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Review

Impacts of warming on tropical lowland rainforests

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Before the end of this century, tropical rainforests will be subject to climatic conditions that have not existed anywhere on Earth for millions of years. These forests are the most species-rich ecosystems in the world and play a crucial role in regulating carbon and water feedbacks in the global climate system; therefore, it is important that the probable impacts of anthropogenic climate change are understood. However, the recent literature shows a striking range of views on the vulnerability of tropical rainforests, from least to most concern among major ecosystems. This review, which focuses on the impact of rising temperatures, examines the evidence for and against high vulnerability, identifies key research needs for resolving current differences and suggests ways of mitigating or adapting to potential impacts.

Tropical rainforests and climate

Until recent clearances, tropical lowland rainforests (TRFs) occupied all land with a mean annual temperature $>20\,^\circ$C, mean annual rainfall >1800 mm and, at most, a brief dry season [1]. Excessively high temperatures do not currently exclude TRF from any land area, so the observed 'climate envelope' is open topped, with no upper limits for warmth. During the 1960s, the warmest TRFs had a mean annual temperature of $28\,^\circ$C, but their absence from warmer areas was apparently controlled by lack of rainfall, rather than excessive temperatures [2]. Hence, the absence of TRF organisms at higher mean temperatures is not evidence that they cannot tolerate warmer conditions: just that this ability is not expressed anywhere at present [3].

Among the climatic threats to TRFs, drought has received most attention [4–6] (Box 1); however, the most pervasive climatic impact in tropical lowlands will be higher temperatures [2,7,8] and this is the focus here. All TRFs will be warmer (by at least 2–4 $^\circ$C by 2100 if current projections are correct), whereas rainfall might increase or decrease, and its prediction is still model dependent. It is not possible, however, to separate warming from changes in water relations. The vapor pressure deficit increases exponentially with a linear rise in temperature, so warming increases water stress even when rainfall is unchanged, although in plants this will be offset, at least partly, by a reduction in transpiration flux as a result of adaptations to rising CO_2 [9]. Conversely, water stress reduces the potential for cooling by transpiration, drought-induced canopy leaf fall increases subcanopy

temperatures and the cloudless skies associated with droughts can increase radiative heating in the canopy. The links between warming and water relations are probably crucial for the carbon balance, considered below, but current understanding of the relationship between leaf-level plant physiology and overall plant hydraulics is still insufficient for an integrated consideration of these factors.

How vulnerable are tropical rainforests?

In general, the TRF pessimists, who believe these forests and their biotas are highly vulnerable, point to the fact that the projected increase in temperature in the lowland tropics will be large relative to present variability [2,10–12], whereas the TRF optimists point to relatively small absolute increases [13,14]. It is not obvious that either of these assumptions is, *a priori*, more accurate, but they predict radically different consequences. If the observed, realized, thermal niches of the TRF biota are used to predict their future survival, then warming by 5 $^\circ$C would lead to an almost 100% loss of biodiversity from the Amazon basin [3]. By contrast, if it is assumed that fundamental thermal niche breadths of tropical lowland species are similar to species from cooler areas, the losses will be much lower. Moreover, if short periods of very high temperature, rather than averages, are the major concern, then lethal temperature spikes are less likely in the equatorial tropics, where diurnal, annual and interannual temperature ranges are all very narrow, than at higher latitudes [15]. Optimists

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Glossary

Acclimation: the process by which an individual organism adjusts to changes in the environment during its lifetime, enabling it to maintain performance.

Adaptation: the evolutionary process by which a population adjusts to changes in the environment over multiple generations, enabling it to maintain performance.

Dynamic global vegetation models (DGVMs): computer models that simulate changes in potential vegetation and ecosystem processes in response to future climate change. Unlike earlier models, which considered only the equilibrium response of vegetation to climate change, DGVMS are able to simulate transient vegetation dynamics. Current DGVMs model a variety of plant processes, including photosynthesis, respiration, stomatal conductance, competition, establishment and mortality, but greatly simplify or omit others, such as seed dispersal, and reduce plant diversity to a small number of plant functional types.

El Niño-Southern Oscillation (ENSO): a quasiperiodic change in the ocean–atmosphere system that occurs at irregular intervals of 2–7 years. ENSO is recognized by coupled variations in sea-surface temperature and air pressure over the tropical Pacific Ocean, but has worldwide consequences for weather and climate.

Transpiration flux: the rate of loss of liquid water contained in a plant to the atmosphere as water vapor.

Vapor pressure deficit: the difference between the amount of water in the air and the amount of water the air can hold when it is saturated.

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Box 1. Droughts and fires in tropical rainforests

The potential modern distribution of TRFs is determined by minimum temperature, rainfall, and the length and severity of the dry season [1], so it is not surprising that drought features prominently among fears for the future of TRFs in a warming world [4,5]. Although many climate models predict an increase in drought frequency and severity in much of the tropics [7], confidence in these predictions is fairly low, in part because of continued uncertainties about the impacts of global warming on ENSO (Box 2). Most existing TRFs already experience a 2–3 month dry season and there is little evidence that this results in damage to plants in normal years, as a result of a variety of adaptive mechanisms, including the hydraulic redistribution of water within the soil profile [27]. However, tree growth and net primary production fall in severe droughts, and tree mortality increases, offsetting the net increase in biomass in non-drought years [5,82]. Comparisons between species that do and do not extend into seasonal forests suggest that the drought sensitivity of many TRF trees reflects physiological traits that result from a performance–tolerance trade-off [83,84]; however, the mechanistic basis of drought-induced mortality is still unclear, with both catastrophic hydraulic failure and gradual carbon starvation plausible [85]. Overall, there is increasing evidence for the sensitivity of Amazonian rainforests to any increase in drought severity [86], but fewer data for regions that lack a regular dry season, such as Borneo, where drought sensitivity appears to be higher [85] but future climate projections are less clear. Drought experiments are a practical way of exploring these issues, but have so far been confined to eastern Amazonia [87].

Undisturbed TRFs do not normally burn, because of high humidity and fuel moisture. In logged or fragmented forests, however, droughts result in peaks in fire frequency and intensity wherever ignition sources are available [88]. Indeed, the frequent co-occurrence of drought and fire can make their individual impacts hard to distinguish, on both the local and regional scales [89]. Even in intact forests, droughts can increase canopy openness and, thus, susceptibility to fires originating elsewhere. These interactions between droughts and anthropogenic fires are probably the biggest single threat to the TRFs worldwide [1]. This positive feedback mechanism might not be inevitable, however, if fire-free farming methods can be first encouraged and then enforced.

can also point to the lack of documented impacts in the tropics so far [7,16], although this is likely to be, at least partly, a sampling bias [17] and greater warming is expected in coming decades.

Plants

Vulnerability to warming for an individual, population, or species depends on the proximity of the current environment to physiological limits [10,15]. Thermal tolerances have been directly assessed for only a tiny and highly non-random selection of TRF species, and no mature tropical tree has been included in these assessments. Evidence for tree tolerances (the key to preserving forest structure and carbon) must therefore be drawn from a variety of other sources, including paleoecology, experiments on seedlings, saplings and branches of adult trees, and mechanistic models.

Paleoecological data suggest that plant diversity was higher during the warmest periods of the Cenozoic and has declined subsequently and that species-rich floras largely persisted through a rapid and short-lived 3–5 °C warming (to an estimated mean annual temperature of 31–34 °C) during the Paleocene–Eocene Thermal Maximum (PETM) [18]. However, the PETM warming appears to have been much slower than that expected over the next century [19] and the 34 million years of cooling since the Eocene and, in particular, the 2.6 million years of the Quaternary, must have relaxed selection for thermal tolerance [20,21]. Moreover, most of the past 800 000 years was considerably cooler than today and the lowest or near-lowest global temperatures were reached at the last glacial maximum, 20 000 years ago [22], with tropical lowland temperatures probably 4–5 °C lower than they are today. There has thus been much stronger selection for cold tolerance than for heat tolerance for millions of years, with the implication that the most heat-tolerant genes and species will have already been eliminated [21]. Many extant rainforest plants and animals diverged from their nearest surviving relatives in warmer climates before the Quaternary [1], when temperatures and CO_2 levels were similar to those projected for 2100, but it is unclear whether species will have retained possibly expensive adaptations to warm conditions that they have not experienced for millions of years.

At above optimal temperatures, photosynthesis is first reversibly inhibited and then suffers increasing damage, from which recovery is slow or impossible [23]. For most C3 plant tissues, heat damage starts between 40 °C and 50 °C, but some desert succulents can tolerate tissue temperatures >60 °C [24]. Leaf temperatures in forest canopies can be considerably higher than the ambient temperature if solar radiation is high and/or the stomata are closed, and this difference increases with leaf size [25,26]. As long as the water supply is adequate, however, TRF canopies are not a particularly hot environment for plants. Most incoming radiation is used for evapotranspiration and, therefore, rainforest canopies are <5 °C cooler than they would be without this transpirational cooling, with reported maximum leaf temperatures typically <40 °C [26,27]. In seasonally dry tropical forests, by contrast, the temperatures of canopy sun leaves in the late dry season can reach 48 °C [28].

Although current and future canopy leaf temperatures in TRF seem unlikely to be high enough to cause irreversible heat damage, the negative correlation between tree growth and minimum daily temperature across a range of tree species [29–32] provides strong evidence for the thermal sensitivity of the carbon balance. Field observations at the leaf, canopy and whole ecosystem levels suggest that this sensitivity occurs because tropical forests already operate near to a high temperature threshold above which net CO_2 uptake declines sharply [29,30,33–36]. This sensitivity seems to reflect largely the fact that the brightly lit leaves that contribute most to tree photosynthesis are warmed to the point where leaf gas exchange is reduced [35]. However, most of these studies have looked at temperature responses over a time period less than the leaf life span and it is not clear whether the plants could acclimate to more gradual warming. It is also possible that rising CO_2 could offset, at least partly, the damaging effects of warming [37–39], although significant warming impacts might occur before CO_2 levels are high enough to be effective. In lowland Bolivia, tree growth across sites is positively related to mean annual temperature, but this is likely to

reflect a strong inverse correlation with the negative impacts of cold fronts near the southern limits of TRF [40].

Current dynamic global vegetation models (DGVMs) do generate lowland vegetation responses to warming, but they omit or greatly simplify key processes and their outputs vary substantially [37]. These weaknesses in turn reflect both the current lack of understanding of the underlying processes (in particular, the omission of the possibility of thermal acclimation of respiration and photosynthesis might make them oversensitive) and the necessity to reduce the biodiversity of TRF to one ('broadleaf evergreen trees') or a few plant functional types and ignore the probable diversity of responses [24]. Although one DGVM was fairly successful in hindcasting the vegetation of the last glacial maximum [39], the use of current DGVMs to assess the vulnerability of lowland rainforests to novel future climates is certainly premature [13,41].

Animals
The thermal tolerances of animals are potentially easier to study than those of trees, but there have been few direct measurements in the tropics. Observations of widespread elevational specialization among tropical animal species are indirect evidence for narrow thermal tolerances [42], but only at temperatures below those current in the lowlands. The limited direct evidence, however, also suggests that many tropical ectotherms have relatively narrow thermal tolerances and are already living near their upper thermal limits [10,15,43–46]. Endotherms can also have well-defined thermal niches, because their stable core temperatures come at a significant energy and water cost [47–49]. In mobile animals (but not their immobile eggs), acclimation to warmer conditions can be behavioral rather than physiological [50], but selecting cooler microclimates can reduce fitness in other ways and the opportunities for this are anyway limited in the forest understorey.

Acclimate, adapt, move, or die
Acclimation is important for long-lived organisms, such as canopy trees, because many individual trees alive today will still be living in 2100. There is evidence for strong acclimation potential in some temperate deciduous trees [51] and warm-temperate eucalypts [38], but a variety of mostly indirect evidence argues against a significant capacity for acclimation to long-term warming in wild populations of tropical plants [28,52]. For animals, too few species have been tested to enable any general conclusions [15,53]. The potential role of rapid evolutionary adaptation to warming is also controversial [54]. In general, species with short generation times, large initial population sizes and high fecundity are expected to evolve faster [55]. However, rates of evolutionary change also depend on the existence of heritable genetic variation in the trait of concern, and this might be low in species that have evolved in the equable lowland tropics [56]. In any case, long generation times rule out rapid evolutionary adaptation to increasing temperature in large trees and the largest vertebrates, even if pre-adapted alleles exist, with 'adaptational lag' expected to be most severe in small, fragmented populations. On the other hand, if all TRF species suffer adaptational lag and there is no potential source of

better-adapted invaders, this might weaken interspecific competition and facilitate persistence under suboptimal conditions [57]. Gene flow via seed and/or pollen from warmth-adapted populations can help adaptation, particularly at the cool edge of a range, but flow from cold-adapted populations could worsen the situation at the warm edge.

Latitudinal temperature gradients are almost flat within the tropics [20], so few species will be able to move far enough by 2100 to track the rate of warming, except in steep topography, where distances to cool refuges are relatively short [2]. This movement potential will be further reduced by immobile edaphic factors, forest fragmentation, loss of dispersal agents for plants [58], and changes in rainfall and other climatic variables. Even in the apparently simple case of moths on Mount Kinabalu, where vertical movements of 127 m would be sufficient to compensate for the warming over 42 years after 1965, species close to major ecological boundaries have retreated at both their upper and lower margins, suggesting constraints on movements [59]. Moreover, some climates, and many more combinations of climate and other environmental factors, such as geology, will disappear completely [8]. In other cases, the new potential range of a species will not be contiguous with the old one, and not within dispersal distance [20].

Impacts above the species level
Few tropical studies have considered climate change impacts on interspecific interactions, despite their acknowledged importance in determining the relative abundances of species and, thus, their potentially large impact on extinction risks. Climate change will both impact existing interactions and create new ones among novel mixes of species. Most attention has been focused on human and wildlife disease, where impacts are expected, but their net effect remains unpredictable [60]. At mid-latitudes, folivory tracked variation in paleotemperature from 59 million to 52.6 million years ago and it has been suggested folivory will increase similarly with anthropogenic warming [61]. However, contemporary spatial gradients of foliage loss with temperature are negative or neutral [62] and warmer TRFs will receive no influx of herbivores from even warmer climates. Phenological mismatches between interacting species are a major concern outside the tropics, but have not been reported yet for TRF, although disruptions to the El Niño-Southern Oscillation (ENSO) cycle are a plausible concern in this regard (Box 2).

It is unlikely that ecosystem-level responses can be predicted from individual thermal tolerances, because thermal adaption can occur not only through individual responses, but also by re-ordering within the community and species immigration from outside [63]. Leaf litter decomposition and nutrient mineralization rates along elevation gradients are controlled largely by temperature, but it is not clear whether this sensitivity will be maintained at temperatures higher than those currently experienced in the lowlands [64]. Thermal adaptation of microbial communities might reduce the impact of warming on soil organic matter content [65]. More generally, the exponential relationship between metabolic rate and temperature in ectotherms means that absolute changes in metabolic rate will be larger in the tropics, where baseline

Box 2. ENSO, climate change and tropical rainforests

ENSO cycles (Figure I) have dramatic effects on TRFs across the tropics, through their impacts on plant and animal reproduction [1], as well as the incidence of droughts and fires (Box 1). The impacts are greatest in Southeast Asia, where ENSO events synchronize supra-annual bursts of reproduction in lowland dipterocarp forests [89], with downstream consequences for much of the forest fauna, and greatly increase the incidence of anthropogenic fires [90]. In effect, ENSO overlays a sort of supra-annual seasonality onto the otherwise aseasonal climates of equatorial Southeast Asia.

The importance of ENSO cycles has led to considerable speculation about the vulnerability of TRFs to changes in ENSO frequency, intensity and other characteristics. Permanent El Niño- or La Niña-like conditions, which have been suggested in some climate projections and paleo-ecological reconstructions [91], could disrupt the synchronization between plants and animals across the tropics, with potentially drastic consequences. In lowland Southeast Asia, for

example, an increase in frequency could reduce the length of the 'fruit famine' between mass fruiting events, potentially benefiting frugivores, such as sun bears [92], while reducing the satiation of seed predators on which successful reproduction of many tree species apparently depends [89]. The close association between ENSO amplitude and sea-surface temperatures in the eastern Pacific over the last millennium and the recent (post-1940) trend towards enhanced ENSO activity are therefore causes for concern [93]. However, ENSO cycles are poorly modeled by existing global climate models (GCMs) and there is no agreement on probable future trajectories. The paleo-ecological record not only suggests considerable variability, making a tight dependence of any TRF taxa on the continuation of historical ENSO patterns very unlikely, but also shows the persistence of ENSO-like cycles under a wide range of climatic conditions, including those predicted for comings decades; therefore, there is a need to understand their effects better [93].
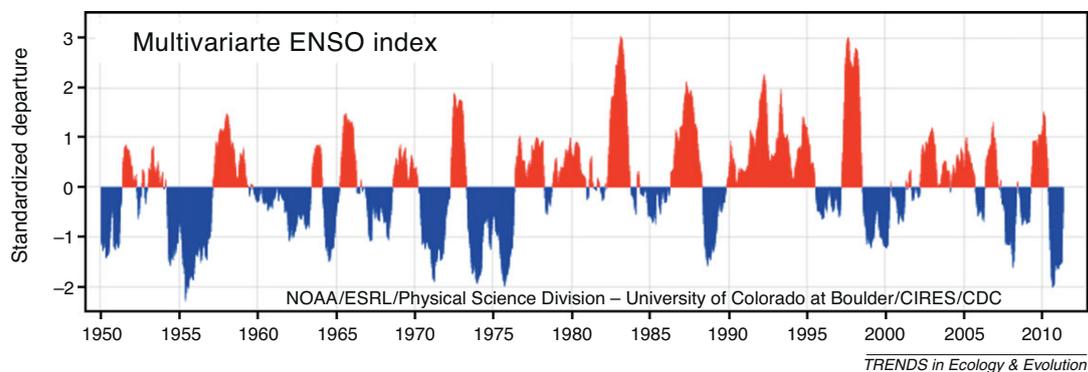

Figure I. Graph of the Multivariate El Niño-Southern Oscillation (ENSO) Index (MEI) showing the irregular fluctuations between El Niño (red) and La Niña (blue) events from 1950 to 2011. Such events have a large impact on tropical rainforest phenology and vulnerability to fire. This has been a period of enhanced ENSO activity. Reproduced, with permission, from the NOAA Multivariate ENSO Index website (http://www.esrl.noaa.gov/psd/enso/mei/).

temperatures are warmer, with largely unexplored consequences for many biologically mediated processes [17].

Research needs

The first research need is to detect the impacts of climate change, both natural and anthropogenic, on TRFs. Given the extent of interannual variability, this will require rigorous, quantitative, long-term (multi-decadal) monitoring [66]. Few, if any, existing monitoring programs reach the necessary standards for quantitative rigor, but many sites have long-term data sets that allow some degree of projection into the past to identify the impacts of recent change [43,59,67]. For rainforest trees, there is a need to start monitoring growth, survival and fecundity on an annual basis, rather than the traditional 4–5-year re-measurement cycle, which smoothes out the effects of year-to-year variation [30,67]. Within-year monitoring of physiological and other processes on various appropriate timescales at the same sites is also needed. Changes in phenology are the most widely reported climate change impacts outside the tropics, but there are few long-term data sets in TRF. Phenological monitoring needs both adequate frequency (fortnightly observations) and sample sizes (at least 15 trees of each species) if relatively small changes are to be detected [68]. Remote sensing data can be used to assess canopy phenology over very large areas, but are most useful in conjunction with ground-based monitoring. Range shifts are the other major reported response outside the

tropics, but there is insufficient information on the current distribution of most tropical species to detect changes [3]. A focus on the distribution of vulnerable species along steep climatic gradients makes most sense [59], along with a push to make all existing distributional information available online.

In addition to monitoring, there is a need for more robust predictions of the impacts of future climate scenarios on species and communities. Current climate-envelope (or niche) models are correlative, relating current distributions to current climate. They can predict exposure to climate change [69], but robust predictions of responses to novel climates are more probable with partly or fully mechanistic models that also incorporate acclimation, interspecific interactions, dispersal limitation and evolutionary adaptation [70,71]. Unfortunately, such models require more knowledge of species biology than is currently available for all but a few species in the tropics. Mechanistic, trait-based models show promise in some cases [48,50]. Another alternative, particularly useful for setting conservation priorities, is to use vulnerability indices, which evaluate the relative vulnerability of species through a systematic, question-based approach [71].

All these approaches to predicting impacts require better information on thermal tolerances of TRF species: both to slowly rising mean temperatures and to short-lived extremes. Research aimed at filling these gaps needs to target explicitly the capacity for acclimation, particularly

in long-lived organisms, and to assess how much heritable genetic variation there is, because this can limit the potential for evolutionary adaption. The simplest (and cheapest) approach is to use existing temporal and spatial variation in the thermal climate as a proxy for long-term changes. Studies that relate long-term records of tree growth to interannual climatic variation are the most promising so far [30,31], but are limited by the narrow range of temperature variation. Short-term studies must make use of spatial variation in climate. Elevational gradients can be used to assess the sensitivity of ecosystem processes to temperature [42,64], but only at temperatures lower than those currently experienced in the lowlands. Thermal climates also vary naturally with distance from the coast [72] and with latitude [40]. Urban heat islands provide an unnatural source of several-degree increases in maximum temperatures over multiple decades, enabling the testing of longer-term acclimation and adaptation responses in urban-tolerant species [73]. On finer spatial scales, canopy disturbances from cyclones or logging provide gradients in maximum temperature, although these are confounded with changes in light and humidity.

The use of existing thermal gradients, natural or anthropogenic, as a proxy for future climate change is limited by their typically narrow range and the lack of control, so controlled experiments are also needed. Published experimental manipulations of whole ecosystems in the tropics have involved only precipitation, but many experiments outside the tropics have manipulated temperature [74]. Responses to brief periods of heat shock in small organisms can often be assessed with simple equipment in the field. Temperature-controlled open-top chambers offer the potential for long-term studies on relatively large

organisms, while minimizing artifacts [51]. Greenhouses and growth chambers offer more control at the expense of more artifacts. Wherever possible, experimental increases in temperature need to be combined with future CO_2 levels, to account for possible interactions [32]. It has been suggested that global change experiments systematically overestimate the magnitude of impacts, with effect sizes tending to decline with time, spatial scale and the number of driver variables tested simultaneously [75], but it is not clear if this is a general problem.

The difficulties of site and canopy access, and the problems of dealing with tree hyperdiversity, mean that a broad regional understanding of climate impacts and carbon-cycle feedbacks will need to depend heavily on the use of high-resolution remote sensing to extrapolate from the few experimental sites [76]. Ongoing attempts to relate the physiological properties of foliage to leaf spectra suggest that this will eventually be possible [77].

Conservation in the face of climate change

Climate change is already underway so researchers cannot wait for a better understanding of the probable impacts before planning for adaptation. In the absence of more detailed predictions for the biodiversity impacts of warming, several types of general management response have been suggested [66]. With tropical conservation already in crisis for other reasons [1], the focus has been on actions that would be beneficial even without the prospect of climate change: so-called 'no regrets' actions. These include minimizing non-climate pressures on TRFs, restoring connectivity to enable movements of genes and species between fragmented populations [54], and restoring canopy cover to reduce temperature maxima [72]. By contrast, actions that

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Box 3. Climate change and alien invasions

Any reduction in the fitness of native species as a result of climate change might provide an opportunity for alien invasives. Most reviews of climate-change impacts on alien invasion have focused on the risks of tropical and subtropical taxa invading areas currently too cool to support them [94]. A similar argument could be made with respect to drought-tolerant tropical taxa invading TRF areas subject to increased drought severity, particularly because such taxa already dominate the ruderal [89] and cultivated [95] floras of equatorial cities, and probably also the faunas associated with them. Any opening of the TRF canopy as a result of climate impacts will favor such drought-tolerant open-habitat species. The effects of warming alone are less obvious, however, because there is unlikely to be a global pool of species adapted to future climatic conditions that have not existed on Earth for millions of years. Aliens that are already successful invaders tend to have growth [96] and dispersal [97] traits that enable them to do well under rapidly changing conditions, including, presumably, those resulting from climate change. However, these traits are also

shared by successful natives [98], so they might not provide a consistent alien advantage. Indeed, it is probably more useful to view climate change as bad for a subset of the native flora, rather than good for aliens.

This discussion presupposes that the current distinction between native and alien species will continue to make ecological sense under novel environmental conditions [98]. When all ecosystems are novel, it will be difficult to make such sharp distinctions [66]. Moreover, alien species could partly compensate for some negative impacts of climate change, as substitutes for poorly adapted native species, although they could also amplify these impacts through negative interactions with natives [99]. It is possible to foresee a future in which the existing black-and-white distinction is replaced by shades of grey (Table I). In particular, it will make no sense to treat better-adapted immigrants from warmer and/or drier areas in the surrounding region, which are likely to retain both natural enemies and mutualists, in the same way as 'naked' invaders from more distant biogeographic regions.

Table I. Degrees of 'alienness' under novel environmental conditions

Degree of alienness	Definition
Viable native	20th-century native species that can still persist under the new conditions
Former native	20th-century native species that cannot persist under the new conditions
Future native	20th-century alien from the regional species pool that can tolerate the new conditions
Beneficial alien	Alien species with net ecological benefits under the new conditions
Harmful alien	Alien species causing net ecological harm under the new conditions

make sense only if current climate change projections are accurate are more controversial. The most general of these recommendations is the need to identify and prioritize for protection (and reforestation if necessary) areas that will be subject to the least damaging climate change (i.e. 'climate refugia') [72]. There is also the need to identify additions to the conservation network that will allow for expected range shifts, for example by extending existing protected areas to higher altitudes or latitudes [78]. Simply enlarging existing protected areas increases the chance that they will contain some areas suitable in the future [66].

Assisted migration is controversial for species [79] but less so for genes. If genotypes adapted to greater warmth are available, their incorporation into the genetic mix for reforestation and reintroduction projects should be a general recommendation [54]. It has been suggested that the aim should be to simulate leptokurtic gene flow dynamics, with most propagules obtained from local sources, some from intermediate sources and a small proportion from far away [80]. With long-lived organisms and rapid climate change, however, natural gene flow is too slow to be a good model and simply matching source populations to expected future climates might be necessary. Current prejudices against novel species combinations are likely to wane in the face of major shifts in species distributions [79] and attitudes to aliens could also change (Box 3). More generally, conservationists will need to abandon the current focus on the preservation and restoration of 20th century reference conditions, which might no longer be relevant in a changing world [71,79]. Finally, given the huge uncertainties in the prospects for TRF biodiversity, a greater investment in *ex situ* conservation makes sense [81]. The fact that this is currently impractical for many species, such as TRF trees with recalcitrant seeds, should not prevent action on those species for which long-term cryopreservation or other *ex situ* strategies are possible.

This review shows that rising temperatures are a definite cause for concern in the lowland tropics. It has also revealed major gaps in current understanding of key issues, including the thermal tolerances and acclimation potential of tropical species and processes. Although the research needed to fill these gaps should receive high priority, it is already possible to make some practical recommendations for conservation planning and management in the face of climate change.

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