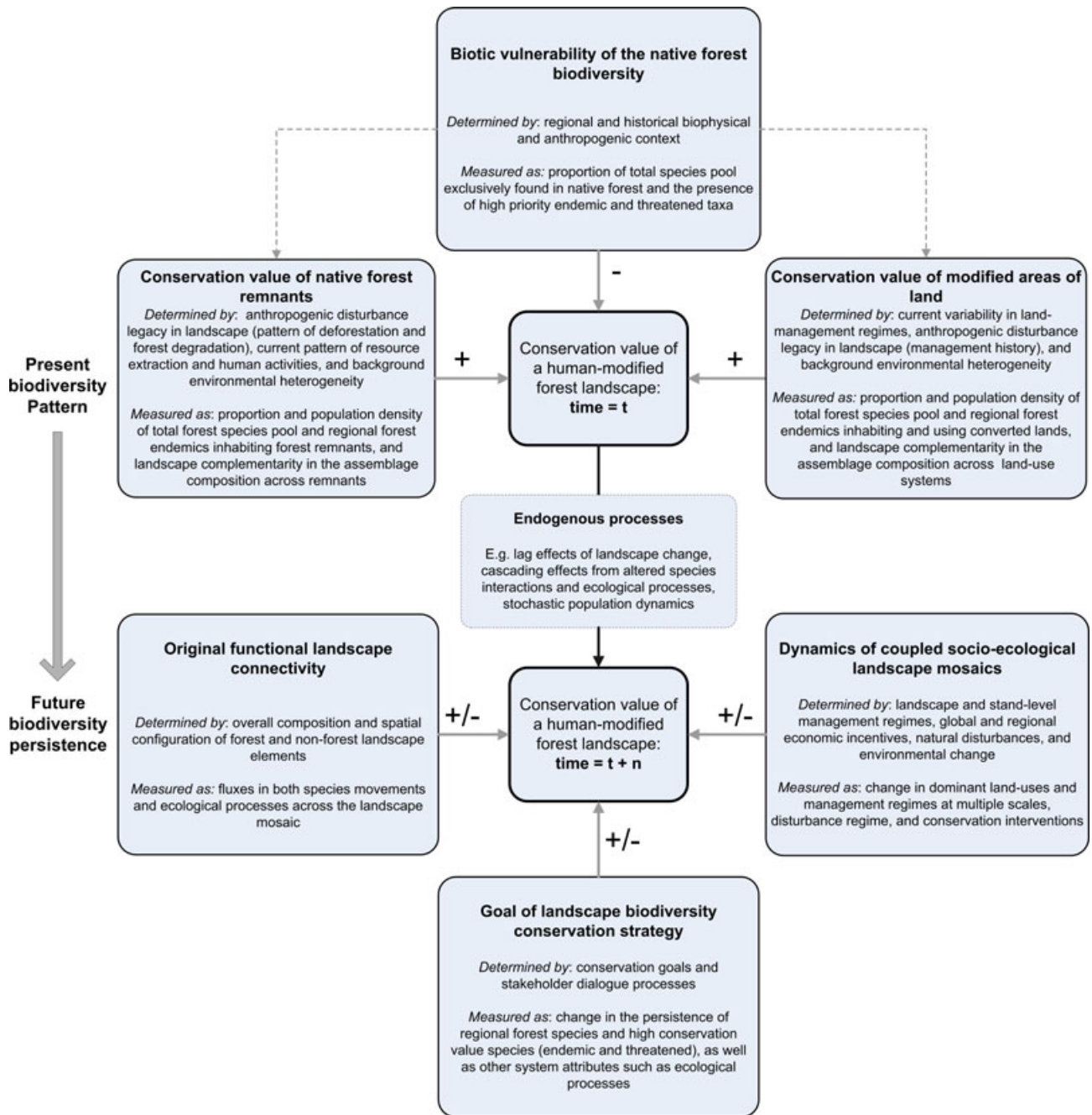
A new conservation science research agenda is required to help meet the challenge of developing sustainable conservation strategies for the human-modified tropics that goes beyond the designation of strictly protected areas and embraces a more holistic, integrated landscape level approach (Chazdon *et al.* 2009). There is much that we do not know, and much existing research may be of little relevance to practical concerns (Meijaard & Sheil 2007). Drawing upon the foregoing synthesis it is clear that context dependency, complexity, and uncertainty are defining characteristics of the challenge that lies ahead. Effectively confronting this challenge requires us to work within a clear and comprehensive framework that builds upon existing knowledge and guides research efforts towards exploiting

newly emerging opportunities for enhancing biodiversity conservation prospects in the human-modified tropics.

Defining the spectrum of opportunity for conserving tropical forest biodiversity in modified lands

Landscapes in varying stages of human modification are receptive to different forms of conservation management (Tschardtke *et al.* 2005). Appropriate management strategies for particular landscapes must be based on an understanding of the relative importance of the interacting human and biological drivers of spatial and temporal dynamics of resident biodiversity (Fig. 1, and foregoing discussion). Yet even if it were possible, achieving this understanding will require decades more research, and urgent conservation action is needed to safeguard the future of tropical forest species. For science to succeed in providing practical guidance to conservation managers it is necessary for theoretical and empirical developments in ecology to be continuously fed into a dynamic planning framework, composed of quantifiable landscape elements and processes, that is able to position individual landscapes on a broad spectrum of opportunity for enhancing biodiversity conservation in modified forest systems (Fig. 6). The framework we propose draws upon the traditional framework of vulnerability and irreplaceability developed within systematic conservation planning (Margules & Pressey 2000), and integrates key lessons learnt from landscape ecology that have thus far been lacking from many science-based

Figure 6 A conceptual framework for understanding the value of human-modified forest landscapes for biodiversity conservation. Evaluating potential conservation prospects in a given landscape requires an understanding of present-day biodiversity patterns as well as the potential for long-term biodiversity persistence. The context-dependent nature of biodiversity in human-modified tropical forest systems is determined by key quantifiable factors that position a given landscape along a broad spectrum of potential conservation opportunity. Challenges for ecological science lie in identifying the components and processes that determine each of these factors, how they relate and interact with each other, and how they can be most reliably measured to provide a practical basis for conservation planners. This framework builds on the critical synthesis presented in this review and provides a working progress towards achieving these goals. An initial appraisal of the relative conservation value of a modified landscape mosaic is provided by assessing the biotic vulnerability of the native forest baseline, which can be measured through the number of species that are found exclusively within large areas of old-growth forest habitat. Although identifying this number is fraught with uncertainty, the greater the number of species that appear to depend upon intact habitat, the lower the conservation return that can be derived from investing in the management of modified land. Landscape-wide patterns of biodiversity value are determined by the composition and configuration of both native forest remnants and converted lands, the value of which is enhanced by the extent to which individual landscape elements are host to any species that occurs in old-growth forest from the regional pool, as well as landscape-wide complementarity (beta-diversity) in species composition (the irreplaceability of individual landscape elements). To understand how biodiversity patterns may translate into long-term patterns of species persistence it is necessary to superimpose our understanding of functional connectivity in species movements and ecological processes across the entire landscape mosaic, and predictions of future landscape dynamics from natural and human-linked disturbance regimes, on the existing structure of the landscape. Understanding species movement potential and landscape dynamics are central ingredients in understanding how well extant biodiversity patterns will persist into the future. A major additional challenge in extrapolating from biodiversity patterns to biodiversity persistence lies in disentangling the importance of lag and cascading effects that are precipitated by past disturbances. Finally, it should be self-evident that any projections of long-term conservation opportunities and landscape dynamics need to be made in the context of clear conservation goals (including any specific target species, vegetation types) and implementation strategies (and associated social, political and economic constraints and uncertainties).



planning discussions (Lindenmayer *et al.* 2008). This simple framework aims to direct the contribution of ecological science in modified landscapes in a world where conservation opportunities vary dramatically from place to place and over time. Two elements are central to our approach. First is the need to recognize modified landscapes as contiguous land-use mosaics, where the benefits of all possible conservation interventions need to be evaluated jointly across the entire landscape, including both protected areas

and the range of land-use and management options that are available outside forest reserves. Second is the need to recognize the highly dynamic nature of modified landscapes, with respect to both internal biodiversity processes and cross-scale human–ecological interactions, by directing our science towards planning for species persistence rather than static biodiversity patterns (see Tscharntke *et al.* 2005; Pressey *et al.* 2007). This is particularly true given the spectre of ongoing climate change.

Defining the potential for biodiversity conservation in human-modified forest systems is only the first step towards achieving actual conservation action on the ground. Science can do no more than provide an informed context for what is ultimately a societal choice. Nevertheless, the conservation opportunities that we outline provide the necessary context-sensitive template upon which the implementation capacity and conservation values of the stakeholders that ultimately determine the nature of any future management regime can be overlain. Recognizing the importance of the coupled social–ecological system within which tropical forest landscapes are embedded is a key step in informing a more useful and context-sensitive sustainability science that can make tangible contributions to the actual implementation of conservation plans (Turner *et al.* 2003).

Looking ahead

Adopting a more holistic framework for identifying conservation opportunities in human-modified landscapes cannot be achieved by a focus on conventional research approaches and methods alone. Alongside identifying key knowledge gaps (see Chazdon *et al.* 2009), a new research agenda needs to be effective at incorporating new tools and approaches, both conceptual and analytical, that have the potential to bridge the divide between theory and practice and translate policies into effective field implementation. Here we highlight five key elements of a revised agenda that can facilitate the development and application of a more holistic framework (Fig. 6), and, if implemented, could go a long way towards addressing the challenges laid out in this review and contribute significantly to the conservation of tropical forest biodiversity.

Recognize and assess land-use trade-offs

Biodiversity conservation in the human-modified tropics will not be successful unless it first recognizes that although some synergies may be possible, fundamental societal trade-offs between competing land-uses exist (DeFries *et al.* 2004). Agroforestry and ecoagriculture offer much promise for conservation in regions that have lost large amounts of native forest and are threatened by further agricultural intensification (Perfecto & Vandermeer 2008), yet the potential biodiversity benefits need to be set against the opportunity costs (in both monetary and rural development terms) of passing over more intensive land-uses that are usually more productive in the short term. Rather than proposing blanket solutions, a more pragmatic approach is to examine how distinct landscapes can be designed to achieve multiple objectives, including biodiversity conservation, the maintenance of ecosystem services and improved human well-being (Lamb *et al.* 2005).

Integrate conservation research and management across entire landscape mosaics

Managing for landscape structure, natural disturbance regimes and restoration invariably needs to occur at the scale of entire landscapes (Tschardt *et al.* 2005; Chazdon 2008; Chazdon *et al.* 2009). It is therefore vital that ecological research adopts the same broad perspective and breaks out of patch and single-process based models to embrace the full conceptual framework of complex interactions among structural and biotic elements of human-modified landscapes (Fig. 1), and how such elements combine into emergent properties that can be evaluated and managed for conservation (Fig. 6). Rapidly developing techniques from decision theory, including optimization modelling can make a significant contribution to the construction of whole-landscape management regimes by evaluating the potential biodiversity benefits (e.g. based on the coverage of a wide range of forest species and analysed based on patterns of species composition) and socio-economic costs of a wide array of alternative management and intervention strategies beyond simple reservation (e.g. Wilson *et al.* 2007). In addition, such approaches can help integrate planning for other ecosystem services (such as carbon sequestration and flood regulation), identify where conflicts lie, and open up the way for novel and potentially significant conservation opportunities through financing initiatives such as reduced emissions from deforestation and degradation (REDD; Miles & Kapos 2008). Finally, synergistic interactions among the drivers of change mean that management interventions may need to operate in unison to be effective (e.g. reservation creation and hunting restrictions; Harvey *et al.* 2006), yet we have few data on the benefits of integrated conservation strategies.

Recognize and assess the inherent scale-dependency of sustainable land-management strategies

Optimized allocation approaches to land management mean that trade-offs are easier to reconcile at larger spatial scales (Lamb *et al.* 2005), and conservation science in human-modified systems needs to develop in full recognition of the hierarchical and cross-scale influences that define coupled human–ecological systems. The problem of scale-dependency in coupled social–ecological processes means that solutions are frequently developed that are largely insensitive to the contingent properties of the system or problem under question. This in turn gives rise to the endemic problem of inappropriate knowledge transfer (Fig. 5), and the emergence of misleading ‘silver-bullet’ solutions or panaceas (Ostrom 2007). The compilation of comparable data sets from across multiple spatial and temporal scales will likely generate significant insights regarding the drivers of biodiversity change in modified systems. Such endeavours can be assisted by improving the selection of cost-effective

indicators for intensive biodiversity sampling programmes (Gardner *et al.* 2008b). Although such indicator groups cannot, by definition, provide reliable information on changes in non-focal species groups, they can help ensure we gain the maximum amount of ecologically useful information for a limited research budget.

Recognize that change is constant in human-modified systems

Sustainability is concerned with managing for persistence under uncertainty. Change is an inevitable and pervasive characteristic of all complex systems, and its quantification through the integrated study of successional dynamics, variable and dynamic threats and spatial-temporal mosaics, evolutionary processes and climate uncertainty needs to become a research priority for conservation work (Pressey *et al.* 2007; Lindenmayer *et al.* 2008).

Embrace other disciplines

Calls for interdisciplinary research have reached a crescendo in recent years, and this could not be more relevant in modified tropical forests characterized by high levels of threat, biotic diversity and social-ecological complexity. Working with social and political scientists and agronomists is crucial for understanding both current and future patterns of land use, and which proposed interventions are most likely to be effective when implemented in human-modified landscapes (Knight *et al.* 2006).

Adopt an inclusive and flexible approach to learning

Enhancing our capacity to learn is a basic research priority that should underlie any research agenda. Pluralism and adaptability are central tenets of an interdisciplinary science that is capable of delivering robust and context-sensitive conservation strategies. Taking a pluralistic approach to research involves exploring a large portfolio of options and approaches to enhancing biodiversity in managed tropical forests beyond straightforward land purchasing, as well as a diverse number of ways of evaluating them. Being adaptive means viewing modified forest landscapes as research arenas and collecting comprehensive monitoring information that can be fed back into revised programmes of management and research. We will threaten the credibility of science and fail to exploit many novel conservation opportunities if we cannot effectively report on management performance and respond to emerging opportunities (such as REDD) or threats.

Concluding remarks

The challenge of safeguarding the future of tropical forest species is daunting. Spatial and temporal patterns of biodiversity are the dynamic product of a myriad of interacting human and ecological processes which vary

radically in their relative importance within and among regions, and have effects that may take years to become fully manifest. Ecologists have little option to avoid the challenge of untangling this complexity as very few, if any, tropical forest species exist in isolation from human interference. To avoid being overwhelmed it is necessary to step back and visualize the full extent of the problem. Here we have outlined a clear and comprehensive conceptual framework which can help identify the specific contributions of both individual research efforts and interventions to conserve biodiversity in modified systems. We show, for example, ways in which the interpretation of biodiversity research findings is frequently made difficult by constrained study designs, low congruence in species responses to disturbance, shifting baselines and an over-dependence on comparative inferences from a small number of well studied localities. We further illustrate how landscape and region-wide differences in biotic vulnerability and anthropogenic disturbance legacies can generate marked spatial and temporal heterogeneities in the likely prospects for biodiversity conservation. By building a more holistic understanding of the relative importance of individual drivers of biodiversity change under different contexts, as well as the factors that determine the reliability of individual research findings, it is possible to draw a line under largely resolved issues, discard unproductive directions of enquiry, and direct future conservation research and action to where it is most needed. Ultimately conservation scientists need to hold sustainability as a vision for human-modified tropical forests and maintain the principle of continuous ecological improvement as the driving force behind efforts to enhance the prospects for tropical forest biodiversity in an increasingly human-modified world.

ACKNOWLEDGEMENTS

We thank Renata Pardini, Júlio Louzada, Julieta Benítez-Malvido, Lian Pin Koh, Jason Tylianakis, Richard Bardgett, Ben Phalan and two anonymous referees for valuable comments that helped improve earlier versions of this manuscript. T.A.G. thanks Fundação de Amparo à Pesquisa do Estado de Minas Gerais, N.S.S. the Sarah and Daniel Hrdy Fellowship, and R.L.C. the U.S. National Science Foundation (DEB-0639393) for funding while writing this manuscript.

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Editor, Marcel Rejmanek

Manuscript received 30 October 2008

First decision made 16 December 2008

Manuscript accepted 3 February 2009