Introduction and synthesis: plant phylogeny and the origin of major biomes

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Phylogenetic trees based upon DNA sequence data, when calibrated with a dimension of time, allow inference of: (i) the pattern of accumulation of lineages through time; (ii) the time of origin of monophyletic groups; (iii) when lineages arrived in different geographical areas; (iv) the time of origin of biome-specific morphologies. This gives a powerful new view of the history of biomes that in many cases is not provided by the incomplete plant fossil record. Dated plant phylogenies for angiosperm families such as Leguminosae (Fabaceae), Melastomataceae *sensu stricto*, Annonaceae and Rhamnaceae indicate that long-distance, transoceanic dispersal has played an important role in shaping their distributions, and that this can obscure any effect of tectonic history, previously assumed to have been the major cause of their biogeographic patterns. Dispersal from other continents has also been important in the assembly of the Amazonian rainforest flora and the Australian flora. Comparison of dated biogeographic patterns of plants and animals suggests that recent long-distance dispersal might be more prevalent in plants, which has major implications for community assembly and coevolution. Dated plant phylogenies also reveal the role of past environmental changes on the evolution of lineages in species-rich biomes, and show that recent Plio–Pleistocene diversification has contributed substantially to their current species richness. Because of the critical role of fossils and morphological characters in assigning ages to nodes in phylogenetic trees, future studies must include careful morphological consideration of fossils and their extant relatives in a phylogenetic context. Ideal study systems will be based upon DNA sequence data from multiple loci and multiple fossil calibrations. This allows cross-validation both of age estimates from different loci, and from different fossil calibrations. For a more complete view of biome history, future studies should emphasize full taxon sampling in ecologically important groups, and should focus on geographical areas for which few species-level phylogenies are available, such as tropical Africa and Asia. These studies are urgent because understanding the history of biomes can both inform conservation decisions, and help predict the effects of future environmental changes at a time when biodiversity is being impacted on an unprecedented scale.

Keywords: molecular clocks; long-distance dispersal; plant biogeography; animal biogeography

1. INTRODUCTION

The papers in this volume represent the proceedings of a Royal Society Discussion Meeting held on 15–16 March 2004. The purpose of the meeting was to bring ecology and phylogenetics together by exploring what can be inferred of the history of major, species-rich biomes from molecular phylogenies of plants. The Earth's biodiversity is not randomly distributed over the planet's surface but is clustered into several biomes. Understanding the origin, history and present-day maintenance of biomes is therefore an important aspect of ecology. However, biomes are composed of species, each of which has an individual evolutionary history. This is the point of connection between the ecology of

biomes and phylogenetics, but it is a connection that has previously been little explored.

Understanding the history of biomes can inform conservation decisions, and perhaps more critically, help predict the effects of future environmental changes. Perhaps we should value ancient biomes more highly than more recent ones. Similarly, following arguments for the consideration of phylogenetic history in conservation decisions (e.g. Mace *et al.* 2003), biomes containing more history in the form of ancient lineages ('museums') might be prioritized more highly than those whose species richness merely reflects geologically recent radiations. By contrast, we may also wish to conserve 'cradles' of diversity where dated phylogenies tell us the evolutionary process is active. Most importantly, a deeper understanding of the Earth's biodiversity is vital in an age of projected species loss and global environmental change. The nature and distribution of present-day biomes determines, in large part, the functioning of the global

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ecosystem. Biomes are now being impacted by anthropogenic environmental change on an unprecedented scale, and one means of understanding how their component species will react is to study the effects of past environmental changes.

The aims of this introduction and overview are to guide the reader through the following papers, to synthesize their principal conclusions and to suggest some future directions for research. The meeting generated lively discussion, and because of the volume, range and complexity of the discussion points raised, we have taken the decision not to include verbatim transcripts. Instead, we have used the discussion generated at the meeting to inform the editing of the manuscripts and have also noted in this paper some of the key points raised.

2. WHAT IS A BIOME?

One problem with a multi-author and multi-disciplinary volume such as this is agreeing on a common definition of 'biome', a word with a long history and a multitude of uses. We decline to be prescriptive or to give a single definition, as the utility of the concept lies to a certain extent in its flexibility. Instead, we give an overview of how the term has been used.

The word biome was coined by Clements as early as 1916, but it was not taken up widely until Clements expanded on the concept in a book (Clements & Shelford 1939); it was also promoted by Carpenter (1939). Clements equated it to his concept of plant formation, but with the addition of animals. As it only referred to a biotic community, Clements excluded soil and climate from the biome concept. In this, Clements was enforcing the distinction between abiotic and biotic that he considered so important. It was a reaction against this rigid distinction between abiotic and biotic that prompted Tansley (1935) to coin the term 'ecosystem', which included abiotic and biotic components. It was ecosystem that came into currency as the basic unit of ecology, whereas biome was generally used for community classification at the macroscale to indicate biotic commonality, particularly in physiognomy, even over relatively diverse conditions of soil and climate.

An example of a recent definition of the world's major biomes was provided by Olson *et al.* (2001), who modified the definitions of Dinerstein *et al.* (1995) and Ricketts *et al.* (1999). Olson *et al.* recognized 14 global biomes.

- (i) Tundra (arctic, humid).
- (ii) Boreal forests-taiga (subarctic, humid).
- (iii) Temperate coniferous forests (temperate cold, humid).
- (iv) Temperate broadleaf and mixed forests (temperate, humid).
- (v) Temperate grasslands, savannahs and shrublands (temperate, semi-arid).
- (vi) Mediterranean forests, woodlands, and shrub (temperate warm, humid).
- (vii) Tropical and subtropical coniferous forests.
- (viii) Tropical and subtropical moist broadleaf forests.
- (ix) Tropical and subtropical dry broadleaf forests.
- (x) Tropical and subtropical grasslands, savannahs and shrublands.
- (xi) Deserts and xeric shrublands.
- (xii) Mangrove.

- (xiii) Flooded grasslands and savannahs.
- (xiv) Montane grasslands and shrublands (high altitude).

Perhaps because many biological and conservation problems are considered locally rather than globally, there has been a tendency to use the term biome in a more restricted sense, as it is used by most authors in this volume. Subdivision of the biome may be obtained by incorporating geographical and environmental data, or data on taxonomic composition. An example of this process is the coining of the term 'ecoregion', an ecologically relatively homogeneous region possessing a single biome. The ecoregion was developed in Canada by Crowley (1967) and extended by Bailey (1989). More recently, the ecoregion has been adopted by the World Wide Fund for Nature (formerly World Wildlife Fund, WWF) for global conservation planning purposes (<http://www.worldwildlife.org/science/ecoregions.cfm>), and is becoming an influential concept. The WWF scheme defines 223 significant ecoregions (the Global 200: Olson & Dinerstein 1998, 2002). These are identified by using as starting points the 14 major terrestrial biomes listed above. These are then divided among the seven biogeographical realms (Afrotropical, Australasia, Indo-Malayan, Nearctic, Neotropical, Oceania, Palaearctic; modified from Pielou (1979) and Udvardy (1975)). Ecoregions are then defined within each biome for each biogeographic realm (Olson *et al.* 2001).

The focus on a single geographical area in the ecoregion is a marked departure from the concept of global biomes, which may be widely disjunct. However, it allows incorporation of local features of importance to conservation such as endemism, and they are intended to have a unique biotic composition. The biota of these ecoregions could be considered biomes in Clements' sense, but might be better termed a 'sub-biome' to preserve 'biome' for macro-level use.

More recently the concept of biome has been used in a special sense in response to influences from remote sensing. With the pressing need to consider terrestrial biota globally, as a response to global environmental change, there has been a need to integrate biome information with the demands of remote observation. This has led to a movement to define biomes solely on observable qualities of the biota (usually the physiognomy and phenology of vegetation), as argued by Woodward *et al.* (2004) in the first paper in this volume. There are advantages and disadvantages to this approach. The advantages are that biomes are easily and objectively definable, they can be monitored readily, and huge amounts of data can be gathered cost effectively. Furthermore, removing local environmental factors from the definition of biome allows hypotheses about the distribution of biomes in respect to the environment to be tested without circularity. However, the disadvantages of this approach are that a huge amount of information has to be disregarded and fine-scale analyses are not possible. For a volume such as this one, which attempts to bring together phylogenetic information about taxa and ecological approaches, the physiognomy- and phenology-based global approaches that ignore taxonomic composition raise a significant challenge. This paper, and the others in this volume (e.g. Crisp *et al.* 2004; Pennington & Dick 2004; Plana 2004; Burnham & Johnson 2004; Jacobs 2004) use biome in a geographically restricted sense (sub-biomes and ecoregions as defined above), which

allows better incorporation of phylogenetic and taxonomic information.

3. HOW DO BIOMES CHANGE THROUGH TIME?

Biomes are unstable in geological time: they are dependent on ecological and phylogenetic constraints for their characteristic features. As ecological conditions change and as organisms evolve and become extinct, so biomes disappear or change composition and new biomes appear. The lycopsid-dominated coal-forming swamp biome of the Carboniferous is a well-known example of a biome that no longer occurs. By contrast, the Miocene swamp-forest of Borneo is a biome that is still present today, essentially unchanged (Demchuk & Moore 1993).

If ecological conditions do not change and there is no influx or evolution of different clades of organisms with different morphologies, then biomes will remain stable. At the global biome level, therefore, it is the addition of a different life form that causes a biome to change. The addition or extinction of species of the same life form is not relevant because a biome is a physiognomic rather than taxonomic or geographical concept at the global scale. However, at a more restricted geographical level (the sub-biome or ecoregion level as defined above), addition and extinction of species of the same life form is significant. For example, broadleaf evergreen forest in southeast Asia is characterized by the abundance of the plant family Dipterocarpaceae. If dipterocarps in the forest were to be replaced by another dominant of the same life form, its nature and the fine-scale functioning of the ecosystem would be changed.

Thus, all biomes can be said to have an origin in time, even though this may be ill defined. This origination process is likely to involve: (i) *in situ* evolutionary change in the morphology and diversity of organisms present in the precursor biome; (ii) changes of relative abundance of organisms already present; (iii) invasion of lineages representing different life forms; and (iv) *in situ* evolution of invading lineages. As (i), (iii) and (iv) are likely to leave a phylogenetic footprints, phylogenetics, particularly of the dominant plants of biomes, is a tool for the study of their origin, and potentially allows us to date the key events.

4. WHAT CAN DATED PHYLOGENIES HELP US INFER ABOUT BIOME HISTORY?

Until recently, the fossil record was the only source of information to answer questions such as when did rainforests originate, how has their floristic composition changed through time, and whether their species richness is a recent phenomenon, or has been building slowly through geological time. This is problematic because some biomes, for example those in tropical arid areas, leave few fossils. Furthermore, the fossil record is far too incomplete to address questions of the time of origin of individual species in most terrestrial plant groups. This means that the fossil record is often at its weakest as a record of the history of the most species-rich biomes, the focus of this volume, where we need to understand the history of a multitude of extant lineages.

New theoretical developments (e.g. Sanderson 1997, 2002; Near & Sanderson 2004; Thorne *et al.* 1998; Thorne & Kishino 2002) offer a means of placing a dimension of

absolute time on phylogenetic trees derived from DNA sequence data. Potentially, this provides a powerful new 'ecological telescope' to view biome history that may be able to resolve issues that the fossil record cannot. If an age can be assigned to a single node in a phylogenetic tree using external evidence, these new methods allow the estimation of the ages of all the other nodes. This allows observation of the pattern of accumulation of lineages through time, estimation of when specific monophyletic groups originated, and when lineages arrived in different geographical areas. In addition, key morphologies (biome-specific physiognomies) can be mapped onto robust molecular phylogenies and their origins dated. The same is true of geographical information, which can be mapped to infer ancestral areas. Ecology has been impacted already by the phylogenetic revolution (e.g. Ackerly & Donoghue 1998; Webb *et al.* 2002) and these impacts are poised to spread to our understanding of biomes.

5. METHODOLOGICAL ISSUES

Methods used to add a dimension of absolute time to molecular phylogenetic trees make considerable assumptions, not least that the initial calibration often relies upon the fossil record. They also have to accommodate the problem that the accumulation of mutations in DNA sequences is often far from constant, meaning that a simple 'molecular clock' cannot be invoked. Two of the early papers in this volume (Near & Sanderson 2004; Renner 2004) deal with these methodological issues.

(a) *Calibrating nodes*

Much attention has been paid in the literature to techniques and algorithms that enable the calculation of relative ages in a molecular phylogenetic tree, even in the absence of rate constancy (e.g. Sanderson 1997, 2002; Thorne *et al.* 1998; Thorne & Kishino 2002). Less attention has been paid to how we might calibrate these phylogenies by assigning ages to individual nodes, but calibration is potentially the largest source of error in the dating of phylogenetic trees. Two principal methods of calibration have been used, taking information from:

- (i) fossils (see, for example, Wikström *et al.* 2001; Renner 2004; Lavin *et al.* 2005; Bremer 2000);
- (ii) ages of geological events such as the opening of ocean barriers (see, for example, Becerra 2003; Crisp *et al.* 2004), completion of land bridges (Richardson *et al.* 2001a), creation of volcanic oceanic islands (Richardson *et al.* 2001b; Plana 2004).

The high frequency of long-distance dispersal events indicated for many plant groups by authors in this volume (Richardson *et al.* 2004; Plana 2004; Renner 2004; Lavin *et al.* 2004; Pennington & Dick 2004; see further discussion in § 6 below) highlights the danger of the use of geological events, especially old ones, as calibration criteria. For example, Renner, Plana and Lavin *et al.* demonstrate that endemic radiations of Melastomataceae *sensu stricto*, *Begonia* and Leguminosae (*Ormocarpopsis*, *Indigofera*) on Madagascar date only from the Miocene. This is an age pattern that reflects over-water dispersal rather than tectonic history. Hence, the distinctiveness of the Madagascan flora cannot solely reflect its long isolation after splitting

from Africa and India, which is the conventional view, but reflects a unique amalgamation of lineages of diverse geographical origin through time.

(b) *Multiple calibration points*

It would appear that well-identified fossils represent the most objective means of assigning ages to nodes. It is clearly desirable to be able to assign fossils to multiple nodes, because this provides a means of cross-validating age estimates. This approach is used in this volume by Near & Sanderson (2004), Lavin *et al.* (2004) and Renner (2004; who uses fossil and geological calibrations). Near & Sanderson (2004) present a useful new algorithmic technique that in the presence of multiple fossil calibrations identifies those that suggest significantly deviant ages, and which may be misleading the analysis. These could be removed from the analysis entirely, but it may be that these have been assigned to an incorrect node, and that careful reconsideration of their morphology is necessary.

It is unfortunately true for most studies, especially those at the species level, that at best a single fossil calibration might be available. Near & Sanderson (2004) acknowledge this, but suggest that the limits to accurate age estimation must continue to be tested in the context of a few carefully chosen systems that offer numerous fossil calibrations. Such systems will help to reveal the exact extent of substitution rate variation in sequence evolution, and the ability of different methods to cope with it. Near & Sanderson (2004) point out that it is possible that such studies might result in the disappointing conclusion that accurate divergence time estimates require multiple reliable calibrations.

(c) *Data and algorithms*

Plant phylogenies are now often generated using DNA sequence data from multiple loci, which ideally come from the different genomes of the chloroplast, nucleus and, more rarely, mitochondrion. This has the theoretical benefit of increased phylogenetic accuracy. However, most published studies dating molecular phylogenies have used DNA sequence data from only a single locus. This may present problems because different loci can evolve distinctly, which can result in different age estimates (Yang & Yoder 2003). However, although rates may vary in different ways among multiple loci, their divergence times from a common ancestor are shared. This means that analysing multiple loci, as well as using multiple calibration points, in theory may improve age estimation (Yang & Yoder 2003).

The Bayesian algorithm of Thorne & Kishino (2002) implemented by Renner (2004) in this volume offers considerable flexibility in the analysis of multiple loci in estimating divergence times. It also allows easy calculation of confidence limits around estimates. Interestingly, Renner's thorough analysis of *Melastomataceae sensu stricto* using multiple loci and multiple calibrations produced age estimates that differed little from those calculated using a single locus, single calibration, and also assuming a strict molecular clock (Renner *et al.* 2001). By contrast, Yang & Yoder (2003), using the same Bayesian method, showed that the dates of the divergence of mouse lemurs produced variable dates when different partitions of mitochondrial DNA sequence were analysed. In this case the partitions were different codon positions rather than different genes. The disparity of results presented by Renner (2004) and

Yang & Yoder (2003) suggests that any conclusion that multiple loci are required for accurate dates may not be general. The more accurate estimates of Yang & Yoder (2003) based upon multiple loci might just reflect the loci and taxa studied. There is a clear need for more empirical studies on systems that offer both numerous calibrations and loci to assess the desirability of basing age estimates on multiple loci and calibrations. We suggest that it is sensible to calculate ages based upon separate loci to cross-validate them (e.g. Lavin *et al.* 2005) before carrying out any combined analysis, just as individual datasets are examined for differing phylogenetic signals before combination in phylogenetic analysis (e.g. Johnson & Soltis 1998).

Finally, concern about precise methodology such as the model of sequence evolution used to calculate branch lengths, and the algorithm used to calculate ages may be somewhat trivial relative to the choice of loci. It is vital that there is a good level of nucleotide substitution for the terminal taxa studied. If terminal taxa are separated by few nucleotide substitutions, and branch lengths in a molecular phylogenetic tree are short, all algorithms will produce age estimates for adjacent nodes with wide confidence limits that overlap. This makes estimation of the sequence of cladogenesis in absolute time impossible.

6. STUDIES OF MAJOR FAMILIES AND LIFE FORMS: LONG-DISTANCE DISPERSAL VERSUS TECTONIC HISTORY

Many biomes have a global distribution (Woodward *et al.* 2004), therefore understanding their history requires a global approach. Similarly, even island continents have received immigrant taxa during their history from diverse areas (Pennington & Dick 2004; Renner 2004; Crisp *et al.* 2004; Hill 2004), so understanding their biotic history requires a broad geographical outlook. This breadth of geographical view is the strength of the studies of species-rich, cosmopolitan, ecologically important families presented here by Renner (*Melastomataceae sensu stricto*), Lavin *et al.* (*Leguminosae*) and Richardson *et al.* (*Annonaceae* and *Rhamnaceae*).

Melastomataceae sensu stricto (3000 species) are generally pioneer and understorey trees and are an important component of rainforest in the Neotropics, but also found in Africa and Asia. Subsequent papers (Lavin *et al.* 2004; Richardson *et al.* 2004) present dated phylogenies for *Annonaceae* (2500 species), *Rhamnaceae* (900 species) and *Leguminosae* (18 000 species). *Annonaceae* are ubiquitous in the understorey of the world's tropical rainforests, whereas *Rhamnaceae* are virtually cosmopolitan in tropical and subtropical xeric regions.

A clear message emerging from all these studies is that long-distance, transoceanic dispersal has been a major force in determining plant distributions. It had previously been considered that in the cases of legumes, *Annonaceae* and *Melastomataceae sensu stricto*, distributions largely reflected processes of continental drift (e.g. Raven & Axelrod 1974). However, in all cases, dated phylogenies show clear evidence of recent long-distance dispersal events. For example, Renner (2004) shows *Melastomataceae sensu stricto* having reached Madagascar only in the Miocene when the Mozambique channel, separating it from Africa, was 400 km wide (its present-day distance). Richardson

et al. (2004) show that *Annona* (Annonaceae) dispersed from the Neotropics to Africa *ca.* 13.9–16.3 Myr ago, despite the fact that it belongs to an ancient family (82–91 Myr old), whose biogeography was certainly influenced by continental drift. The most extreme examples are Rhamnaceae and Leguminosae, which are shown to have undergone multiple transoceanic dispersal events.

The paper by Lavin *et al.* (2004) on legumes estimates the ages for 59 ‘transcontinental crown clades’. Each is a monophyletic group that comprises sister clades separated by an oceanic barrier or large expanse of continental area, such as one clade in North America, and its sister in South America. Most of these clades are 6–16 Myr old, and only eight have a mean age of over 25 Myr. This age distribution precludes any influence of continental vicariance on producing these distribution patterns, and long-distance dispersal is likely to be the primary explanation. Lavin *et al.* (2004) suggest that the unified neutral theory of biodiversity and biogeography of Hubbell (2001) might be a potential explanation of the geographical and ecological structure in the legume phylogeny because it is a dispersalist theory that makes predictions about phylogenetic structure. This hypothesis requires further testing.

The predominance of long-distance dispersal in legume biogeography is a highly significant result for biome history. Leguminosae are the third largest family of the flowering plants, dominating the tropical rainforests, dry forests and woody savannahs of the Neotropics and Africa, both in terms of species numbers, and numbers of individuals. It is clear that long-distance dispersal must have had a substantial influence on the historical construction of the tree flora of these biomes.

It should be pointed out that other plant groups do show the biogeographic imprint of tectonic events, and perhaps a lesser role of long-distance dispersal. For example, a dated phylogeny has been used to corroborate the hypothesis that Crypteroniaceae rafted northward on India to colonize Asia (Conti *et al.* 2002). This scenario is also suggested for Dipterocarpaceae (Ashton & Gunatilleke 1987), and the topology of molecular phylogenetic trees is consistent with it (Ducousso *et al.* 2004), but given the prevalence of long-distance dispersal in other groups, this scenario must be tested by dating these phylogenies. Similarly, Mark Chase (Royal Botanic Gardens, Kew) pointed out during a discussion at the meeting that molecular phylogenetic trees of Orchidaceae (e.g. Cameron *et al.* 1999; Whitten *et al.* 2000; Van den Berg *et al.* 2004) show clear continental geographical structure, but whether this is consistent with continental vicariance also needs testing by dating these phylogenetic trees.

(a) *Epiphytes*

Orchidaceae are the largest family of flowering plants, but their importance for understanding biome history does not lie wholly in their large number of species. Many orchids are epiphytes, and are characteristic elements of tropical rain and cloud forests. Elucidating the evolutionary history of these epiphytes, and the factors that have driven their diversification is an important element of understanding the historical assembly of these species-rich habitats. Gravendeel *et al.* (2004) use phylogenies of orchids and some other major epiphytic groups to elucidate this. However, they also turn the question on its head and ask

whether the epiphytic habit promotes diversification. They conclude that it does and therefore the origin of rain and cloud forest biomes, home to most epiphytes, has had a massive impact on global biodiversity by promoting diversification of species-rich epiphyte clades.

7. STUDIES OF INDIVIDUAL BIOMES

The bulk of the remaining papers adopt the approach of reviewing what is known of the history of species-rich biomes, ranging from the Cape of Africa (Linder & Hardy 2004), Australia (Crisp *et al.* 2004), the rainforests of west Africa (Plana 2004), the Amazon rainforest (Pennington & Dick 2004) to Northern Hemisphere temperate forests (Donoghue & Smith 2004). In the cases of Africa (Jacobs 2004), the Neotropics (Burnham & Johnson 2004) and Australia (Hill 2004), there are palaeontological reviews. These are essential for two reasons. First, as outlined above (see § 5), in most cases the basis for calibration of phylogenies is the fossil record, and all these papers provide important reviews for botanists seeking published information of fossils in their specialist groups. Second, it is vital that inferences made from dated phylogenies are compared with what is known from the fossil record. One major aim of the Discussion Meeting was, therefore, to bring together palaeobotanists and plant molecular systematists.

(a) *Australia*

The papers of Hill (2004) and Crisp *et al.* (2004) tackle the origin of the Australian vegetation by using palaeobotanical and phylogenetic data, respectively. Australia is particularly interesting in this context because it is an ancient and discrete landmass, isolated from other continents since 25 Myr ago. Hill (2004) traces a Gondwanan element in present-day biomes, particularly in the gymnosperms. However, this element has been much influenced by *in situ* evolution, apparently driven by Australia’s massive post-Gondwanan environmental shifts. Whereas Hill (2004) uses palaeobotany to look forward in time to present-day biomes, Crisp *et al.* (2004) extrapolate historical patterns through the collation and examination of numerous phylogenetic analyses. They note that lineages in different biomes have different histories, and many appear to have a post-Gondwanan origin in Australia. Lineages in the aseasonal-wet biome are species-poor and appear to have been depleted by extinction during the onset of dry conditions after the continental separation of Australia (from 25 Myr ago). At the same time, taxa characteristic of the sclerophyll biomes such as *Banksia* and *Eucalyptus* underwent rapid radiation. During the more recent hyper-aridification which gave rise to the arid communities (Eremean biome), there has been rapid radiation of certain characteristically Eremean lineages. These include *Lepidium* and Chenopodiaceae, which have dispersed into Australia from overseas, again emphasizing an important role for long-distance dispersal.

(b) *African rainforests: ancient versus recent speciation*

Jacobs (2004) reviews the palaeontological history of African rainforest, woodland and savannah biomes. She concludes that biomes corresponding with contemporary rainforest and woodland did not originate until the Eocene, when there is clear evidence for the presence of families

such as Leguminosae that characterize them. Despite the presence of grass pollen in the Palaeocene, the savannah biome did not begin to expand until the Middle Miocene (*ca.* 16 Myr ago), and did not become widespread until the Late Miocene (*ca.* 8 Myr ago). This review provides a background and time-scale against which Plana (2004) evaluates evidence for the time-scale of species diversification in West African (Guineo-Congolian) rainforests, though her review also touches upon savannahs and East African rainforests.

The high species richness of tropical rainforests was quickly noted by nineteenth-century naturalists. As early as 1878, Alfred Russell Wallace suggested a central role for stable tropical climates in explaining high tropical diversity: 'The equatorial zone, in short, exhibits to us the result of a comparatively continuous and unchecked development of organic forms; while in the temperate regions there have been a series of periodical checks and extinctions'. This inspired later papers from Dobzhansky (1950) and Fischer (1960) that led to an influential viewpoint that the high diversity of tropical rainforests resulted from long periods of stable tropical climates resulting in low extinction rates, meaning that species accumulated through time. With Jacobs' time-scales in mind, this would allow *ca.* 40–50 Myr for the accumulation of species in African rainforests.

The concepts of stable tropical climates so crucial to the ideas of Wallace (1878), Dobzhansky and Fischer were radically challenged in the 1960s and 1970s. Fossil pollen data from Africa and the Neotropics showed that during the Ice Age climates became drier and cooler (Aubréville 1962; Van der Hammen 1974). This led to suggestions that rainforests must have become restricted in extent, while drought-adapted seasonally dry forest or savannah vegetation became more widespread. In an influential paper, Haffer (1969) suggested that populations of rainforest species would have become isolated in 'refugia', restricting gene flow and causing divergence that would ultimately lead to speciation. In his original paper, Haffer (1969) proposed that this process was the principal speciation engine that had driven the production of high species numbers of birds in the world's most species-rich rainforests of the Amazon Basin. This was followed by suggestions that Pleistocene climate changes had similarly influenced the evolution of plant species (Prance 1987; Whitmore 1987), though these authors clearly envisaged a burst of speciation in the Pleistocene after older speciation events. Although the basis of 'refuge theory' has been heavily criticized, especially for the Neotropics (Colinvaux *et al.* 1996, 2001), it remains influential, particularly for Africa, where there is evidence that Pleistocene climatic changes were severe (reviewed by Plana 2004).

Plana (2004) evaluates the evidence from the few available dated phylogenies of African rainforest plant species for Pleistocene species diversification. She presents strong evidence for recent Pleistocene speciation, which may therefore have been driven by climatic changes, in genera such as *Aframomum* (Zingiberaceae) and *Begonia*, which are largely confined to rainforest. This stands in stark contrast to the review of Moritz *et al.* (2000), which focuses upon global patterns of rainforest animal speciation, and which found little evidence for such recent speciation. The recent patterns documented by Plana have also been

shown for the species-rich Neotropical tree genus *Inga* (Leguminosae; Richardson *et al.* 2001a), and for *Goniothalamus* (Annonaceae; Richardson *et al.* 2004) in Southeast Asia. Similarly, Linder & Hardy (2004) indicate that 15% of modern species diversity of the Fynbos biome evolved during the Pleistocene, and 40% since the beginning of the Pliocene. Crisp *et al.* (2004) review dated phylogenies that show massive speciation over the past 5 Myr in taxa such as Chenopodiaceae, Brassicaceae and *Gossypium* that are characteristic of the arid communities (Erebean biome) of Australia. Recent, rapid speciation has clearly played a role in producing a substantial proportion of the plant species diversity we see in rainforests and other species-rich biomes.

Plana (2004) is, however, careful to point out that in African *Begonia*, many of the key evolutionary events in this large genus date to the Miocene, and that in other genera such as *Acridocarpus* (Malpighiaceae) that have both rainforest and savannah species, that the rainforest species are often phylogenetically basal members of Miocene lineages. Clearly, the species richness of African rainforests is the result of a combination of both relatively ancient and more recent speciation, a conclusion echoed in a study of seasonally dry forest in the Neotropics (Pennington *et al.* 2004), and in this volume for the Fynbos (Linder & Hardy 2004) and Australian sclerophyll biomes (Crisp *et al.* 2004).

(c) *Amazonian rainforest: the importance of immigrants*

In contrast to Plana (2004), Pennington & Dick (2004) use plant phylogenies to identify immigrant plant lineages in the world's most species-rich rainforests of the Amazon basin. Burnham & Johnson (2004) review palaeontological data that show no clear evidence in terms of morphological features and taxonomic composition for rainforest in South America until the early Tertiary. At this time, South America was an island continent, and had been isolated since it split from Africa *ca.* 100 Myr ago. It had been widely assumed that the contemporary flora of the Amazon rainforest was derived almost entirely from lineages isolated by this vicariance event (Gentry 1982; Young *et al.* 2002). However, Pennington & Dick (2004) show that the Amazon tree flora contains a substantial proportion (*ca.* 20%) of species that are members of groups shown by molecular phylogenies to have arrived in South America long after the west Gondwanan vicariance event. They review various migration routes by which these taxa may have arrived, but conclude that long-distance, transoceanic dispersal may have played a predominant role, echoing the conclusion reached in the studies of major families (Lavin *et al.* 2004; Richardson *et al.* 2004).

(d) *The Cape Floristic Region*

The 'Fynbos Biome' of the Cape Floristic Region is noted for its high levels of plant species diversity and endemism that is limited to relatively few clades. Some authors even consider its number of endemic genera and families sufficient to warrant describing it as a floristic kingdom (Good 1974). The origin of this diversity is thought to be a response to progressive aridification in the Pliocene and Late Miocene that eliminated the tropical flora that once occupied this region (Levyns 1964; Linder *et al.* 1992; Goldblatt 1997; Goldblatt & Manning 2000; Linder

2003). What was known about the history of these continental radiations was based upon a sparse fossil record that did not provide precise details of their initiation. Now we can use molecular data in combination with the fossil record and geological events to get more precise information concerning the timing of these radiations. Linder & Hardy (2004) present a phylogenetic analysis of the largest clade of Restionaceae that is found in the Cape and demonstrate that radiation was initiated between 20 and 42 Myr ago. The starting dates for the radiation of seven other clades were also evaluated with an estimated range of between 7 and 20 Myr ago. Linder and Hardy suggest that these clades radiated in response to the Fynbos vegetation increasing its extent in the Cape due to climatic change. These data allow a critical evaluation of the Levyns (1964) and Goldblatt (1997) hypotheses that state that the modern species richness of the Cape flora is the result of radiation into the arid habitats of the western portion of the Cape Floristic Region. The initiation of these radiations appears to be lineage specific starting in the Late Oligocene, and continuing through the Late Miocene into the Pliocene. Molecular phylogenetic studies of the taxa that are found in this biome allow us to develop a clearer picture of how its modern diversity has accumulated through space and time.

(e) Northern Hemisphere forests: plant versus animal biogeography

Donoghue & Smith (2004) take a phylogenetic approach to analyse biogeographic patterns within the northern temperate forest biome. This biome, when considered in terms of taxonomic composition, may be broken up into distinct biogeographic units: east Asia, western north America, eastern North America and Europe. However, many lineages are common to two or more of these areas, implying an exchange of biota between areas at some point in the past. Phylogenetic analysis points to the origin of most of these lineages in east Asia followed in many cases by migration across the north Pacific at various times during the past 30 Myr, possibly by a Beringian land bridge.

Donoghue & Smith (2004) also contrast biogeographic patterns and ages of disjunctions of plants in Northern Hemisphere forests with those reviewed for animals in the same areas by Sanmartín *et al.* (2001). There are striking differences. For example, the general pattern of movement out of Asia is not found for animals, and east Asia – eastern North America disjunctions are more recent (less than 30 Myr ago) for plants than animals. Similarly, in a study of Southern Hemisphere biogeography, Sanmartín & Ronquist (2004) reported plant disjunctions to be younger than those in animals. Pennington & Dick (2004) also suggest that the vertebrate fauna of South America contains fewer immigrant lineages than the flora. We agree with Donoghue & Smith (2004) that it may be premature to conclude that there are truly major biogeographic differences between plants and animals, because of analytical problems such as the few taxa sampled, biases towards species-poor groups and taxa such as angiosperms and insects, and differences in the methodology of age estimation. However, if plants do show repeated intercontinental movements more recently than animals, perhaps due to greater capacities to disperse over long distances and establish founder populations (Pennington & Dick 2004),

this has major implications for community assembly and coevolution (Donoghue & Smith 2004). For example, Donoghue & Smith (2004) point out that if animals have been present in an area longer than plants, this implies a need for rapid adaptation on the part of animals as new plant immigrant lineages enter a community.

8. WHY ARE SOME BIOMES MORE SPECIES RICH?

The final paper (Davies *et al.* 2004) takes a different approach and asks why some biomes contain more species. There may be contemporary ecological explanations for this phenomenon in that different biomes may allow differing numbers of species to coexist. However, why did more species evolve (or less become extinct) in different biomes? Davies *et al.* (2004) take a global perspective to try to determine some of the causes of these patterns. One pattern that has been observed is that species richness tends to decline towards the poles. Davies *et al.* (2004) investigate the possibility that high levels of environmental energy promote higher species richness nearer the Equator. The amount of energy input into a system may limit the number of species that coexist in an area or influence evolutionary rates. Davies *et al.* (2004) demonstrate that angiosperm families that are exposed to a high-energy load tend to be both more species rich and possess faster evolutionary rates, although it is not known whether one drives the other. They also highlight the case of Iridaceae, which demonstrates that the effects of the environment can vary among lineages. This may be due to interactions between biological traits and the environmental conditions in which the lineage is found. Diversification rates are therefore likely to be dependent upon many interacting factors. To get a better overview of the effects of this range of factors a broader sample across multiple lineages is required.

9. CONCLUSIONS: WAYS FORWARD

The contributions in this volume demonstrate the power of phylogenetic trees based upon DNA sequence data to illuminate the history of biomes, especially when calibrated with a dimension of time. We believe that such studies will become more widespread, just as phylogenetics is becoming increasingly influential in ecology (Hubbell 2001; Webb *et al.* 2002). In this final section we highlight some research areas that we see as especially important.

(a) The importance of fossils and morphology

Because dating phylogenies relies on assessing amounts of change in DNA sequences, much attention has been focused upon issues such as correcting for deviations from a strict 'molecular clock' (Sanderson 1997, 2002; Thorne *et al.* 1998; Thorne & Kishino 2002; Near & Sanderson 2004). However, much discussion at the meeting, including points raised by Michael Donoghue (Yale University), Susanne Renner (Ludwig Maximilians University Munich) and Sir Peter Crane (Royal Botanic Gardens, Kew) highlighted the vital role to be played by both fossils and morphological data.

Crane pointed out that though the method presented by Near & Sanderson (2004) provides a means of identifying possibly misleading fossil calibrations, this should not substitute for careful study of fossils before they are used in an analysis. Different fossils will have different values as calibration points, which can be assessed before analysis by

considering issues such as: (i) reconstructed fossil plants based upon multiple organs will be easier to assign to a specific phylogenetic node because they have more character information than isolated organs; (ii) the age precision offered by fossils varies greatly, representing an age range rather than an absolute date, and the best fossils for calibration will have smaller age ranges.

Crane also highlighted the importance of the analysis of morphological data to accurately position fossils in a phylogenetic framework. The theoretical ideal might be to score the fossil and extant taxa for morphological characters, and infer the placement of the fossil taxa from a morphological (Crepet & Herendeen 1992) or simultaneous morphological–molecular phylogenetic analysis. Problems with this are the limited phylogenetic resolution often obtainable from morphological characters (Scotland *et al.* 2003), and missing data for fossils in a simultaneous analysis because their DNA cannot be sequenced. This may cause their position in the resulting phylogenetic trees to be unstable (Platnick *et al.* 1991). However, these approaches will be impossible in most cases simply because the fossils are fragmentary and can be scored for few characters (Lavin *et al.* 2005). In this case, the best that can be done is to use the few characters the fossils possess to assign them to extant clades. To be done accurately, this requires careful morphological characterization of extant taxa, and a clear picture of the character states (synapomorphies) defining clades. This ideally requires morphological characters to be scored for extant taxa and included in a simultaneous molecular–morphological phylogenetic analysis, allowing individual morphological character states to be assigned to nodes in the resulting phylogenetic tree. The placement of fossils can then be inferred from their character states. This approach should be more precise than simply assigning fossils to the stem of the clade to which they belong, a tendency in many studies, as pointed out by Donoghue & Smith (2004), which will underestimate divergence times.

It is clear that assigning fossils to phylogenetic nodes requires not only careful morphological consideration of the fossils, but also of their extant relatives. To a large extent, the recent emphasis on molecular systematics has diminished the volume and profile of traditional comparative morphological systematics (Wortley *et al.* 2002). This will make it difficult to place relevant fossils, which ironically will result in poorly calibrated molecular phylogenies.

(b) *The value of phylogenetic studies of ecologically important groups*

The purpose of this volume is to investigate the history of biomes, but many of the phylogenetic studies presented arose originally from unrelated studies focused on the systematics of different groups. The papers in this volume by Lavin *et al.* (2004; Leguminosae), Renner (2004; Melastomataceae *sensu stricto*), Plana (2004; *Begonia*), Linder & Hardy (2004; Restoniaceae), Richardson *et al.* (2004; Annonaceae and Rhamnaceae), Gravendeel *et al.* (2004; Orchidaceae) attest to the much wider value of such systematic work, and to the urgency of its continuation and completion. These groups are ecologically important as different life forms in different biomes and geographical areas. For example, leguminous trees are canopy dominants in Neotropical and African rainforests. Annonaceae are generally small trees that form an important component

of the rainforest understorey virtually worldwide. *Begonia* species are ubiquitous terrestrial herbs or trunk epiphytes in tropical rainforests worldwide. Phylogenies of these groups are complementary because they permit inference of the history of different aspects of the rainforest biome. However, for all these taxa, the full potential of their phylogenies will not be realized until taxon sampling is more complete. For example, sampling of *Begonia* species outside of Africa–Madagascar is sparse (Plana *et al.* 2004), meaning the *Begonia* phylogeny cannot yet be used to study the history of the herbaceous flora of Neotropical and Southeast Asian rainforests.

Unfortunately, despite the increasing ease of gathering DNA sequence data, increasing taxon sampling in phylogenetic studies is difficult. Field collection of all 1200 Neotropical and Asian *Begonia* species would be a massive undertaking. The collection of tall, legume trees is even tougher. However, the scientific value of better-sampled phylogenies would repay the investment.

(c) *Geographical areas with few phylogenies*

It is clear that much more information is available for some biomes and geographical areas than for others. Donoghue & Smith (2004) review phylogenies from 66 clades of Northern Hemisphere temperate forest plants, and Crisp *et al.* (2004) found 50 published phylogenies of the Australian vascular flora presenting chronograms or phylograms allowing an assessment of radiation history. Linder & Hardy (2004) review evidence from eight phylogenies for clades largely endemic to the Cape Region of South Africa, and a recently established collaborative network for the study of the evolution of the Cape flora will ensure that more phylogenies will appear soon (J. A. Hawkins, personal communication). By contrast, the review of the main expanse of African rainforest in the Guineo-Congolian region by Plana (2004) deals with phylogenies of two plant genera. Similarly, we are aware of very few reasonably sampled species-level phylogenies for plants of Southeast Asian rainforests. The answers to key questions such as why African rainforests are less species rich than those in Asia and the Americas (Richards 1973; Gentry 1993) may lie in the history of these rainforests, so more phylogenies of their component plants are desirable.

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