Cambridge University Press
978-1-107-04185-1 - Forests and Global Change
Edited by David A. Coomes, David F. R. P. Burslem and William D. Simonson
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CHAPTER ONE

Forests and global change: an overview

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1.1 Introduction

Forests provide a range of goods and services upon which humanity depends, from local (e.g. flood prevention) to global (e.g. carbon sequestration). Yet some 13 Mha of forest is lost each year, mostly in the tropics (Canadell & Raupach 2008). Considerable political, media and scientific attention has focused on this forest destruction and fragmentation and its implications for livelihoods, biodiversity and ecosystem services. However, human influences on forests now go beyond deforestation and degradation, to changing the states of atmosphere and climates and altering biogeochemical cycles, which in turn bear heavily on the functioning and composition of forest ecosystems. A range of disciplines are required to chart such change, understand how it works and predict where it is going. They span a broad range of scales from photosynthetic machinery in leaves, to the dynamics of forests across wide regions, to global atmospheric circulation. Integration of these multiple strands and scales of investigation has only recently begun, and this volume makes an important contribution to weaving them together into a more cohesive, albeit still incomplete, picture.

The story is told in three parts, beginning with a collection of perspectives on the global environmental drivers of forest change, the complexity of their interaction and effects, and important feedbacks. The second section concentrates on species-level traits and trade-offs, and how these explain the composition and dynamics of forests in a changing world. Finally, a number of approaches and tools are presented for measuring forest change and forecasting its future direction.

1.2 Forest dynamics and global change

Global forest decline has important implications for the atmosphere and climate. Forests are intimately coupled to the atmosphere by both physical

Forests and Global Change, ed. David A. Coomes, David F. R. P. Burslem and William D. Simonson.
Published by Cambridge University Press.

and biological processes and feedbacks (Charney, Stone & Quirk 1975). These ecosystems have very different properties in this respect from pastures and croplands, and the widespread conversion of forests to other land-uses is not only contributing directly to climate change, but also compromising the potential for forest-based climate mitigation in the future. In Chapter 2 Grace describes from first principles the fluxes of energy, water, carbon dioxide and other gases between forest canopies, the atmosphere and soil. The importance of albedo in the energy and water balance is highlighted, as is canopy roughness, which helps to explain the difference between forests and vegetation of shorter stature. The predictions derived from parameterising and solving equations for stands are supported by observational data for regions, but at larger scales additional complexities become significant, including the spatial organisation of deforestation activity; cloud formation; phenological change; and teleconnections between different parts of the world (Avissar & Werth 2009). Chapter 2 reviews progress using global circulation model simulations, which predict reduced rainfall and increased temperatures, although only above certain ‘tipping points’ of deforestation (Walker *et al.* 2009). Evidence and explanation is also given for forests operating as carbon sinks, even as old-growth systems, although we are warned that a switch in function from sinks to sources is possible as a result of climate warming and drought. The conversion of forests also has important implications for the production of non-CO_2 greenhouse gases, as well as aerosols and other chemically important gases. Land-use policy and forest management need to keep pace with our understanding of these systems, and the rapid increase in area of fast-growing tropical plantations (FAO 2011), including oil palm, gives rise to important ethical as well as practical considerations.

In Chapter 3, Valladares *et al.* explore the ways in which the Mediterranean biome responds to environmental change, showing that we require not only ecophysiological understanding of individual species responses, but also consideration of biotic interactions – both antagonistic and facilitative – and the non-additive interplay of multiple drivers. The mechanisms that confer resilience on vegetation communities in the short term can collapse when threshold situations are reached. Valladares *et al.* show that differential species responses to abiotic stress may exacerbate negative interactions (e.g. when pathogen life cycles are accelerated by warming) or alleviate them (e.g. when phenological mismatching breaks down the onslaught of a natural enemy). Facilitative effects can also be either enhanced or compromised. For example, the amelioration by shrubs of harsh abiotic conditions for woody seedling establishment is a well-known phenomenon in the Mediterranean, but evidence is mounting that such facilitation may not hold as stress levels increase (Maestre & Cortina 2004). Positive animal–

plant interactions may also be compromised by climate change; the behaviour of animal dispersers of seed and fruit in the face of environmental change, including fragmentation, can be as critical to plant population dynamics as any more direct effect arising from a changing climate.

Shifting land-use is one of the main agents of change in Mediterranean forests, and its implications for biodiversity are significant in a region where the biota has been tightly linked to traditional land-use practices over a very long time (Blondel, Aronson & Bodiou 2010). Forest fragmentation is prevalent, leading to reduction of habitat area, increase in isolation and altered physical environment, with implications for population genetics and species ecology. But it furthermore seriously restricts the survival options for species coping with climate change: these options are either acclimation/adaptation to local conditions, or migration to more favourable areas. Fire suppression and lack of timber management in fragments, for example, can lead to wood accumulation which mediates the long-term effects of climate change on fire regimes. Even a small shift in climate can cause major shifts in flammability (Pausas & Paula 2012). The woodlands of Mediterranean mountains are considered to be particularly vulnerable to changing fire regimes if the regime is afflicted by more severe droughts in the future, as predicted by most global warming models. Changes in fire frequency and intensity are likely to have more profound consequences than the direct effects of drought stress on physiology (Fyllas & Troumbis 2009). The cultural landscapes of the Mediterranean region are a notable example of how a long history of human occupation and land-use shapes forests and other ecosystems.

In the emergent geological epoch of the ‘Anthropocene’, all of the Earth’s ecosystems are affected by human activity. In Chapter 4, Phillips and Lewis document field-based evidence for the world’s tropical forests undergoing rapid change as a result of anthropogenic influences on the atmosphere–biosphere system. Such change is more subtle than forest conversion, and can be picked up by persistent, on-the-ground monitoring at fixed locations. Results of diameter at breast height (dbh) measurements in permanent plots across Amazonia (the RAINFOR network), complementing similar networks across Africa (AfriTRON) and Asia (e.g. the Center for Tropical Forest Science, CTFS), are reviewed. Evaluation of change in the plots appears to indicate an increase in biomass carbon, equivalent to 1.3 PgC yr^{-1} in the 1990s when scaled up to the total global old-growth forest area (Lewis *et al.* 2009). These findings have become the subject of much debate and intense scrutiny: it is argued that the statistical noise associated with estimating diameters, heights and wood density is not routinely propagated through biomass-estimation functions, potentially leading to poor estimates of the mean and variance of carbon stocks (see Chapter 14). It is also argued that intense

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natural disturbances are not picked up by short-term measurements in small plots (the 'slow in, rapid out' argument of Korner 2003 and Coomes *et al.* 2012), which may cast doubt on the magnitude of the tropical forest sink (Chambers *et al.* 2013). Phillips and Lewis use the chapter to lay out the evidence that supports their case. For example, they argue that the plots lack the basic signatures of forests recovering from large disturbances. Instead, they maintain that the trend of biomass gain can be explained in terms of an increase in primary productivity as a result of more available resources such as carbon dioxide (Lewis *et al.* 2004). Other changes to the forests, including increased dynamism (higher rates of mortality and recruitment) and shifts in species or functional group composition (notably an increased prevalence of lianas), are considered to be more consistent with such explanations.

The network of Amazonian plots allows Phillips and Lewis to explore the consequences of a 'natural experiment' – a severe drought that hit the region in 2005. The frequency of droughts in the Amazon seems to be increasing, in line with forecasts made by some global warming models, leading to dire predictions about the fate of the rain forests (Cox *et al.* 2004). These plot-based analyses provide the first glimpses of what might actually happen. Pre- and post-drought plot data suggest that this region lost aboveground biomass of the order of 0.59 Mg ha^{-1} as a result. This represents a loss of between 1.21 and 1.60 PgC for the Basin as a whole (Phillips *et al.* 2009). A switch from being a carbon sink to a carbon source is a scenario for tropical forests that may become more widespread in the future, and the chapter ends by reviewing some of the complexities, related to water shortage, photosynthesis/respiration and composition, relevant to modelling such changes.

In temperate forests, the effects of climate change are even harder to predict because forest composition and function are so strongly driven by anthropogenic disturbance and pollution, and by the legacy of historical management; many factors contribute simultaneously to change, and careful analysis is needed to disentangle them. As Canham explains in Chapter 5, drawing on examples from the northeastern United States, any signal for climate change must be decoupled from contemporaneous effects of a range of additional context-dependent factors such as cycles of land clearance and re-colonisation, herbivore dynamics, changes in fire regimes, logging, introductions of non-native pests, pathogens and plants, and pollution. The tree-specific sensitivity to temperature rise and N deposition (Quinn Thomas *et al.* 2009) illustrates the point. In general, a decline in N deposition of 3 kg ha^{-1} yr^{-1} would largely neutralise the effect of a 3 °C temperature increase, yet the net impact of these two factors will vary in magnitude and even direction for different tree species. He explains how, in principle, individual-based succession models such as SORTIE (Pacala *et al.* 1996) can be parameterised to

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capture the impacts of these factors on tree demography and make predictions about the future under various realistic scenarios. However, setting realistic initial conditions is critical in such simulations, as successional trajectories depend closely upon them. For this reason it is important to characterise the identity and spatial distribution of trees surviving anthropogenic disturbance events (Papaik & Canham 2006), and this requires spatially explicit data for all species over large areas.

Hence, this section on forest dynamics and global change draws to a close with a key insight: that to understand how a forest responds to global change drivers, it is necessary to understand that overall forest change is the cumulative result of the interacting responses of multiple species and individuals. We need to consider not just the sum of the parts, but the parts themselves: the characteristics, or 'traits', of species.

1.3 Species traits and responses to changing resource availability

It is increasingly recognised that characterising the plant functional traits within a forest provides a powerful tool for understanding responses to global change (e.g. Diaz & Cabido 1997; Morin *et al.* 2011). If the traits of individuals vary less within species than they do between species, it becomes possible to describe species traits, and, from species composition of forests, derive predictions about forest functioning and response to change drivers founded on a better understanding of underlying mechanisms.

This is first illustrated for Amazonia by Chave (Chapter 6). This region remains a poorly understood component of the global carbon cycle. It has been predicted that by the end of the twenty-first century, large areas of the Amazonian forest will dry out and convert into open vegetation (the 'Amazonian dieback' scenario; Malhi *et al.* 2009). These predictions result from simulations in which atmospheric global circulation models are coupled with dynamic global vegetation models (DGVMs). Empirical evidence for this scenario remains tenuous, and so it is important to explore some of the key assumptions made by the current generation of DGVMs. One of the key features of these models is that they adopt a coarse description of tropical forest vegetation, with only a few plant functional types (Sitch *et al.* 2003). However, the 'biodiversity insurance hypothesis' predicts that species-poor ecosystems are more susceptible to marked shifts than species-rich ones (Yachi & Loreau 1999). DGVMs, as currently constructed, ignore the interspecific variability characteristic of species-rich ecosystems, as well as phenotypic plasticity and adaptive potential. A finer-grained description of tropical forest vegetation dynamics would allow for a more accurate description of interspecific and inter-individual variability. Chave (Chapter 6) reviews the literature on past environmental shifts in Amazonia and describes the method currently used to delineate functional types for tropical forest trees.

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Some aspects of plant physiology that are currently overlooked in the definition of plant functional types are then considered, focusing on the role of stems and branches in conducting fluids towards the leaves while controlling for possible drought stresses. This review emphasises the need for a whole plant perspective, incorporating a greater range of (non-leaf) traits in order to understand the contribution of tropical forest to biogeochemical cycles.

In Chapter 7, Purves and Vanderwel provide a theoretical framework for understanding global change biology that builds on classic models of community dynamics. They point out that coexistence is no longer a paradox from a theoretical perspective: neutral theory demonstrates that it can take many thousands of years for populations of functionally identical species to drift to extinction, while various ‘niche’ theories show that mono-dominance is avoided so long as traits that affect fitness are influenced by some form of negative feedback (Dislich, Johst & Huth 2010). This rich theoretical background provides a useful resource for understanding global change, they argue. Purves and Vanderwel introduce a traits–states–rates (TSR) framework for helping forest ecologists to understand the coexistence of multiple species in forest communities. Within this framework, a ‘trait’ is any property of an individual that does not depend on the current state of the community, or that reacts so slightly to the state of the community that it does not affect population dynamics and hence coexistence (Purves & Vanderwel, Chapter 7); ‘states’ refer to the state variables of a model of a community (e.g. population size and size distribution, soil nutrients, pathogen abundance) and ‘rates’ refer to the rate of change of each state variable. Traits combine with states to give rates, which in turn leads to new states. The TSR scheme is illustrated by reference to classic Lotka–Volterra modelling, before moving on to more complicated size-structured communities, using a relatively simple but realistic forest model: the ‘perfect plasticity approximation’ model, PPA (Purves *et al.* 2008; Strigul *et al.* 2008). By parameterising a PPA model using vast forest inventory datasets from the United States, Purves and Vanderwel provide a glimpse of the mechanisms that might, and might not, plausibly promote species coexistence in forested landscapes. With recognition that the traits themselves are not constant, but are affected by environmental change, they show how it is possible to use the TSR approach to explore species composition, forest structure, carbon dynamics and biogeochemistry in the context of global change (Purves & Pacala 2008).

Recent analyses have shown that the consequences of biodiversity loss for ecosystem services are of comparable magnitude to the effects of other global change drivers (Hooper *et al.* 2012). Chapter 8 concentrates on the functional role of biodiversity in forests, and the biological mechanisms behind it, providing a historical perspective before appraising a number of published reviews of the subject of biodiversity and ecosystem functioning (BEF) published since 2005 (Nadrowski, Wirth & Scherer-Lorenzen 2010; Scherer-Lorenzen, Körner & Schulze 2005; Thompson *et al.* 2009). Amongst all possible drivers relating to diversity, the reviewed studies concentrate on tree species richness, and show a predominately positive effect of tree mixes on growth, wood production and other ecosystem processes. Such studies for forests represent a tiny fraction of those for all ecosystems, and indeed pose certain challenges. Silvicultural trials have generally been limited to monoculture versus two-species mixture comparisons, while the applicability of experimental manipulations of forests ('synthetic communities') to real world situations is sometimes questioned (Srivastava & Vellend 2005).

Observational studies and modelling represent complementary approaches to the experiments. The value of national forest inventories for exploring BEF is increasingly recognised, and positive BEF effects have been quantified after accounting for environmental covariates (e.g. Vilà *et al.* 2013). Comparative studies where a similar number of plots per diversity level are deliberately chosen are another form of observational study. The latter are serviced by a growing number of different tools such as forest growth models, process-based succession models, structural equation modelling or mixed-effect models. Although there is still much to understand, the combination of these three different lines of investigation allows some tentative conclusions to be drawn. Whereas individual tree growth, biomass production and diversity of associated organisms are often positively associated with tree species diversity, other ecological functions, such as those related to biogeochemical cycling, seems to be more strongly controlled by site conditions. Perhaps most importantly in the context of species traits, the identity and functional traits of dominant tree species often have strong impacts on ecosystem functions. The functional differences between tree species are the basis for any relationship between biodiversity and ecosystem processes, emphasising the value of trait-based approaches for understanding the biotic control of ecosystem processes.

The evolution and ecology of Brazil's seasonally dry tropical communities, which lie to the south and southeast of the equatorial rain forests, are the focus of Chapter 9. By analyses of a large dataset of woody plants, Oliveira-Filho *et al.* seek to determine whether seasonally dry woodlands (caatinga) and savanna woodlands (cerrado) have distinct phylogenetic structures, and to ascertain which traits and climatic variables are most strongly associated with this structuring. They find that the two floras are phylogenetically distinct, reflecting several million years of divergence and suggesting that these two types of dry-adapted vegetation have different evolutionary histories. The factor that is most strongly associated with the pairwise phylogenetic difference between sites is the leaf trait of deciduousness, which has already been established as shaping plant communities in eastern Brazil (Oliveira-Filho, Jarenkow & Rodal 2006; Santos *et al.* 2012). This result suggests that phenology is phylogenetically conserved ('phylogenetic niche conservatism'; Donoghue 2008; Crisp *et al.* 2009) and contributes to differential community assembly in this setting. The dry woodlands are critically important for the Amazon region in terms of forecasting which species might thrive there in the drier and more seasonal climates predicted of the future.

As we have already seen (Chapters 6 and 7), functional diversity may play an important role in the resilience of tropical forests to global change. Some climate projections forecast increases and decreases in annual rainfall and length of the dry season for different tropical regions (Hulme & Viner 1998) as well as increases in the frequency of extreme weather events (IPCC 2007), although these predictions are highly uncertain. In the search for predicted responses to increased drought, Comita and Engelbrecht (Chapter 10) review work on the effects of water availability, including experimentally induced drought, on tropical tree regeneration, dynamics and distribution. There are now documented cases of natural drought events causing increased mortality rates of tropical trees and their seedlings (e.g. Condit *et al.* 1995; Potts 2003; Phillips *et al.* 2010), and it is reasonable to propose that changing frequency of drought will result in changes to tree species composition and ecosystem processes.

Comita and Engelbrecht show that there is huge variation among species in their responses to drought, which contributes directly to where seedlings are located within the landscape. Classic studies of the mechanisms of drought resistance differentiate species according to the extent that they avoid or tolerate drought conditions, and search for traits that are associated with these mechanisms. However, the review finds very limited evidence of a consistent role for traits associated with *drought avoidance*, such as deep or extensive root systems, water storage, stomatal responses, cuticular conductance or deciduousness, in promoting differential drought resistance of tropical tree seedlings under field conditions. Instead, mechanisms of *drought tolerance* are decisive in determining differential seedling responses. Thus traits such as turgor loss point, rigidity of cell walls, solute concentrations at full turgor, vulnerability of xylem to cavitation and ability to refill embolised cells seem to be important in determining survival, whereas 'soft traits' often measured by ecologists seem to have little bearing on drought response.

Following considerations of water availability in Chapter 10, Kobe *et al.* (Chapter 11) explore the importance of soil nutrient availability in interpreting and predicting how forests respond to global change. This is because soil resources are major determinants of tree growth and forest productivity, and human activity is changing the availability of key soil-borne resources through atmospheric nitrogen deposition, which accelerates soil acidification and may lead to enhanced leaching losses of phosphorus and nutrient cations.

Nutrient losses may also occur through intensification of tree harvesting, especially when tree bark and leaves are removed, and in response to increases in fire frequency. Kobe *et al.* also show that soil nutrient and water availability are important determinants of the limits to tree species distributions and may influence the response of tree distributions to changing climatic conditions. Pollen records provide evidence that postglacial colonisation of infertile soils in eastern North America by *Pinus contorta* rather than *Abies* or *Picea* species was driven by the edaphic preferences of these taxa rather than the suitability of the climate (Whitlock 1993). Similarly, the physiological response of temperate forest trees to extreme temperature or precipitation is modulated by nutrient supply, leading to declining function under conditions of nutrient imbalance (St.Clair, Sharpe & Lynch 2008). Hence soil resource availability influences the response of forests to facets of global change both directly through responses to atmospheric N deposition, and indirectly through interactions with other abiotic environmental factors.

The scope for these interactions is illustrated by recent research on tree communities in temperate deciduous forests in eastern North America and tropical forests in Costa Rica. One focus has been to understand the balance of nutrient limitation of tree growth and forest productivity by N, P and base cations, as a test of the widespread generalisation of N limitation in temperate forests and P limitation in tropical forests. Contrary to this, Kobe *et al.* conclude that there may be significant limitation of these processes by base cations in both temperate and tropical forests (Baribault, Kobe & Finley 2012; Baribault, Kobe & Rothstein 2010). The identity of the limiting element may vary in response to soil mineralogy, ontogenetic stage, and species or functional group, and different elements may determine contrasting physiological or demographic variables (e.g. wood production, leaf production, seedling growth or reproductive output). The diversity of responses to soil resource availability reflects the multiple mechanisms that trees use to acquire nutrient pools within the soils, which includes translocation of base cations from deep soil horizons to the surface (Dijkstra & Smits 2002), exudation of carbon into the rhizosphere to support the activity of soil organisms (Kobe, Iyer & Walters 2010) and the ubiquitous associations of trees with mycorrhizas. These conclusions support other recent research in temperate and tropical forests based on long-term fertilisation experiments (Kaspari *et al.* 2008; Wright *et al.* 2011) and short-term pot experiments (Burslem, Grubb & Turner 1995; Denslow, Vitousek & Schultz 1987) highlighting an important role for base cations as well as N and P in biogeochemical cycling and identifying contrasts and highly variable within- and between-species responses to nutrient heterogeneity. Understanding these processes within

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978-1-107-04185-1 - Forests and Global Change
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forest ecosystems is important because they will influence the ways in which tree distributions respond to climate change, the management of forest carbon stocks across edaphic gradients and the responses of forests to increased atmospheric N deposition.

1.4 Detecting and modelling global change

Throughout this overview of forests and global change, it will have become apparent that building better dynamic models, and servicing them with better empirical data, is critical for understanding current and predicting future trajectories of change. The need to integrate different approaches for more realistic modelling has also been underlined. For example, in Chapter 6 we saw that combining individual-based models with dynamic global vegetation models is necessary to bridge the gap between ecosystem science and community ecology and better understand crucially important future changes to Amazonian forests (Fisher *et al.* 2010). Earlier, in Chapter 3, it was suggested that the coupling of niche envelope models for plants and their animal interactors (e.g. seed dispersers, herbivores) can greatly enhance our understanding of how plant populations will respond to future changes. In this latter case, parallel modelling approaches in which plant models largely ignore animal effects, and animal models only consider plants in terms of vegetation habitat suitability, can underestimate the influence of interactions on the distribution of each species under new climates. Coupled models would be inherently complex because of the scope for high dimensionality, but would help to overcome these limitations.

In this final section, detecting and modelling change comes under greater focus, and from a number of different angles, beginning with an aerial perspective using imaging spectrometers (Chapter 12). One of the key challenges in current forest research is to improve our measurement, mapping and understanding of species diversity and how this is responding to global change. In this chapter Asner describes an innovative approach to this question involving remote sensing of foliar chemical traits. Drawing from pioneering results from the Carnegie Airborne Observatory, he shows how interspecific variation in the hyperspectral signatures of tropical forest species allows for their discrimination in airborne imagery (Asner & Martin 2009). Canopies that appear monotonous green carpets to the naked eye become a kaleidoscope of spectral variation on the basis of leaf chemicals fulfilling the three independent functions of light capture and growth, longevity and defence, and maintenance and metabolism. Crucially, Asner advocates that more variation in the leaf chemistry and spectral reflectance properties is found between species than within species in tropical systems, opening up the possibility of taxon-specific mapping from the air. The power of such an approach for a range of applications is emphasised in the chapter,