

Patterns in the assembly of temperate forests around the Northern Hemisphere

Michael J. Donoghue* and Stephen A. Smith

Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT 06520, USA

Recent studies of Northern Hemisphere biogeography have highlighted potentially significant differences between disjunction patterns in plants versus animals. To assess such differences, we compiled a larger sample of relevant plant phylogenies from which disjunction patterns, ancestral areas and directions of movement could be inferred. We considered 66 plant clades with species variously endemic today to eastern Asia (EA), Europe (including southwestern Asia), eastern North America (ENA), and/or western North America (WNA). Within these clades we focused on 100 disjunctions among these major areas, for 33 of which absolute divergence times have also been inferred. Our analyses uphold the view that disjunctions between EA and ENA are exceptionally common in plants, apparently more so than in animals. Compared with animals, we find few disjunctions between EA and WNA, consistent with increased extinction in WNA or failure of some groups to colonize that region. Taken at face value, our data also support the view that many temperate forest plant groups originated and diversified within EA, followed by movement out of Asia at different times, but mostly during the last 30 Myr. This favours Beringia over a North Atlantic land bridge as the primary path between the Old World and the New World. Additional studies are needed, especially to evaluate the impacts of differential extinction on these patterns, to more confidently establish divergence times, and to assess the statistical significance of these findings. Fortunately, many more plant groups show relevant disjunction patterns and could soon be added to such analyses.

Keywords: temperate forests; Tertiary relict floras; historical biogeography; phylogeny; plants; animals

1. INTRODUCTION

The distribution of the temperate forest biome is discontinuous around the Northern Hemisphere, being well developed today in EA, ER and ENA and, to a much lesser extent, in WNA (figure 1). How did this distribution arise, and how were temperate forest communities in these regions assembled over time? Our aim is to explore these questions from the standpoint of historical biogeography, bringing to bear rapidly improving knowledge of plant phylogeny.

The phylogeography of the Holarctic region of the Northern Hemisphere has attracted considerable attention in the past (Gray 1859; Li 1952, 1972; Graham 1972; Boufford & Spongberg 1983; Davidse 1983; Tiffney 1985*a,b*) and has recently been revisited using phylogenetic tools (Wen 1999; Manos & Donoghue 2001). Botanists have long recognized several major disjunction patterns (e.g. Thorne 1972; Wood 1972; Raven & Axelrod 1974; Axelrod 1975; Liston 1997), but especially a connection between EA and ENA (reviewed by Wen 1999; Manos & Donoghue 2001; Milne & Abbott 2002). The standard explanation put forward for this pattern is the existence earlier in the Tertiary of a widespread vegetation type (the 'boreotropical forest' or, more recently in time, the 'mixed

mesophytic forest') followed by increased extinction in WNA due to drying climates, and in ER, more recently, owing to glaciation (Wolfe 1975; Tiffney 1985*a,b*, 2000; Manchester 1999; Wen 1999; Sanmartín *et al.* 2001; Tiffney & Manchester 2001; Milne & Abbott 2002). Adopting this view, EA and ENA have retained greater diversity and, owing to extinction elsewhere, species from these areas will appear to be directly phylogenetically connected to one another. Related species from EA and ENA may also have retained greater morphological similarity compared with related species in other areas owing to their prolonged occupation of similar, relatively stable environments ('morphological stasis': Parks & Wendel 1990; Wen 2001; Milne & Abbott 2002). The generation and retention of particularly great diversity in EA, compared with the other major Holarctic areas of endemism, has been attributed to topographic and climatic circumstances, and to the greater refuge area available there (Latham & Ricklefs 1993; Ricklefs & Latham 1992; Guo *et al.* 1998; Qian & Ricklefs 1999, 2000; Harrison *et al.* 2001; Qian 2001).

Although this explanation is in many ways quite satisfying, it has not yet been thoroughly tested and it leaves open several important questions. In earlier studies, a detailed knowledge of phylogenetic relationships was generally lacking, offering the possibility that the basic disjunction patterns themselves may not have been properly identified (Wen 1999). Among other things, it has not been clear whether and to what extent temperate plant species in different areas are related to plants outside the Holarctic, such

* Author for correspondence (michael.donoghue@yale.edu).

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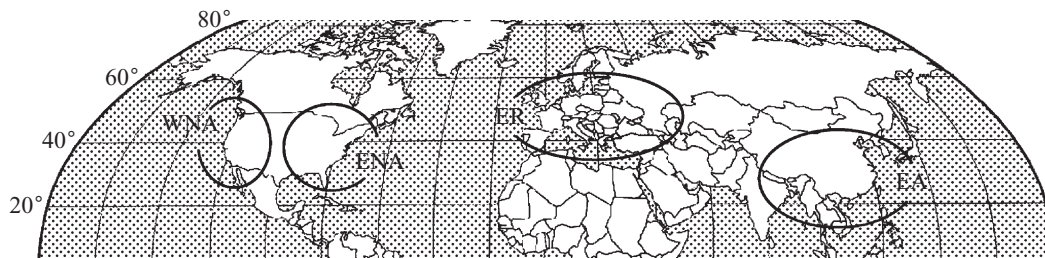


Figure 1. Map of the Northern Hemisphere showing the four major areas of temperate forest endemism that are the focus of the present analysis; EA: eastern Asia; ER: Europe (including southwestern Asia); ENA: eastern North America; WNA: western North America.

as from adjacent subtropical or tropical regions (Wen 1999, 2001; Fritsch *et al.* 2001; Lavin *et al.* 2001; Davis *et al.* 2002a). The standard view also does not directly address the question of the movement of individual clades, or whether there are general patterns in where temperate forest clades originated, or in the direction of movement, whether through Beringia or through a North Atlantic land bridge (Tiffney & Manchester 2001; Xiang *et al.* 2001; Donoghue *et al.* 2001). Finally, despite its great importance (Donoghue & Moore 2003), information on the timing of disjunction events has been limited. Fossils of some relevant groups have provided valuable insights into their whereabouts at different times (Manchester 1999), but these have typically not been integrated with phylogenetic data to estimate lineage divergence times (Manchester & Tiffney 2001).

Several recent studies of Northern Hemisphere plant geography have attempted to integrate all of these elements, namely recently derived phylogenetic hypotheses, inferences of ancestral areas and directions of movement, and age estimates (see Manos & Donoghue 2001; Milne & Abbott 2002). These studies have upheld elements of the traditional view, but have called into question or contradicted others. Notably, recent botanical studies have supported earlier observations of EA–ENA disjunctions, and the origination of many temperate plant clades in Asia and their subsequent movement to the New World (Wen 1999; Xiang *et al.* 2001; Donoghue *et al.* 2001). However, where dates for relevant plant clades have been reported in the literature (Xiang *et al.* 2000; Donoghue *et al.* 2001), these have placed Old World–New World disjunctions at several different times, mostly within the last 20 Myr. This supports the idea of iterated movement through Beringia, as opposed to through the North Atlantic, as the more common route for dispersion.

Animal clades are well known to show similar disjunction patterns around the Holarctic, and have been subjected to several cladistic biogeographic analyses (Enghoff 1995; Sanmartín *et al.* 2001). In a groundbreaking study of 57 animal (mostly insect) taxa, Sanmartín *et al.* (2001) integrated phylogenetic information, ancestral area reconstructions and age estimates. Their analyses yielded several results that contradict the traditional botanical perspective and recent botanical studies. For example, they documented more disjunctions between EA and WNA than between EA and ENA. The latter disjunction, they also concluded, mostly originated relatively early in the Tertiary (before *ca.* 30 Myr ago), which might support movement across the North Atlantic. Regarding directions of movement, they found

evidence of asymmetry in some disjunctions (more movement from WNA to ENA than in the reverse direction, and also from EA to ER), but not a general pattern of movement out of Asia, as has been postulated for mammals earlier in the Tertiary (Beard 1998) and for several plant groups more recently (e.g. Xiang *et al.* 1998b, 2001; Donoghue *et al.* 2001).

Are there genuine differences between Holarctic biogeographic patterns in plants and animals, or are the apparent discrepancies a function of the limited samples analysed so far? Plant studies have been sufficient to document the complexity of the problem, and have clearly demonstrated a variety of different disjunction patterns and the attainment of the same pattern at different times during the Tertiary (pseudocongruence: see Cunningham & Collins 1994; Donoghue & Moore 2003). However, they have been insufficient in number to establish much in the way of generalities about disjunction patterns, directions of movement and the timing of events. The aim of the present study was to expand the sample of relevant Northern Hemisphere plant groups and to compare our analyses with those of Sanmartín *et al.* (2001) on animal clades.

2. DATA AND METHODS

Studies of relevant plant taxa were assembled from the literature, based first on the presence of endemic species in two or more of the major Holarctic centres of endemism: EA, ER, ENA and WNA. Our search strategy relied heavily on previous compilations on Northern Hemisphere biogeography (Li 1952; Thorne 1972), and especially on several recent reviews (Wen 1999; Milne & Abbott 2002) and contributions to a recent symposium (Manos & Donoghue 2001). In general, we relied on geographical range information provided by authors, but in some cases we referred to additional taxonomic literature to determine distributions. Several studies included one or more species from outside the four major Northern Hemisphere regions of interest; these were retained only if they created no confusion in identifying disjunction patterns. This process resulted in the assembly of an initial list of 198 plant taxa of potential use (available at www.phylodiversity.net/ssmith/biogeography.html).

From this list we culled 125 groups for which we could not identify a recent phylogenetic study. From the remaining 73 studies we omitted seven for which taxon sampling was judged insufficient to address the biogeographic problem investigated. For example, in published studies of *Acer* (Ackerly & Donoghue 1998; Suh *et al.* 2000) taxon sampling has been too sparse for one or

more geographical regions. Phylogenies of the remaining 66 clades were assembled and searched for unambiguous disjunctions among any two of the major areas of endemism. We omitted cases in which phylogenetic relationships were not clearly resolved, and those in which distribution polymorphisms within or outside of the clade of interest precluded a clear-cut assignment to one of the following disjunctions: EA–ER, EA–ENA, EA–WNA, ER–WNA, ER–ENA, WNA–ENA. For comparison, we did not tally disjunctions between a particular area and a composite of two or more areas, such as EA–WNA + ENA (though several such cases are discussed and are represented in table 2). This process yielded the 100 disjunctions recorded in table 1.

Ancestral areas and directions of movement were inferred by using DIVA (Ronquist 1996, 1997). DIVA results were recorded only for those portions of trees that were fully resolved, and we avoided areas where conflicting results were reported in different studies (e.g. differences between nuclear and chloroplast DNA results for *Chamaecyparis*; Li *et al.* 2003; Wang *et al.* 2003). Limits were not imposed on the number of areas assigned to internal nodes, nor did we attempt to choose among alternative optimal area assignments. In this respect our analyses are not fully comparable to those of Sanmartín *et al.* (2001). They considered each alternative optimal area assignment and down-weighted each possibility such that the sum of all alternatives corresponded to a single unambiguous reconstruction. Our strategy was simply to omit such ambiguous results and to focus instead only on clear-cut cases.

Inferred divergence times for disjunction events were obtained entirely from the published literature. Methods used to obtain divergence times varied among studies. In some cases molecular phylogenies were calibrated by the placement of one or more fossils (Donoghue *et al.* 2001). In other cases, however, estimates relied on a rate of substitution for a given gene obtained from another fossil-calibrated group of organisms. For example, Xiang *et al.* (2000) obtained a rate of substitution for *rbcL* from a fossil-calibrated *Cornus* phylogeny, and used this to obtain estimates for disjunctions in 10 other clades. Table 2 summarizes age estimates for 33 disjunctions obtained from 28 plant clades.

3. RESULTS AND COMPARISONS

(a) Disjunction patterns

Based solely on current physical connections, one might expect more disjunctions within continental areas (that is, between EA and ER within Eurasia and between ENA and WNA) than those spanning the oceans that separate the Old and New Worlds. Likewise, for those disjunctions that do cross oceans, one might expect more between adjacent regions (EA–WNA, ER–ENA) than between the more widely separated areas (EA–ENA, ER–WNA).

These expectations are only partly met by our plant disjunction data, summarized in figure 2a. The two within-continent disjunctions (EA–ER, ENA–WNA) are almost equal in number, and outnumber three of the four intercontinental disjunction patterns by approximately four or more times, including the two disjunctions between adjacent regions on different continents and the ER–WNA disjunction. However, considered from the standpoint of area connectedness, three other results seem

counterintuitive. First, the number of disjunctions between EA and WNA seems low in general, even in comparison with the corresponding ER–ENA pattern. Second, the number of disjunctions between ER and WNA, corresponding to the Madrean–Tethyan pattern (Axelrod 1975; Liston 1997), is equal in our data to that between the adjacent ER and ENA regions. Finally, and by far the most obviously, the number of disjunctions between the physically disjunct EA and ENA regions is exceptionally high. Fifty out of our 100 disjunctions fall in this category, which is 2.5 times the number in the next highest category (ENA–WNA) and 10 times the number in the corresponding ER–WNA pattern.

The prevalence of EA–ENA disjunctions accords well with the experience of botanists, perhaps, but not with the animal data assembled by Sanmartín *et al.* (2001). Their results, shown in figure 2b, generally match expectations based on spatial contiguity and the distances separating areas. The largest numbers of animal disjunctions are found within the two continental areas, but in this category ENA–WNA disjunctions clearly outnumber ER–EA disjunctions. Many fewer span the oceans, but it is noteworthy that there are more than twice as many EA–WNA disjunctions as there are ER–ENA disjunctions. Sanmartín *et al.* (2001) found the lowest numbers of disjunctions between the disjoint areas EA–ENA and ER–WNA.

Figure 2 highlights two major ways in which our results appear to be positively at odds with those of Sanmartín *et al.* (2001). First, in our data, by far the largest disjunction category is EA–ENA, whereas this is almost the smallest category in Sanmartín *et al.* (2001). Second, we found the smallest disjunction category to be EA–WNA, whereas this emerged as a major, and perhaps unexpectedly large, category in Sanmartín *et al.* (2001). Taken at face value, these contrasting results imply that plant and animal clades have been subjected to different processes, perhaps at different times, and perhaps especially in WNA.

(b) Ancestral areas and directions of movement

Directionality results for our plant datasets are summarized in figure 3a, where arrowheads indicate the direction of movement when this could be inferred from DIVA analyses, and lines without arrowheads represent cases that could not be unambiguously assigned a direction. Whereas one might initially predict an approximately equal number of migration events going in different directions between areas, there appear to be several major asymmetries. Most importantly, to the extent that we are able to assess ancestral areas, clades showing the EA–ENA pattern are predominantly reconstructed (at a ratio of 20 : 1) as having originated in EA and later spread to ENA. This finding accords well with results from several recent analyses, including Xiang *et al.* (2001) and Donoghue *et al.* (2001). Likewise, in all cases where we were able to make a positive determination, clades showing disjunctions between EA and ER appear to have originated in EA.

The comparable results from Sanmartín *et al.* (2001) are shown in figure 3b. It is important to note that they partitioned ambiguous DIVA results into one of two directions according to the frequency of alternative reconstructions, and their results therefore lack lines without arrowheads. Within limits (given the small sample in some categories) they obtained rather similar numbers of dispersal events in

Table 1. Sixty-six plant clades with 100 disjunctions assigned to one of the six two-area categories. (For each taxon the number of unambiguous disjunctions in each category is listed. Where it was possible to unambiguously infer an ancestral area using DIVA, the abbreviation for the ancestral area is given (number of cases in parentheses); when only a number appears, an ancestral area could not be determined. References refer to the original phylogenetic studies from which data were obtained.)

taxa	EA-ER	EA-ENA	EA-WNA	ER-WNA	ER-ENA	WNA-ENA	reference(s)
<i>Aesculus</i>	EA (1)					2	Xiang <i>et al.</i> (1998a)
<i>Anemone</i>		EA (1)		1			Hoot (1995)
<i>Aralia</i>						1	Wen (2000)
<i>Arbutoideae</i>				WNA (1)			Hileman <i>et al.</i> (2001)
<i>Asarum</i>		EA (1), 1				1	Kelly (1998)
<i>Boykinia</i>		1				1	Xiang <i>et al.</i> (1998b); Xiang & Soltis (2001)
<i>Brachyelytrum</i>		EA (1)				1	Saarela <i>et al.</i> (2003)
<i>Buckleya</i>						1	Li <i>et al.</i> (2001a); Donoghue <i>et al.</i> (2001)
<i>Calycanthus</i>		1				1	Xiang & Soltis (2001)
<i>Campsis</i>						2	Xiang <i>et al.</i> (2000)
<i>Cardamine</i>	EA (2)	EA (1)					Sweeney & Price (2000)
<i>Carpinus</i>		1				1	Yoo & Wen (2002)
<i>Caulophyllum</i>		1				1	Kim <i>et al.</i> (2004); Xiang <i>et al.</i> (2000)
<i>Cercis</i>		1			1		Davis <i>et al.</i> (2002b)
<i>Chamaecyparis</i>		1				1	Wang <i>et al.</i> (2003); Li <i>et al.</i> (2003)
<i>Chelidoniaceae</i>		2					Blattner & Kadereit (1995)
<i>Chrysoplenium</i>		EA (1)				1	Soltis <i>et al.</i> (2001)
<i>Clethra</i>		EA (1)				1	Fior <i>et al.</i> (2003)
<i>Cornus</i>	1	EA (1)			EA (1)		Xiang <i>et al.</i> (1996, 1998b); Fan & Xiang (2003)
<i>Corylus</i>	EA (1)				1		Forest & Bruneau (2000); Whitcher & Wen (2001)
<i>Cypripedium</i>		3					Pridgeon <i>et al.</i> (1999)
<i>Datisca</i>		1		1			Swensen <i>et al.</i> (1994)
<i>Decumaria</i>		EA (1)					Xiang <i>et al.</i> (2000)
<i>Diervilleae</i>					EA (1)		Donoghue <i>et al.</i> (2001)
<i>Erythronium</i>	1						Allen <i>et al.</i> (2003)
<i>Fagus</i>	EA (1)						Manos <i>et al.</i> (2001)
<i>Gleditsia</i>	1						Schnabel <i>et al.</i> (2003)
<i>Gymnocladus</i>		1					Schnabel <i>et al.</i> (2003)
<i>Halesia</i>		EA (1)					Fritsch <i>et al.</i> (2001)
<i>Hamamelis</i>		EA (1)					Li <i>et al.</i> (2000); Kim & Kim (2001); Donoghue <i>et al.</i> (2001)
<i>Ilex</i>		EA (1), 1					Cuenoud <i>et al.</i> (2000)
<i>Illicium</i>		EA (1)					Oh <i>et al.</i> (2003); Hao <i>et al.</i> (2000)
<i>Juglans</i>		1				WNA (1)	Stanford <i>et al.</i> (2000)
<i>Liquidamber</i>							Li & Donoghue (1999); Donoghue <i>et al.</i> (2001)
<i>Liriodendron</i>		1					Azuma <i>et al.</i> (2001)
<i>Magnolia</i>		EA (1), 1					Qui <i>et al.</i> (1995a, b); Azuma <i>et al.</i> (2001)
<i>Menispermum</i>		1					Lee <i>et al.</i> (1996); Xiang <i>et al.</i> (2000)
<i>Mitchella</i>		1					Xiang <i>et al.</i> (2000)
<i>Moraceae</i>	EA (1)						Bell & Donoghue (2003)

(Continued.)

Table 1. (Continued.)

taxa	EA-ER	EA-ENA	EA-WNA	ER-WNA	ER-ENA	WNA-ENA	reference(s)
<i>Nyssa</i>		1					Fan & Xiang (2003)
<i>Onoclea</i>		EA (1)					Gastony & Ungerer (1997)
<i>Osmundaceae</i>		3					Yatabe <i>et al.</i> (1999)
<i>Ostrya</i>	EA (1)						Chen <i>et al.</i> (1999); Yoo & Wen (2002); Balthazar <i>et al.</i> (2000)
<i>Pachysandra</i>	EA (1)	1					Sang <i>et al.</i> (1997)
<i>Paeonia</i>		EA (1)					Wen & Zimmer (1996); Xiang & Soltis (2001)
<i>Panax</i>		1					Lee <i>et al.</i> (1996); Xiang <i>et al.</i> (2000)
<i>Penthorum</i>		1					Lee <i>et al.</i> (1996); Xiang <i>et al.</i> (2000)
<i>Phryma</i>							Liston <i>et al.</i> (1999)
<i>Pinus</i>	1			1			Xiang <i>et al.</i> (2000)
<i>Podophyllum</i>		EA (1)					Cameron & Chase (1999)
<i>Pogoniinae</i>		ENA (1)					Manos <i>et al.</i> (2001)
<i>Quercus</i>	3						Miller <i>et al.</i> (2001)
<i>Rhus</i>							Schultheis & Donoghue (2004)
<i>Ribes</i>			WNA (1)				Eriksson & Donoghue (1997)
<i>Sambucus</i>	EA (1)						Hao <i>et al.</i> (2001)
<i>Schisandra</i>		EA (1)					Li <i>et al.</i> (2002)
<i>Stewartia</i>		EA (1)					Fritsch (2001)
<i>Styrax</i>		EA (1)		1			Wen <i>et al.</i> (1996); Xiang & Soltis (2001)
<i>Symplocarpus</i>		EA (1)				ENA (1)	Li <i>et al.</i> (2001c)
<i>Taxus</i>	EA (1)					1	Xiang <i>et al.</i> (1998b)
<i>Tiarella</i>						1	Li <i>et al.</i> (2001b)
<i>Torreya</i>						1	Xiang <i>et al.</i> (1998b); Xiang & Soltis (2001)
<i>Trautvetteria</i>						1	Osaloo & Kawano (1999)
<i>Trillium</i>		2				2	Donoghue <i>et al.</i> (2001)
<i>Triosteum</i>		EA (1)				ENA (1)	Donoghue <i>et al.</i> (2004); Winkworth & Donoghue (2004)
<i>Viburnum</i>	EA (2)	EA (2)					
total (100)	19	50	1	5	5	20	

Table 2. Thirty-three disjunctions from 28 plant taxa for which age estimates were obtained from the literature (references in table 1).

(Disjunction patterns are divided into two broad time categories; disjunctions dating within the past 30 Myr are likely to have been preceded by migration through Beringia; those before 30 Myr might have passed through a North Atlantic land bridge. In three cases the estimated divergence refers to a split between EA and a North American clade present in both WNA and ENA.)

taxa	more than 30 Myr	less than 30 Myr
<i>Aesculus 1</i>	WNA–ENA	EA–ER
<i>Aesculus 2</i>	WNA–ENA	
<i>Aesculus 3</i>		
<i>Aralia</i>		EA–ENA
<i>Boykinia</i>		EA–WNA + ENA
<i>Buckleya</i>		EA–ENA
<i>Calycanthus</i>		EA–WNA + ENA
<i>Campsis</i>		EA–ENA
<i>Caulophyllum</i>		EA–ENA
<i>Cercis</i>		ER–ENA
<i>Cornus</i>		EA–ENA
<i>Decumaria</i>		EA–ENA
<i>Diervilleae</i>		EA–ENA
<i>Gleditsia</i>		EA–ENA
<i>Gymnocladus</i>		EA–ENA
<i>Hamamelis</i>		EA–ENA
<i>Liquidamber</i>	ER–ENA	
<i>Liriodendron</i>		EA–ENA
<i>Magnolia</i>		EA–ENA
<i>Menispermum</i>		EA–ENA
<i>Mitchella</i>		EA–ENA
<i>Osmunda 1</i>	EA–ENA	
<i>Osmunda 2</i>	EA–ENA	
<i>Osmunda 3</i>	EA–ENA	
<i>Pachysandra</i>		EA–ENA
<i>Penthorum</i>		EA–ENA
<i>Phryma</i>		EA–ENA
<i>Podophyllum</i>		EA–ENA
<i>Styrax</i>		EA–ENA
<i>Symplocarpus</i>		EA–ENA
<i>Torreya 1</i>		EA–WNA
<i>Torreya 2</i>		EA–WNA + ENA
<i>Triosteum</i>		EA–ENA

the two directions for all but two disjunction categories. In the case of the EA–ER pattern they reconstructed around twice as many movements from EA to ER as in the reverse direction, and for ENA–WNA they found somewhat more movement from WNA to ENA.

Figure 3 provides a comparison between our directionality results and those from Sanmartín *et al.* (2001). One clear similarity is the predominance of movement from EA to ER. The most obvious difference, despite the number of ambiguous results, is that in the plant data we see considerable movement out of EA, both to ER and to ENA, but very little movement into EA from elsewhere. By contrast, in animals there is no clear ‘out-of-Asia’ pattern—the numbers going into and out of EA are about the same. Sanmartín *et al.* (2001) specifically concluded that they found no significant difference between EA and ENA as the source area for the EA–ENA pattern. Some additional evidence for an out-of-Asia pattern in plants is provided by examination of the 16 unresolved WNA–ENA disjunctions. Consistent

with results from Xiang *et al.* (1998b), in 9 of these 16 cases (*Aesculus*, *Aralia*, *Asarum*, *Boykinia*, *Calycanthus*, *Rhus*, *Tiarella*, *Torreya*, *Trautvetteria*) the WNA–ENA clade appears to be most closely related to one or more species from EA, and in some of these cases (e.g. *Aralia*) it is clearly nested within EA. Likewise, one of the four unresolved WNA–ER disjunctions (*Styrax*) is nested within EA.

(c) Ages of disjunctions

Estimated divergence times for 33 disjunctions spanning the Old World and the New World are recorded in table 2 in two age classes, before and after 30 Myr. Based on geological and palaeoclimatological evidence (reviewed by Tiffney 1985a,b, 2000; Tiffney & Manchester 2001) we regard lineages with Old World – New World divergence times younger than *ca.* 30 Myr as unlikely to have passed through a North Atlantic land bridge, and instead more likely to have moved through Beringia. Twenty-seven of these 33 disjunctions are inferred to have occurred within the past 30 Myr, leaving only six cases in the older category, three of these within the fern *Osmunda*. Twenty-four of the 33 dated disjunctions are between EA and ENA, which reflect a focus in the literature on these cases. It is noteworthy, nevertheless, that all but the three *Osmunda* EA–ENA disjunctions (which date to the mid-Mesozoic) fall in the younger time class. Moreover, the three dated splits between EA and North America (WNA + ENA) also fall in the young category. Taken at face value these data argue in favour of the passage of most of these groups through Beringia as opposed to through the North Atlantic or, perhaps less likely, transoceanic seed dispersal.

How do these results compare with those of Sanmartín *et al.* (2001)? Out of the 57 animal clades that Sanmartín *et al.* (2001) included, they recorded at least some dating information on 39. In 27 of these 39, dates were based on fossil evidence, molecular clock estimates, or non-Holarctic biogeographic events, whereas in the 12 remaining clades the ages of various Holarctic biogeographic events were used. Inferred divergence times ranging from 1 to 150 Myr were placed by Sanmartín *et al.* (2001) into one of several age classes for comparison among different disjunction types. In contrast to our plant clades, within which most divergences are estimated at less than 30 Myr, almost one-third of the inferred animal divergence times fell into a category between 70 and 150 Myr, and less than one-quarter were in the 3–20 Myr age class. Many of their EA–WNA disjunctions were inferred to have occurred within the 1–20 Myr period, but most of their EA–ENA disjunctions were older. Specifically, in their most detailed temporal analysis they found that most of their EA–ENA disjunctions fell in the 45–70 Myr interval, which they interpreted as favouring movement across a North Atlantic land bridge.

Sanmartín *et al.* (2001) noted the contrast between their data and the much younger intercontinental divergence times recorded for plant clades by Xiang *et al.* (1989a,b) and Wen (1999). Our results, based on a larger sample, amplify this difference. If we accept the age estimates reported in these studies, EA–ENA disjunctions in many plant groups are younger than those in many animal groups.

4. DISCUSSION AND CONCLUSIONS

Our results, based on a much larger sample of plant clades and disjunctions, are consistent with those obtained from

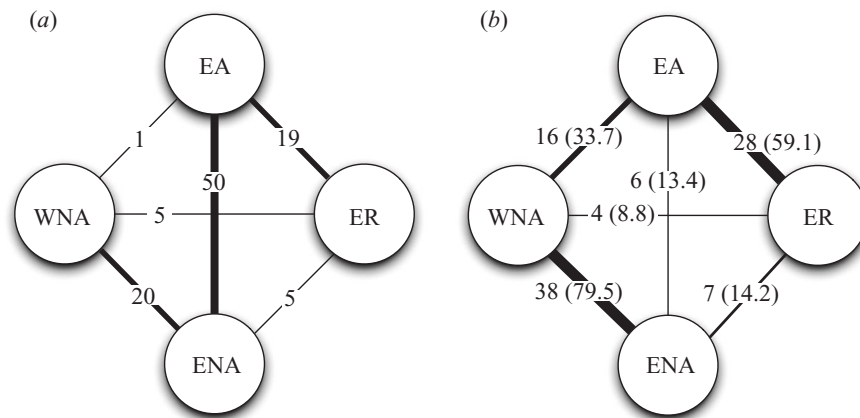


Figure 2. Comparison of disjunction patterns among the four major Holarctic areas of endemism (figure 1) for (a) plants (this study) and (b) animals (Sanmartín *et al.* 2001); line thickness is proportional to the percentage in each category. (a) Plants, from table 1; for 100 disjunctions the absolute number and percentage are equivalent. (b) Animals, redrawn from Sanmartín *et al.* (2001); the first number is the percentage of the total in that category; the number in parentheses is the absolute number from Sanmartín *et al.* (decimals result from the partitioning of reconstruction ambiguities in the original study; see § 2).

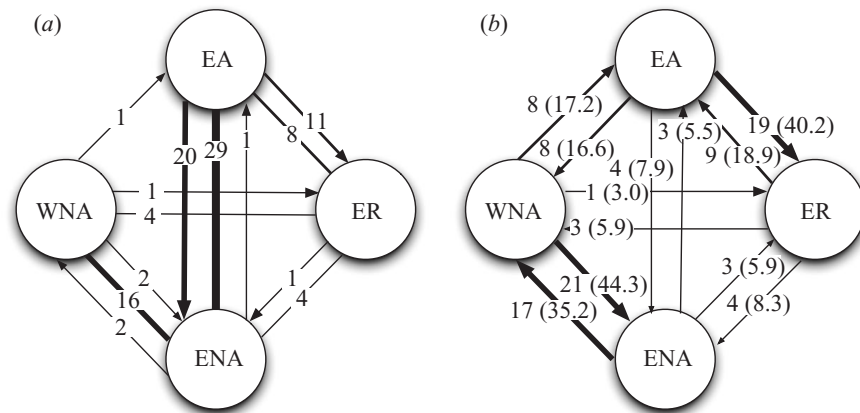


Figure 3. Inferred ancestral areas and directions of movement among the four major Holarctic areas of endemism (figure 1) for (a) plants (this study) and (b) animals (Sanmartín *et al.* 2001); line thickness is proportional to the percentage in each category, arrows point from the inferred ancestral area to the inferred derived area. (a) Plants, from table 1; for 100 disjunctions the absolute number and percentage are equivalent. Lines without arrowheads represent cases for which an unambiguous inference of ancestral area was not possible. (b) Animals, redrawn from Sanmartín *et al.* (2001); the first number is the percentage of the total in that category; the number in parentheses is the absolute number from Sanmartín *et al.* (decimals result from the partitioning of reconstruction ambiguities in the original study; see § 2).

recent botanical studies that have integrated phylogenies, ancestral areas, and ages. However, taken at face value, our findings for plants are at odds, in several major ways, with those of Sanmartín *et al.* (2001) for animals. Where we find an excess of EA–ENA disjunctions, they found few. Where we find few EA–WNA disjunctions, they found many. Where we find a general pattern of movement out of Asia, they did not. Where we find most Old World – New World disjunctions, and most EA–ENA disjunctions in particular, to be rather recent (less than 30 Myr), they found many of these to be older.

What do these results imply about the assembly of temperate forests? First, they indicate that the standard explanation, which posits that current disjunction patterns mainly reflect extinction in clades that became widespread around the Northern Hemisphere early in the Tertiary, is oversimplified. Instead, it would appear that there were movements at different times, some more recent than

previously supposed. Under the traditional view, temperate plants within different regions have coexisted for many millions of years, with losses through extinction and adaptation to changing climates occurring to a greater or lesser extent in different regions. By contrast, under the view suggested by our analyses, some species may have coexisted for a long time, but others have filtered into the regional species pool at different times. Some species therefore have come together only relatively recently.

This perspective has important consequences for our understanding of competition, coevolution and cospeciation in these forests, among the plants themselves and among the plants and the animals in the system. For example, if insect clades have truly been present within an area longer than the plants, this implies a high degree of host switching and rapid adaptation on the part of the insects as new plants have entered a community from elsewhere. Another implication, it would seem, is that

plants have been better able than many animal groups to transcend physical and climatic barriers and to successfully migrate longer distances more recently. At the same time, however, they may have suffered greater extinction in some regions, especially in WNA and ER, whereas many animal groups were better able to maintain their presence and adapt to climatic and other changes.

In this context it is fascinating to note that Sanmartín & Ronquist (2004) have reported similar results for Gondwanan biogeography based on their analysis and comparison of 54 animal clades and 19 plant clades. In this case it may also be that the plant and animal patterns differ significantly, with plant disjunctions often being younger than those in animals and perhaps best attributed to more recent patterns of dispersal.

Before getting carried away with such thinking, however, it is important to reflect on possible artefacts and sources of bias. It is, of course, quite possible that the sample sizes are still too small or too biased for the plants and/or the animals to recover an accurate picture. Although 100 disjunctions from 66 plant clades seem respectable, this is still a small proportion of the relevant plant disjunctions that exist. In preparation for the present analysis, for example, we compiled a list of nearly 200 plant clades with species endemic to two or more of the major Holarctic regions. The true number is probably in the 1000s, and we presume that the same is true for animals, not to mention for fungi (Mueller *et al.* 2001) and other life forms.

Our sample is clearly also biased in several ways. Perhaps most importantly, it reflects the idiosyncratic interests of the plant systematics community, where there has been long-standing interest in the EA–ENA pattern in particular. There is also a bias towards species-poor groups, both because these make attractive phylogenetic studies in the first place and because we have consciously excluded highly incomplete phylogenies for many larger groups. For these reasons we may well be over- and under-representing certain patterns. We can safely conclude, based now on new phylogenetic information, that there are many EA–ENA disjunctions, but it is harder to gauge how surprised we should be about the numbers (see discussion of null hypotheses below). Other results may be more surprising, such as the paucity of EA–WNA disjunctions in our dataset. However, this may also reflect a concentration on groups that are represented in both EA and ENA, and therefore a bias against plant clades that are especially well represented in WNA. Here, it is worth noting that the one instance we have recorded of the EA–WNA disjunction, and of movement from WNA to EA, is in *Ribes*, which has diversified extensively in WNA. To rectify this situation, we will need to concentrate specifically on such clades, of which there are many. *Symphoricarpos* (Caprifoliaceae) is as a case in point, with perhaps 15 species in WNA and just one in EA. The inclusion of more speciose WNA clades by Sanmartín *et al.* (2001) may partly account for their larger number of EA–WNA disjunctions.

Another bias in our sample is the concentration on angiosperms. The fact that the fern clade *Osmunda* stands out as providing several much older EA–ENA disjunctions, suggests that we might get a different perspective by broadening the representation of ferns, mosses, and liverworts, to name just a few non-angiosperm plant groups that are well known to exhibit Holarctic patterns. Aquatic flowering

plants might also provide important insights (Les *et al.* 2003).

The animal sample is also relatively small and biased. Forty-one of the 57 studies included in Sanmartín *et al.* (2001) are of insect groups; of these 32 are holometabolous insects, and 17 are Coleoptera. Only 11 vertebrate clades are included: five fishes, three birds and three mammals. One wonders how the outcome would be affected by adding more vertebrates (such as amphibians and lizards, which are absent from their sample), or other arthropods.

There are also possible biases associated with ancestral areas and directions of movement. In our study, and in Sanmartín *et al.* (2001), ancestral area reconstructions have relied on DIVA, which attempts to minimize costs associated with dispersal and extinction. Leaving aside possible debates about the costs assigned to these events, it is important to appreciate that DIVA works only with fully resolved trees and with the sample of taxa included in the phylogeny at hand, and the results may be quite sensitive to alternative resolutions of phylogenetic ambiguity or variously incomplete sampling. Of special interest in the applications reported here is the possibility of systematic biases introduced by the failure to include fossil species and their distributions. It is possible, as we have supposed, that many plant clades originated and radiated within Asia before spreading to other regions. This is consistent with other arguments to the effect that transitions to living in the temperate zone may have been fostered in Asia owing to its geological and climatological history compared with other Holarctic regions (Latham & Ricklefs 1993). However, we must also consider the possibility that Asia has falsely been identified as the ancestral area due to the retention of the greatest number of species in that area, and the selective extinction of species in other regions. Our feeling is that the circumstances that would result in consistent error may rarely be realized, but the possible misleading effects of differential extinction in different areas will need to be thoroughly examined using simulations, and then evaluated from the standpoint of the relevant palaeobotanical data (Manchester 1999).

In this context, it is worth noting that our analyses do appear to support the standard view that many plant species went extinct in WNA, probably owing to drying climates. We see few EA–WNA disjunctions, and if many plant groups now showing the EA–ENA disjunction originated in Asia and moved to the New World through Beringia, it is natural to assume that they were once also present in WNA. There is excellent fossil evidence for this in some cases (Manchester 1999). It is possible, however, depending on palaeoclimatic factors, that at least in some of these lineages movement from Beringia to ENA occurred more directly, without ever becoming established in WNA.

It is also important to appreciate possible sources of bias in estimating the ages of various disjunctions. Although an understanding of the absolute timing of events is crucial for historical biogeography (Donoghue & Moore 2003), and although methods for inferring divergence times have improved dramatically (Sanderson 2002; Thorne & Kishino 2002), in most cases we are still a long way from achieving confidence in age estimates and will therefore need to cope with major margins of error. In some cases rather different age estimates have been reported for

disjunction events within the same phylogeny, depending on the data and methods used. In *Liquidambar*, for example, the Old World – New World disjunction was dated at 7–16 Myr by Hoey & Parks (1991) but at 30–40 Myr by Donoghue *et al.* (2001) when fossil information was integrated. Some of the age estimates tallied here were obtained from molecular phylogenies in which fossils were included for calibration (for example, most of those from Donoghue *et al.* 2001). However, the estimates in other cases relied on extrapolating a rate of nucleotide substitution obtained from a phylogeny that was calibrated using fossils (for example, most of those from Xiang *et al.* 2000). The situation is even more confusing for the animal datasets in Sanmartín *et al.* (2001). Some of the animal estimates incorporated fossils, but in other cases Sanmartín *et al.* (2001) relied directly on apparent concordance with particular biogeographic events to which dates could be assigned. Moreover, they extrapolated dates for many nodes using a ‘branching clock’ method that imposed equal time durations between speciation events.

We look forward to the assembly of datasets that incorporate more standardized and more confident age assessments. In the meantime, it is important to ask whether the datasets that have been assembled are likely to be systematically biased, and specifically whether animal ages might for some reason be overestimated and plant ages underestimated. For animals, it is possible that the use of biogeographic barriers in assigning divergence times could overestimate lineage splitting times. For plants, we worry about how fossils are typically placed within phylogenies. Where fossils are incomplete and cannot be assigned with confidence to any particular branch within a crown clade, the tendency is to place them along the stem of the entire clade, which has the effect of underestimating divergence times (Bell & Donoghue 2004). We doubt that such factors account entirely for the different ages reported for plants versus animals, but they clearly require further study.

Finally, all of the preceding comments suggest the need to compare our numbers (and those of Sanmartín *et al.* (2001), etc.) with expectations generated under a suitable null model. It is tempting (as suggested by a reviewer of this paper) to derive an expected number of disjunctions of each type based solely on the number of species that we sampled from each region. This might yield comforting results (suggesting, for example, that there are more EA–ENA and fewer EA–WNA disjunctions than expected), but it disregards too many other relevant variables to be very convincing. For example, the underlying numbers of species in the different regions should be taken into account, along with the sizes of the areas and the distances among them, and how these have varied through time. Unfortunately, we lack the necessary data or the analytical machinery to generate meaningful expectations for this particular problem, which makes it difficult to interpret the statistical significance of the numbers we have obtained. We can only hope that the patterns documented here will stimulate the development of worthy null hypotheses.

For all of the reasons we have outlined, we think it is too early to conclude that there are truly major biogeographic differences between plants and animals around the Northern Hemisphere. Nevertheless, this study focuses attention on the possibility of discord, and makes it harder to attribute differences only to limited sampling. A critical

test requires additional data, assembled with an eye toward reducing the possible sources of bias just noted. In addition to improving our knowledge of the plant clades included here, many more disjunctions could be added simply by resolving phylogenetic relationships in the many other clades with relevant distribution patterns. In the meantime, it will also be important to assemble comparable data on ecological characteristics of the taxa in question (including life-history traits and dispersal mechanisms), and also on the details of their geographical ranges (Peterson 2001). Already there appear to be interesting correlations within particular clades between distribution pattern, timing and direction of movement, and traits such as whether plants are evergreen or deciduous (Fritsch *et al.* 2001; Manos & Stanford 2001). It remains to be seen whether major generalities can be made along these lines (Milne & Abbott 2002).

Cladistic biogeographers have paid more attention to the Southern Hemisphere than to the Northern Hemisphere, reflecting in part the relative simplicity of the geological/climatological history of Gondwana compared with Laurasia. The break-up of Gondwana yielded widely separated landmasses, among which biotic interchanges would be difficult, whereas the development of Laurasia left various land connections in place and fluctuating climates rendered these passable at various times. One might expect, therefore, to find greater concordance of plant and animal phylogenies in the Southern than in the Northern Hemisphere, and to some extent this is born out by comparing the results of our study and Sanmartín *et al.* (2001) on the Northern Hemisphere with those of Sanmartín & Ronquist (2004) on the Southern Hemisphere. However, in comparing the present analysis with Sanmartín & Ronquist (2004) we are struck by the possibility of another pattern, namely that in both the Northern and the Southern Hemispheres there may be significant differences between plants and animals, with plant groups tending to show repeated intercontinental movements more recently than animal groups. If true, this would have major implications for community assembly and coevolution. Additional biogeographic comparisons among plants, animals, and other organisms are clearly needed to investigate this possibility.

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GLOSSARY

- DIVA: dispersal–vicariance analysis
 EA: eastern Asia
 ENA: eastern North America
 ER: Europe
 WNA: western North America