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Opinion Article

Last chance to see: the role of phylogeography in the preservation of tropical biodiversity

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Abstract
Habitat loss and anthropogenic climate change are primary threats to global biological diversity and ecosystem stability. International efforts to halt the effects of climate change and to slow the loss of biodiversity are now focused on the tropical biome. Specifically, and in recognition of the substantial contribution to climate warming made by deforestation in developing countries, the UN-REDD+ programme has been established to provide incentives for stopping tropical deforestation. This programme also places emphasis on rewarding measures for the conservation of biodiversity. However, the effective integration of carbon storage and biodiversity conservation goals in countries participating in the REDD+ programme will require greater research effort. In particular, in order to maximize our chances of preserving biological diversity, it will be essential to consider diversity at a population level, as well as at a species and ecosystem level. Phylogeographic studies should be an integral part of this population-level research effort as they can be used to document regional biological diversity, provide baseline genetic data to monitor changes in genetic diversity, allow the identification of evolutionary refugia, and provide evolutionary context for current patterns of diversity. The REDD+ initiative has the potential to provide an internationally well-supported framework for reducing forest habitat loss and protecting tropical diversity, and may, therefore, provide the impetus needed for increased biodiversity research effort. In conjunction with the recent development of the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES), phylogeographic research may now be considered more explicitly in the development of national environmental policies and in planning for biodiversity conservation.

Keywords: biodiversity, evolutionary refugia, phylogeography, REDD+, tropical deforestation

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Last chance to see

> 'In short, although there are many uncertainties about the trajectories of individual populations and species, we know where biodiversity will go from here in the absence of a rapid, transformative intervention: up in smoke; toward the poles and under water; into crops and livestock; onto the table and into yet more human biomass; into fuel tanks; into furniture, pet stores, and home remedies for impotence; out of the way of more cities and suburbs; into distant memory and history books.'
>
> – Ehrlich and Pringle, 2008[1]

Global biodiversity is in precipitous decline. The current rate of species extinction has been estimated at 100 to 1000 times the natural background rate [2], driven by human-mediated exploitation and toxification of natural habitats. The impact of human activity on natural ecological systems and species diversity cannot be overstated, and yet, despite international recognition of the unfolding ecological crisis through the Convention on Biological Diversity, there has been little practical progress toward halting rates of species extinction and deforestation. In fact, vertebrate extinction risk has accelerated [3] and rates of deforestation have shown a net increase over the past two decades [4].

Habitat loss is the primary cause of declines in biological diversity and ecosystem stability; however, anthropogenic global warming now compounds the effects of habitat fragmentation. There is already empirical evidence connecting recent climate change with declines in population sizes [e.g., 5-6], changes in species phenology [e.g., 7], and shifts in species distributions [e.g., 8-9]. Dramatic changes in the dynamics of disease in natural populations have also been attributed to anthropogenic climate change [e.g., 6]. Increases in temperature and changes in weather patterns are likely to cause further, unpredictable interactions between species and their habitats, resulting in the destabilization of natural ecological systems and the production of 'no-analogue' communities [10].

For example, changes in community composition may occur due to trophic mismatches in phenological synchronicity between species, disrupting the co-evolved interdependence required for their survival [11]. Additionally, populations forced to seek suitable climatic 'space' through physical shifts in their geographic range may be constrained by the fragmentation and degradation of surrounding natural habitat. For some populations it may be impossible to find appropriate climatic conditions, as has been predicted for montane species [12]. Alternatively, interspecific differences in dispersal rates may result in an uneven competition for available climatic niches, increasing the extinction risk for poor dispersers [13].

Hopes of halting or reversing the effects of climate change and slowing the loss of biodiversity are now focused on the tropics. Almost half of the world's remaining forests are found in the tropical biome [4], as well as half of the world's species [14]. Global human population growth and material consumption in developed countries are driving the destruction of these forests through increased logging and the conversion of forested land to pasture and crops [15]. However, large sections of the human population in the tropical biome live in developing countries, relying on small-scale, low-technology farming for subsistence. These countries are now in the paradoxical position of producing an estimated 12 to 17 percent of global greenhouse gas emissions [16-17], and under intense international pressure are being forced to integrate local economic goals with global imperatives for the mitigation of climate change and biodiversity loss.

A rapid, transformative intervention?

In recognition of the substantial contribution made by tropical deforestation to climate warming, a proposal for an international scheme to reduce this source of emissions was put forward in 2005 during the Conference of the Parties to the United Nations Framework Convention on Climate Change

(COP 11). From this proposal, the UN-REDD (Reducing Emissions from Deforestation and Degradation) programme was conceived. REDD was an attempt to place a financial value on forest carbon stores and to provide policy support and incentives for stopping tropical deforestation [18]. It was thought that financial incentives provided through the REDD framework would allow developing countries to benefit from reducing the clearing of forests by increasing investment in other, more sustainable means of development. The original emphasis of the REDD initiative on stopping large-scale deforestation has now broadened to reward measures for the active conservation and sustainable management of forests. This programme, REDD+, has increased emphasis on the maintenance of healthy forest ecosystems and ecosystem services, as well as on the conservation of biodiversity.

There are still fundamental issues to be resolved concerning the potential benefits and pitfalls associated with REDD+ [19]. These include how carbon stocks will be measured, how financial values for these stocks and other ecosystem services will be determined, how payments will be distributed, and how the territorial rights of indigenous people will be safeguarded. There are many uncertainties and it is inevitable that there will be difficulties ahead [e.g., 20]. However, REDD+ offers a relatively 'holistic' approach to reducing forest degradation through the recognition that forest conservation for carbon stocks should be integrated with initiatives for the conservation of biodiversity.

Additionally, the international spotlight on both biodiversity conservation and good forest governance in biologically diverse Afrotropical, Neotropical, and Indo-Malayan countries, as well as the potential for increased financial support for environmental services and protected areas, may provide an important focus for increased research effort in these regions. Such research will be essential for the integration of carbon storage and biodiversity conservation goals in REDD+ programmes. For example, areas marked for initiatives to reduce carbon emissions will need to overlap with areas in which biodiversity will also benefit, even if there is a tradeoff in the efficiency of carbon storage [21]. This may be through targeting regions with relatively few areas of intact forest but high species diversity, such as Indonesia [22], or montane regions such as the tropical Andes and the Himalayas [21].

Population-level thinking

In order to maximize our chances of preserving tropical biological diversity and to measure the extent and speed with which it is being lost, it is essential to consider the rate and magnitude of population extinction [23]. Traditionally, levels of biological diversity have been considered and measured in numbers of species. Applying phylogeographic methods to studies of natural populations makes clear that high levels of geographically structured genetic diversity exist within species due to the effects of historical environmental change. The observed depth of genetic divergence has led to a re-evaluation of the level at which conservation effort should be directed in order to maintain independently evolving lineages [24].

In the tropics, levels of genetic divergence indicating the geographic isolation of populations over a time scale of millions of years have been observed in a range of taxonomic groups [e.g., 25-28]. Hence, as the effects of tropical habitat fragmentation on population persistence are compounded by those of global climate change, emphasis should be placed on the preservation of divergent evolutionary lineages, or, evolutionarily significant units (ESUs *sensu* [29]). The maintenance of this intraspecific genetic variability will be critical to maintaining the raw material for functional adaptation [30].

It is well accepted that findings from phylogeographic and population genetic studies should be used to inform practical conservation efforts. In many tropical regions, however, poor economic, political and logistical capacity has historically limited the number and extent of these kinds of studies [31]. Even the basic documentation of biological diversity has been impeded by the difficulties of conducting research in regions with poor access and infrastructure. Thus, it is likely that the greatest proportion of the world's undescribed species occur in regions where tropical forests have undergone minimal anthropogenic disturbance [32]. In these ecologically complex landscapes, species are also more likely to have small geographic ranges with narrow environmental niches and a correspondingly high extinction risk [32].

Given the fundamental importance of genetic diversity to the maintenance of higher levels of biological diversity, phylogeographic studies are an obvious source of information for conservation planning and biodiversity management in tropical regions. Indeed, the protection of diversity at the genetic level has been recognized as a specific goal by the Convention on Biological Diversity. Yet a recent review of international efforts to meet the Convention Targets for 2010 highlighted the lack of progress toward this goal [33]. Hence, under international initiatives that claim to benefit tropical biodiversity, such as REDD+, there is now an opportunity to explicitly consider genetic diversity in planning and management decisions and to support further biodiversity research at the genetic level.

The role of phylogeography

There are three ways in which phylogeographic studies can provide information for the conservation of biodiversity and intersect with the priorities of global initiatives such as REDD+.

1. *Fine-scale documentation of the diversity of species and populations in a region*. Due to the structural and ecological complexity of tropical forests, There is likely a high proportion of currently unrecognized intraspecific diversity in tropical regions. The consequences of widespread population extinction for global ecosystem stability should be considered as serious as the consequences associated with species extinction [34]. Phylogeographic studies have an important role to play in providing baseline data for the cataloguing and mapping of intraspecific and cryptic species diversity, through either single-species or comparative studies. These data are critical for monitoring the effects of current and future anthropogenic activities on tropical forest populations; increased efforts to collect spatial genetic data now will ensure more realistic estimates of the effectiveness of policy and planning decisions on future genetic diversity.

2. *Identification of genetic lineages for the maintenance of evolutionary potential within species*. Studies of species in the Andes [e.g., 35], New Guinea [e.g., 27] and the Philippines [e.g., 36] illustrate the complexity of genetic structuring of populations that may arise in geologically and geographically heterogeneous tropical regions. Upward shifts of geographic range in response to climate change have already been documented for some tropical montane species [e.g., 9]; thus, it is likely that many populations isolated at high elevations will be threatened with extinction as they attempt to find suitable climatic conditions. The loss of these genetically unique populations, or evolutionary lineages, will seriously deplete the genetic potential available to the species. In conjunction with the basic documentation of population diversity, phylogeographic analyses allow the identification of ESUs and prioritization of populations for the preservation of genetic diversity [30]. Comparative phylogeographic studies can also be used to identify evolutionary refugia, regions where high levels of genetic variation occur within a number of taxa or where many relictual and endemic species occur. The inclusion of these refugia in protected areas is critical to the maintenance of the process of evolution under future scenarios of climate change [37].

3. *Elucidation of the historical processes driving changes in species range and abundance*. It is likely that species will have idiosyncratic responses to climate change due to differences in their ability to find or recolonise suitable habitat [e.g., 38]. Phylogeographic approaches allow consideration of the effect of historical climate change on species diversity and distributions, and findings from these studies can be used to inform, and to some extent predict the response of species to contemporary habitat change [39]. Inferences of historical demographic change based on phylogeographic data can provide important context for present trends in population abundance and distribution, as well as a better appreciation of the extent to which current extinction rates differ from the past [40]. Multi-

taxon phylogeographic studies will therefore be needed to appreciate the variation among species in patterns of genetic diversity and levels of intraspecific divergence.

There are an increasing number of examples in which phylogeographic methods have been used to guide conservation management decisions. These include the documentation of regional biological diversity and the provision of baseline genetic data for assessing changes in genetic diversity [e.g., 41], and the identification of ESUs or other types of management units [e.g., 42-43]. DNA barcoding surveys using mitochondrial DNA have also shown promise for both rapid assessment of phylogenetic diversity and the identification of evolutionary lineages [44-45, but see 46]. Nevertheless, the consideration of phylogeographic patterns in practical conservation programmes is still limited, even in developed countries. Under large-scale initiatives such as REDD+, there is now potential for increased consideration of ecological and land-use data [e.g., 47]. These data could be integrated with regional spatial genetic data generated through a phylogeographic approach for management and planning purposes.

For example, phylogeographic information may be incorporated into mapping 'tools' used in environmental project development and assessment [e.g., 48], and for refining the boundaries of regional biogeographical zones, which may be used to map changes in forest cover [e.g., 49]. Additionally, although boundaries of protected areas are often decided by socio-political rather than research-based imperatives, proposals for the extension of protected areas would be better informed by DNA barcoding studies [e.g. 45] and targeted studies of the spatial genetic structure in key forest species. These targeted studies may include comparative phylogeography [e.g., 50], species distribution modeling [e.g., 51], or phylogeographic studies of surrogate species [e.g., 52]. While the choice of taxa will depend on the spatial scale of the study, in tropical regions, low vagility endemic invertebrate taxa have been shown to be adequate surrogates for conservation values across a range of species groups [52].

Into distant memory and history books?

There is no question that biological diversity is in serious trouble. Field guides for well-known taxonomic groups already serve as history books for a significant number of the world's species. At current rates of deforestation in tropical countries, it is likely that many more species and populations will be extinct before they have been documented [34]. REDD+ may offer one of the most well supported international frameworks to date for reducing forest habitat loss and protecting tropical diversity. Additionally, the current international focus on the tropical biome may improve transparency in the local and national management of protected areas. In conjunction with the recent establishment of the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES), there is also now greater opportunity for the integration of scientific research into the development of national environmental policies in tropical countries.

Combined, the REDD+ and IPBES initiatives may engender further collaborations and in-country capacity building in the area of population-level biodiversity research. There are many successful examples of these types of research collaborations between international or national institutions and conservation organizations in developing countries [e.g., 53-55]. There will now be more opportunities for these types of collaborations to grow. Already, the development of an evolutionary approach to biodiversity science and assessment has been formalized as a 'Core Project' of the scientific committee (DIVERSITAS) within the IPBES. This project specifically recognizes the need to understand the evolutionary patterns and origins of biodiversity and to integrate this understanding into practical conservation and local training programmes [56]. The incorporation of evolutionary science, including phylogeographic concepts and methods, into planning for the protection of biodiversity is long overdue, and it is critical if we are to preserve global diversity for the future.

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