

Comparative phylogeography of unglaciated eastern North America

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Abstract

Regional phylogeographical studies involving co-distributed animal and plant species have been conducted for several areas, most notably for Europe and the Pacific Northwest of North America. Until recently, phylogeographical studies in unglaciated eastern North America have been largely limited to animals. As more studies emerge for diverse lineages (including plants), it seems timely to assess the phylogeography across this region: (i) comparing and contrasting the patterns seen in plants and animals; (ii) assessing the extent of pseudocongruence; and (iii) discussing the potential applications of regional phylogeography to issues in ecology, such as response to climatic change. Unglaciated eastern North America is a large, geologically and topographically complex area with the species examined having diverse distributions. Nonetheless, some recurrent patterns emerge: (i) maritime – Atlantic vs. Gulf Coast; (ii) Apalachicola River discontinuity; (iii) Tombigbee River discontinuity; (iv) the Appalachian Mountain discontinuity; (v) the Mississippi River discontinuity; and (vi) the Apalachicola River and Mississippi River discontinuities. Although initially documented in animals, most of these patterns are also apparent in plants, providing support for phylogeographical generalizations. These patterns may generally be attributable to isolation and differentiation during Pleistocene glaciation, but in some cases may be older (Pliocene). Molecular studies sometimes agree with longstanding hypotheses of glacial refugia, but also suggest additional possible refugia, such as the southern Appalachian Mountains and areas close to the Laurentide Ice Sheet. Many species exhibit distinct patterns that reflect the unique, rather than the shared, aspects of species' phylogeographical histories. Furthermore, similar modern phylogeographical patterns can result from different underlying causal factors operating at different times (i.e. pseudocongruence). One underemphasized component of pseudocongruence may result from the efforts of researchers to categorize patterns visually – similar patterns may, in fact, not fully coincide, and inferring agreement may obscure the actual patterns and lead to erroneous conclusions. Our modelling analyses indicate no clear spatial patterning and support the hypothesis that phylogeographical structure in diverse temperate taxa is complex and was not shaped by just a few barriers.

Keywords: molecular phylogeography, Pleistocene glaciation, pseudocongruence, refugia, regional phylogeography

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Introduction

In the nearly 20 years that have passed since the term 'phylogeography' was first used (Avice *et al.* 1987a), this

field has expanded quickly and now encompasses a vast literature. The rapid accumulation of data for diverse species has made it possible to compare phylogeographical structure among co-distributed species as a means to assess past geographical distributions and the processes that may have shaped those distributions (Soltis *et al.* 1997; Avice 1998; Comes & Kadereit 1998; Schaal *et al.* 1998;

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Table 1 Phylogeographical hypotheses for unglaciated eastern North America

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- I. Given the size of the region and its geological and ecological complexity, phylogeographical history will also be complex, with numerous patterns evident.
- II. Major phylogeographical breaks will be associated with major barriers, including Apalachicola Bay, the Appalachian Mountains, and the Mississippi River.
- III. The dispersibility of both plants and animals varies greatly, resulting in similar patterns of phylogeographical structure.
- IV. Plants and animals survived in several of the same long-proposed glacial refugia; additional refugial areas are also likely.
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Avise 2000; Brunsfeld *et al.* 2001; Hare 2001; Hewitt 2001; Knowles & Maddison 2002; Petit *et al.* 2002, 2005; Heads 2005). Regional phylogeographical studies involving co-distributed animal and plant species have now been conducted for several areas of the world, notably Europe (Taberlet *et al.* 1998; Petit *et al.* 2002), the Pacific Northwest of North America (Soltis *et al.* 1997; Brunsfeld *et al.* 2001), the southeastern United States (Avise 2000), the California Floristic Province (Calsbeek *et al.* 2003), and the eastern European Alps (Tribsch & Schonswetter 2003).

In Europe, largely congruent phylogeographical patterns have emerged for animals and plants. This might be expected due to the east-to-west orientation of the major mountain ranges in Europe, providing only a few possible migration routes and refugial areas during glaciation. The conditions experienced during Pleistocene glaciation in Europe would have resulted in extreme bottlenecks across the biota of the region and congruent patterns of recolonization during subsequent climate warming.

In contrast to Europe, the physiographic setting of much of unglaciated eastern North America has been defined by the Appalachian Mountains that run north to south. The area is also geologically and ecologically complex. Hence, a diverse array of population genetic phenomena could result in a variety of patterns that reflect numerous evolutionary processes, including historical barriers to gene flow, dispersal capacity, population size, and other life-history characteristics. Fossil data suggest that pockets of hardwood forests existed in the Lower Mississippi Valley during the last glacial maximum, a finding that many researchers have interpreted as a full glacial refugium for displaced temperate taxa (Davis 1981; Delcourt & Delcourt 1984). Due to limited fossil localities, however, the geographical extent of these forests is still controversial (Jackson *et al.* 2000). If diverse organisms had retreated to and shared these refugial areas, some degree of phylogenetic patterning would be expected.

Hypotheses and goals

When ecological, biological, and geological factors are all considered, perhaps it is not surprising that phylogeographical analyses so far conducted in eastern North America have revealed complex patterns. Recent studies for plants from unglaciated eastern North America suggest

both similarities to and differences from the phylogeographical patterns reported for animals. As a result of a rapidly growing database, the time is ripe to review the phylogeographical patterns observed in this area, integrating studies of plants and animals.

Although there is convincing evidence that biogeographical barriers played an important role in structuring genetic diversity in some taxa in unglaciated eastern North America (e.g. Gulf/Atlantic drainages in some amphibian species, Kozak *et al.* 2006), it is not clear whether general phylogeographical patterns exist across the diverse taxa that inhabit unglaciated eastern North America. Based on the physiographic history of eastern North America (reviewed below), we pose several hypotheses for the phylogeographical history of this region (Table 1).

Through a critical review of the robustness of patterns reported in the literature and a spatial model that addresses the distinctness among patterns, we asked: (i) are plant patterns different from any of the emerging patterns for animals, and are any of these patterns sufficiently distinct to formalize a specific set of physiographic hypotheses? (ii) what is the role of pseudocongruence among patterns? (iii) what are the potential applications of regional phylogeography to major issues in ecology (e.g. response to climatic change)?

We use pseudocongruence here to emphasize two different aspects of the data. Our first approach to pseudocongruence follows the traditional usage of spatially congruent patterns generated at different times (Hafner & Nadler 1990; Cunningham & Collins 1994; Xiang & Soltis 2001); we do this using only a qualitative perspective because it was not possible to obtain and reanalyse the original data to assess pattern and obtain age estimates. The second approach addresses the concept that spatially congruent patterns may in fact be a mixture of patterns. Here, we quantitatively assess this type of pseudocongruence by assuming that the broadest splits in published phylogeographies are robust and different from one another.

Materials and methods

Overview of physiography

The physiographic setting for the unglaciated region of eastern North America is largely defined by two factors: (i)

past changes in climate, especially during the peak of the last continental glaciation, approximately 18 000 ¹⁴C BP (or 21 500 calendar years BP; Jackson *et al.* 2000), when the Laurentide Ice Sheet extended south to about 39°N (Delcourt & Delcourt 1987); and (ii) a modest degree of topographic relief. There is strong evidence to support a historical scenario of northern vegetation types (e.g. boreal forest) moving south, creating compressed zones of vegetation types that harboured a unique blend of biota, including the highly endemicized flora and fauna observed today (Martin *et al.* 1992–1993), to the currently more widespread elements of the mixed mesophytic (hardwood) forest and its associated fauna (Braun 1950). Within the Mississippi Valley, river bluff habitats of the southernmost drainages have been considered glacial refugia of the mesophytic plant community (Delcourt & Delcourt 1981), although recent studies suggest that pollen data are inconclusive on the location and abundance of glacial refugia (Jackson *et al.* 2000). Despite the uncertainty, the generality of the paradigm holds: much of the current biota north of the extent of glaciation is derived from ancestral populations distributed in more southerly areas.

The north–south alignment of the Appalachian Mountains and the presence of continuous, low-relief land areas to the north and south of the Appalachians (extending in the south to the tropics) have made the eastern USA both a rich source and pathway for a wide range of biota (Graham 1999). The Appalachian Mountains and their component highlands (the highest being the Blue Ridge Province that reaches northeastern Georgia and its associated foothills, the Valley and Ridge Province to the west, and the Piedmont Plateau Province to the south and east) resulted in drainage patterns and major rivers that flow south (e.g. Mississippi, Tombigbee, Apalachicola, Suwanee) to the Gulf of Mexico or southeast (Santee, Savannah, Altamaha) to the Atlantic Ocean (Fig. 2a). High levels of biodiversity are associated with the rivers of the Gulf Coast, and phylogeographical breaks in freshwater fauna have been noted to occur in and around this area, such as east and west of the Apalachicola River. Although the role of watersheds as a differentiating force for the terrestrial biota is less obvious than for freshwater fauna, the bluffs of the Apalachicola have been known to contain relict and often somewhat differentiated populations of more widespread plant taxa (e.g. Parks *et al.* 1994) and also form a well-known break for many animal species (Neill 1957; Blainey 1971; Swift *et al.* 1985).

Freshwater biotic breaks, exchanges, and subsequent dispersions of taxa were strongly affected by changes in sea level. During the cooler climates of the Pliocene and Pleistocene, sea-stands were > 150 m lower than at present; subsequent warming trends resulted in greater alluvial definition of the coastline and a decrease in drainage in paludal areas along the coastal plain (Watts 1980). For terrestrial organisms, changes in climate and ecology closed a

putative range gap between temperate, continental taxa that were once isolated to the west and north of the peninsula with subtropical taxa of the south to form a ‘suture zone’ (Remington 1968; Avise 2000). While secondary contact zones were produced on land, a barrier to gene flow was formed among certain marine taxa, creating well-documented range disjunctions in temperate, marine taxa of the Gulf and Atlantic (Avise 2000). Tropical biota are recent additions to the peninsula, within the last 5000 BP, and with the exception of marine taxa, most terrestrial taxa of tropical affinities have distributions peripheral to the area under study (Long 1984; Gunderson & Loftus 1993; Thorne 1993).

Literature base

We first searched the Web of Science using the keyword ‘phylogeography’ for an initial estimate of the number of studies produced since the last comprehensive review by Avise (2000). To focus the review, the following journals, *Systematic Biology*, *Systematic Botany*, *Marine Biology*, *Journal of Biogeography*, *Molecular Ecology*, *Evolution*, *The Auk*, *Journal of Ornithology*, and *American Journal of Botany*, were surveyed from 2000 to the first 4 months of 2006.

We have deliberately limited our discussion to organisms largely occurring in unglaciated eastern North America because of both the rich phylogeographical history of this area, as well as the sheer scope of the region. This area includes the southeastern USA, an area that represents the focus of the pioneering phylogeographical research of Avise and co-workers (reviewed in Avise 2000). Some organisms discussed here may have a portion of their ranges outside of the unglaciated eastern USA (e.g. northern USA, Canada, and western North America); some marine organisms occur broadly across the Caribbean. Phylogeographical studies are also emerging for plants occurring in once-glaciated and arctic eastern North America (e.g. Tremblay & Schoen 1999; Chung *et al.* 2004; Godbout *et al.* 2005), but these areas are beyond the scope of the current review and should best be considered with other arctic/alpine and circumboreal organisms.

Pattern evaluation

The quality of sampling and robustness of data analysis varied greatly among studies, as did the marker employed. Importantly, not all analyses conducted have been phylogenetic in nature; various distance measures have also been used. Even the phylogenetic studies often lack internal support for clades. For each paper that was specifically compliant with the goals of the review, we recorded the type of marker obtained, general pattern reported, and method of data analysis. If a measure of internal support was provided, this too was noted, and bootstrap values of 50% or more are reported when given (Table 2).

Table 2

Taxon	Common name	Markers	Pattern	Method of analysis/Support	References
FISH					
<i>Percina evides</i>	gilt darter	mtDNA seq	E–W Mississippi River (two subclades in west)	network; parsimony, 100% for eastern clade; 60% for western clade	Near <i>et al.</i> (2001)
<i>Percina caprodes</i>	darler	allozymes; mtDNA seq	no structure	parsimony	Turner <i>et al.</i> (1996)
<i>Percina nasuta</i>	darler	allozymes; mtDNA seq	different haplotypes in major drainages of Central Highlands	parsimony, weak support (54–58% for most clades)	Turner <i>et al.</i> (1996)
<i>Percina phoxocephala</i>	darler	allozymes; mtDNA seq	some structure; distinct Arkansas and Red River haplotypes	parsimony; 52% for Arkansas R. Clade; 57% for Red R. clade	Turner <i>et al.</i> (1996)
<i>Cyprinella lutrensis</i>	cyprinid fish	mtDNA seq	E Texas–E Texas & SW Louisiana – north of Texas	parsimony; neighbour-joining; 94% for E Texas, 80% for E Texas & SW Louisiana, 100% north of Texas	Richardson & Gold (1995)
<i>Cottus carolinae</i>	sculpin	mtDNA res. sites	Ozarks – Appalachia & Indiana & Illinois	network; parsimony, < 50%	Strange & Barr (1997)
<i>Fundulus majalis</i> / <i>F. similis</i>	killifish	allozymes	Atlantic Coast–Gulf Coast (break is near Florida-Georgia border)	UPGMA: not given	Duggins <i>et al.</i> (1995)
<i>Fundulus catenatus</i>	studfish	mtDNA res. sites	Ozarks & Indiana – Appalachia	network; parsimony, < 50%	Strange & Barr (1997)
<i>Fundulus heteroclitus</i>	killifish	allozymes; mtDNA res. sites	northeast – southeast sites; microsats	AMOVA; parsimony network; UPGMA, none given	Gonzalez-Vilasenor & Powers (1990); Adams <i>et al.</i> (2006)
<i>Etheostoma (Litocara) sp.</i>	darler	mtDNA res. sites	Ozarks–E of Mississippi River (2 subclades: Cumberland River & Kentucky River)	network; parsimony, 100% for E of Mississippi	Strange & Barr (1997)
<i>Etheostoma beanii</i> / <i>E. bifascia</i>	darler	mtDNA seq	haplotypes show high drainage system affinity	parsimony, no support given	Wiley & Hagen (1997)
<i>Alosa sapidissima</i>	shad	mtDNA res. sites	no structure along Atlantic Coast	AMOVA	Bentzen <i>et al.</i> (1989); Epifanio <i>et al.</i> (1995)
<i>Gambusia affinis</i> / <i>G. holbrooki</i>	mosquito fish	mtDNA res. sites; allozymes	E–W Apalachicola	UPGMA; parsimony, 100% for each clade	Wooten & Lydeard (1990); Scribner & Avise (1993)
<i>Lepomis punctatus</i>	spotted sunfish	mtDNA res. sites	Atlantic Coast–Gulf Coast drainages (E–W of Apalachicola)	UPGMA; parsimony, 100% for western clade; < 50% for eastern clade	Birmingham & Avise (1986)
<i>Lepomis microlophus</i>	reardear sunfish	mtDNA res. sites	Atlantic Coast–Gulf Coast drainages (E–W of Apalachicola)	UPGMA; parsimony, 100% for western clade; < 50% for eastern clade	Birmingham & Avise (1986)
<i>Lepomis gulosus</i>	warmouth sunfish	mtDNA res. sites	E–W Tombigbee River (Alabama)	UPGMA; parsimony, 100% for western clade; < 50% for eastern clade	Birmingham & Avise (1986)
<i>Lepomis macrochirus</i>	bluegill sunfish	mtDNA res. sites; allozymes	Atlantic Coast–Gulf Coast drainages	UPGMA; not given	Avise <i>et al.</i> (1984); Avise & Smithc (1974)

Table 2 *Continued*

Taxon	Common name	Markers	Pattern	Method of analysis/Support	References
<i>Amia calva</i>	bowfin	mtDNA res. sites	E–W Apalachicola	UPGMA; parsimony, 96% for western clade; < 50% for eastern clade	Bermingham & Avise (1986)
<i>Micropterus salmoides</i>	largemouth bass	mtDNA res. sites; allozymes	E–W Apalachicola	UPGMA; parsimony; not given	Philipp <i>et al.</i> (1983); Nedbal & Philipp (1994); Avise (2000)
<i>Cyprinella venusta</i>	blacktail shiner	mtDNA res. sites	E of Apalachicola–Mobile – Chocktawatchee–west of Mobile	neighbour-joining; parsimony, 100% for Mobile, 100% for east Apalachicola, 52% west of Mobile	Kristmundsdottir & Gold (1996)
<i>Stizostedion vitreum</i>	walleye	mtDNA res. sites	unique haplotype in Tombigbee River	sequence divergence	Billington & Strange (1995)
<i>Hypentelium nigricans</i>	northern hogsucker	mtDNA seq	two major clades; Ohio River basin – upper Mississippi River basin	parsimony, bayesian; 80% for Ohio R; 70% for Mississippi R network; parsimony, 100% for Ozarks; 98% for E of Mississippi	Berendzen <i>et al.</i> (2003)
<i>Erimystax dissimilis</i>	streamline chub	mtDNA res. sites	Ozarks – E of Mississippi River (3 subclades: Ohio River, Tennessee River & Green River)	genetic distance; neighbor-joining, not given	Strange & Burr (1997)
<i>Polyodon spathula</i>	paddlefish	allozymes; mtDNA res. sites	Mobile River – Mississippi River and Pearl River	UPGMA; parsimony network; not given	Epifanio <i>et al.</i> (1996)
<i>Acipenser oxyrinchus</i>	sturgeon	mtDNA res. sites	Atlantic Coast–Gulf Coast; small sequence divergence, limited sharing of genotypes between clades	UPGMA; 88%/85% and 85%/70% for Gulf and Atlantic groups with seq and microsats, respectively	Bowen & Avise (1990)
<i>Sciaenops ocellatus</i>	red drum	allozymes	Atlantic Coast–Gulf Coast	UPGMA; not given	Wirgin <i>et al.</i> (2002)
		mtDNA res. sites	High overall similarity (one locus shows Atlantic Coast–Gulf Coast difference)		Bohlmeyer & Gold (1991)
		otolith chemistry	Atlantic Coast–Gulf Coast	AMOVA	Gold <i>et al.</i> (1999)
<i>Pogonias cromis</i>	black drum	mtDNA res. sites	Atlantic Coast–Gulf Coast	MANOVA	Patterson <i>et al.</i> (2004)
<i>Cynoscion nebulosus</i>	spotted seatrout	mtDNA res. sites	Atlantic Coast–Gulf Coast	AMOVA; parsimony, not given	Gold & Richardson (1998a)
				AMOVA; neighbour-joining; parsimony, not given	Gold & Richardson (1998a)
<i>Arius felis</i>	hardhead catfish	mtDNA res. sites	no structure	UPGMA; parsimony	Avise <i>et al.</i> (1987b)
<i>Bagre marinus</i>	gafftopsail catfish	mtDNA res. sites	no structure	UPGMA; parsimony	Avise <i>et al.</i> (1987b)
<i>Anguilla rostrata</i>	eel	mtDNA res. sites	no structure	sequence divergence	Avise <i>et al.</i> (1986)
<i>Brevoortia tyrannus</i> / <i>B. patronus</i>	menhaden	mtDNA res. sites	Atlantic–Atlantic & Gulf (considerable sharing of haplotypes in the Gulf)	UPGMA; parsimony network; not given	Bowen & Avise (1990)
<i>Opsanus beta</i> / <i>O. tau</i>	toadfish	mtDNA res. sites	Atlantic Coast–Gulf Coast	UPGMA; parsimony, not given	Avise <i>et al.</i> (1987b)
<i>Scomberomorus maculatus</i>	spanish mackerel	mtDNA & nuclear seq	no structure along Atlantic/Gulf Coasts	sequence divergence	Buonaccorsi <i>et al.</i> (2001)
<i>Scomberomorus cavalla</i>	king mackerel	mtDNA res. sites	no structure along Atlantic/Gulf Coasts	AMOVA; parsimony	Gold & Richardson (1998a)
<i>Carcharhinus limbatus</i>	blacktip shark	mtDNA & nuclear seq	Atlantic Coast–Gulf Coast (2 subclades)	parsimony network, not given	Keeney <i>et al.</i> (2005)
<i>Myxeroperca phenax</i>	scamp	microsats	no structure along Atlantic/Gulf Coasts	AMOVA; not given	Zatcoff <i>et al.</i> (2004)
<i>Centropristis striata</i>	black seabass	mtDNA res. sites	Atlantic Coast–Gulf Coast	UPGMA; parsimony network; not given	Bowen & Avise (1990)

Table 2 Continued

Taxon	Common name	Markers	Pattern	Method of analysis/Support	References
<i>Epinephelus morio</i> <i>Seriola dumerii</i>	red grouper amberjack	microsats mtDNA	no structure along Atlantic/Gulf Coasts Atlantic Coast–Gulf Coast; but small genetic difference (with AMOVA, not in phylogenetic analyses)	AMOVA; not given AMOVA; parsimony, NJ, not given	Zatcoff <i>et al.</i> (2004) Gold & Richardson (1998a, b)
AMPHIBIAN					
<i>Rana pipiens</i>	northern	mtDNA seq	E–W Mississippi River (much of range once glaciated)	parsimony, 75% for eastern clade; < 50% for western clade	Hoffman & Blouin (2004)
<i>Rana catesbeina</i>	bullfrog	leopard frog mtDNA seq	E–W Mississippi River River (with overlap)	network; maximum likelihood; Bayesian; 100% eastern clade; 65% western clade	Austin <i>et al.</i> (2004)
<i>Pseudacris crucifer</i>	spring peeper	mtDNA seq	east of Appalachians (and north)– west of Appalachians (central clade)– west of the Mississippi River	parsimony; neighbour-joining; 64% eastern clade; 81% centra l clade; 99% western clade	Austin <i>et al.</i> (2002, 2004)
<i>Ambystoma tigrinum</i>	tiger salamander	mtDNA seq	E–W Apalachicola (E–W of Appalachians)	Maximum likelihood, 53% for eastern clade; 95% for western clade	Church <i>et al.</i> (2003)
<i>Ambystoma talpoideum</i>	mole salamander	mtDNA seq	E–W Apalachicola	parsimony, 54% for eastern clade; 64% for western clade	Donovan <i>et al.</i> (2000)
<i>Ambystoma maculatum</i>	spotted salamander	mtDNA seq	largely E–W Apalachicola (E–W of Appalachians); western clade has two subclades	maximum likelihood; parsimony; nested clade; 100% for eastern and western clades	Donovan <i>et al.</i> (2000), Zamudio & Savage (2003)
<i>Eurycea multiplicata</i> <i>complex</i>	plethodontid salamander	mtDNA seq	Ozark Plateau–Ouachita Mts	parsimony; Bayesian, 99% for Ozark and 100% for Ouachita clade	Bonett & Chippindale (2004)
<i>Eurycea bislineata</i> <i>complex</i>	plethodontid salamander	mtDNA seq	complex pattern; north–south clades that agree with ancient rather than modern river drainages	parsimony; 100% for northern and southern clades	Kozak <i>et al.</i> (2006)
<i>Desmognathus wrighti</i>	pygmy salamander	mtDNA seq	4 genetically distinct clusters in southern Appalachians, suggesting long-term isolation	genetic distance; parsimony, maximum likelihood, 100%, 62%, 79%, 96%	Crespi <i>et al.</i> (2003)
<i>Desmognathus marmoratus</i> & <i>D. quadramaculatus</i>	shovel-nosed salamander	mtDNA seq	E–W of Appalachians	Bayesian, parsimony, 0.99/80% (east clade), 1.0/100% (west clade)	Jones <i>et al.</i> (2006)
<i>Pseudobranchius striatus</i>	salamander	mtDNA seq	E–W of Apalachicola; East clade divided into N vs S of Altamaha	maximum likelihood, 92% for east, 100% for west; 97% for north of Altamaha, 100% for south of Altamaha	Liu <i>et al.</i> (2006)
<i>Pseudacris 'nigrita' clade</i>	chorus frog	allozymes; mtDNA seq	E–W of Mississippi River (former with 2 subclades)	parsimony, maximum likelihood, 100% for eastern clade; 70% for western clade	Moriarty & Cannatella (2004)

Table 2 Continued

Taxon	Common name	Markers	Pattern	Method of analysis/Support	References
REPTILE					
<i>Sceloporus undulatus</i>	eastern fence lizard	mtDNA seq	4 lineages including E–W Mississippi River; also western USA and southwestern US	parsimony, maximum likelihood, Bayesian; 90% for western clade	Leache & Reeder (2002)
<i>Elaphe obsoleta</i>	rat snake	mtDNA seq	E of Apalachicola – Central Clade (W of Apalachicola) – W of Mississippi River	parsimony; maximum likelihood, 98% eastern clade; 99% central clade; 100% western clade	Burbrink <i>et al.</i> (2000)
<i>Elaphe guttata</i>	corn snake	mtDNA seq	E of Apalachicola – Central Clade (W of Apalachicola) – W of Mississippi River	maximum likelihood; Bayesian, 100% eastern clade; 100% central clade; 100% western clade	Burbrink (2002)
<i>Alligator mississippiensis</i>	alligator	microsats	East–West Apalachicola	AMOVA; none given	Davis <i>et al.</i> (2002)
<i>Nerodia rhombifera</i> / <i>N. taxispilota</i>	water snake	allozymes	E–W Tombigbee River (Alabama)	UPGMA; parsimony, not given	Lawson (1987)
<i>Sternotherus minor</i>	musk turtle	mtDNA res. sites & seq	E–W Apalachicola (E–W of Appalachians) (the former with 2 subclades)	parsimony; neighbour-joining; 100% for western clade; 52% for part of E clade (res. site data)	Walker <i>et al.</i> (1995)
<i>Sternotherus odoratus</i>	stinkpot (turtle)	mtDNA res. sites	E–W Apalachicola (E–W of Appalachians) (each with two subclades)	parsimony network, not given	Walker <i>et al.</i> (1997)
<i>Kinosternon baurii</i>	mud turtle	mtDNA res. sites	E Apalachicola (peninsular Florida) – Georgia & Virginia	parsimony; neighbour-joining; < 50%	Walker & Avise (1998)
<i>Kinosternon subrubrum</i>	mud turtle	mtDNA res. sites	E Apalachicola (E Appalachians) – peninsular Florida–W of Apalachicola (W of Appalachians = central clade)–W of Mississippi River	parsimony; neighbour-joining; 99% for eastern clade; 100% for central clade; < 50% Florida; western clade has 1 sample	Walker & Avise (1998)
<i>Trachemys scripta</i>	slider (turtle)	mtDNA res. sites	E–W Apalachicola (E–W of Appalachians)	UPGMA; parsimony, not given	Avise <i>et al.</i> (1992)
<i>Macrolemys temminckii</i>	alligator snapping turtle	mtDNA seq	E–W Apalachicola–Suwannee River (Florida)	parsimony; 86% eastern clade; 58% western clade	Roman <i>et al.</i> (1999)
<i>Deirochelys reticularia</i>	chicken turtle	mtDNA seq	E–W Apalachicola – Ozarks	phenogram; not given	Walker & Avise (1998)
<i>Gopherus polyphemus</i>	gopher tortoise	mtDNA seq	E Apalachicola (two subclades) – W Apalachicola	UPGMA	Ostentoski & Lamb (1995)
<i>Malaclemys terrapin</i>	diamondback terrapin	mtDNA res. sites	Atlantic Coast–Gulf Coast (Atlantic break is central Florida)	sequence divergence, not given	Lamb & Avise (1992)
<i>Chelydra serpentina</i>	common snapping turtle	mtDNA res. sites	no structure	parsimony network	Walker <i>et al.</i> (1998)
<i>Chrysemys picta complex</i>	painter turtle	mtDNA seq	south Mississippi drainage (W of Apalachicola) – all northern populations; northern divided into subclades: eastern clade (~E of Appalachians, Georgia–Maine)–upper midwest – Great Plains & NW	parsimony; neighbour-joining; maximum likelihood; 98%MP/99%NJ for southern clade; 61%MP/71%NJ for northern clade	Starkey <i>et al.</i> (2003)

Table 2 Continued

Taxon	Common name	Markers	Pattern	Method of analysis/Support	References
<i>Apalone ferox</i>	softshell turtle	mtDNA seq	no structure	parsimony; neighbour-joining	Weisrock & Janzen (2000)
<i>Apalone mutica</i>	softshell turtle	mtDNA seq	approximately E–W of Mississippi River (Florida & eastern Louisiana–Texas, Arkansas, Iowa)	parsimony; neighbour-joining; 97% western clade; 100% southeast clade	Weisrock & Janzen (2000)
<i>Apalone spinifera</i>	softshell turtle	mtDNA seq	western (New Mexico, Texas)–northern – southeast 1 (Alabama, west Florida, Louisiana, Mississippi)–southeast 2 (north Florida, Georgia)	parsimony; neighbour-joining; 100% western clade; 97% northern; 100% southeast 1; 97% southeast 2	Weisrock & Janzen (2000)
<i>Eumeces fasciatus</i>	five-lined skink	mtDNA seq	[East + ‘Central’]–West of Mississippi River	Bayesian, neighbour joining; 1.0/74% for east + central; 0.62/62% for west	Howes <i>et al.</i> (in press)
BIRD					
<i>Agelaius phoeniceus</i>	red-winged blackbird	mtDNA res. sites	no structure	parsimony network	Ball <i>et al.</i> (1988)
<i>Spizella passerine</i>	chipping sparrow	mtDNA res. sites	no structure	UPGMA	Zink & Dittmann (1993a); Zink (1996, 1997)
<i>Melospiza melodia</i>	song sparrow	mtDNA res. sites	no structure	UPGMA; parsimony	Zink & Dittmann (1993b)
<i>Zenaidura macroura</i>	mourning dove	mtDNA res. sites	no structure	UPGMA; parsimony	Ball & Avise (1992)
<i>Dendrocopos pubescens</i>	downy woodpecker	mtDNA res. sites	no structure	UPGMA; parsimony	Ball & Avise (1992)
<i>Parus carolinensis</i>	carolina chickadee	mtDNA res. sites	E–W Tombigbee River (Alabama)	parsimony network, not given	Gill <i>et al.</i> (1993)
<i>Parus bicolor</i>	tufted titmouse	mtDNA res. sites	no structure	genetic distance	Gill & Slikas (1992)
<i>Geothlypis trichas</i>	yellowthroat	mtDNA res. sites	no structure in E.N.A.	parsimony	Ball & Avise (1992)
<i>Dendroica petechia</i>	yellow warbler	mtDNA res. sites	no structure in E.N.A.	parsimony	Klein & Brown (1994)
<i>Colaptes auratus</i>	northern flicker	mtDNA res. sites	no structure in E.N.A.	parsimony	Moore <i>et al.</i> (1991)
<i>Quiscalus quiscula</i>	common grackle	mtDNA res. sites	no structure	parsimony	Zink <i>et al.</i> (1991)
<i>Ammodramus maritimus</i>	seaside sparrow	mtDNA res. sites	Atlantic Coast–Gulf Coast	UPGMA; parsimony, 100% for each clade	Avise & Nelson (1989)
<i>Ammodramus savannarum</i>	grasshopper sparrow	mtDNA seq; microsats	minimal genetic divergence between Florida populations and others in North America	minimum spanning tree; neighbour-joining; genetic distance, support < 50%	Bulgin <i>et al.</i> (2003)
<i>Aix sponsa</i>	wood duck	mt DNA seq	E–W North America, but no structure in E.N.A.	parsimony network, not given	Peters <i>et al.</i> (2005)
<i>Scolopax minor</i>	woodcock	mt DNA seq	no structure	parsimony network	Rhymer <i>et al.</i> (2005)
<i>Lanius ludovicianus</i>	loggerhead shrike	mt DNA seq	no structure in E.N.A.	mimimum-spanning network	Vallianatos <i>et al.</i> (2001)

Table 2 *Continued*

Taxon	Common name	Markers	Pattern	Method of analysis/Support	References
MAMMAL					
<i>Odocoileus virginianus</i>	white-tailed deer	mtDNA res. sites	southern Florida—the remainder of peninsular Florida, and north—the Florida panhandle west	parsimony; 81% south Florida; 71% for other two clades together; support < 50% for the individual clades	Ellsworth <i>et al.</i> (1994)
<i>Geomys pinetis</i>	pocket gopher	mtDNA res. sites	E–W Apalachicola	parsimony network, not given	Awise <i>et al.</i> (1979)
<i>Blarina brevicauda</i>	short-tailed shrew	mtDNA seq	E–W Mississippi River (former with 2 subclades)	parsimony, maximum likelihood, nested clade; 91% for eastern clade; 100% for western clade	Brant & Orti (2003)
<i>Peromyscus polionotus</i>	beach mouse	mtDNA res. sites	approximately E–W Apalachicola (Central Florida–W Florida, Mississippi, Georgia)	UPGMA; parsimony network; not given	Awise <i>et al.</i> (1983)
<i>Glaucomys volans</i>	flying squirrel	mtDNA seq	some structure; most Florida populations distinct	neighbour-joining; clades weakly supported (65% for most Florida populations)	Petersen & Stewart (2006)
<i>Trichechus manatus</i>	manatee	mtDNA seq	no structure along coasts of Florida	neighbour-joining; maximum parsimony, support < 50%	Vianna <i>et al.</i> (2006)
<i>Canis latrans</i>	coyote	mtDNA res. sites	no structure in E.N.A.	UPGMA; parsimony, not given	Lehman & Wayne (1991)
MOLLUSK					
<i>Loligo pealei</i>	longfin squid	mtDNA RFLPs	Atlantic Coast–Gulf Coast	minimum-spanning network	Herke & Foltz (2002)
<i>Loligo plei</i>	arrow squid	mtDNA RFLPs	East–West Apalachicola	minimum-spanning network	Herke & Foltz (2002)
<i>Busycon perversum</i>	sinestral whelk	mtDNA seq; allozymes; morphology	Atlantic Coast–Gulf Coast	parsimony, < 50% for each clade	Wise <i>et al.</i> (2004)
<i>Brachidontes exustus</i>	scorched mussel	mtDNA & ITS seq	Atlantic Coast–Gulf Coast (plus 2 other clades)	Bayesian PP, parsimony, Gulf 0.75/51%; Atlantic 0.91/84% (nuclear); and Gulf 1.00/100%, Atlantic 1.00/100% (mtDNA)	Lee & Foighl (2004)
<i>Geukensia demissa</i>	mussel	allozymes; morphology	Atlantic Coast–Gulf Coast	UPGMA: not given	Sarver <i>et al.</i> (1992)
<i>Crassostrea virginica</i>	oyster	mtDNA res. sites	Atlantic Coast–Gulf Coast	UPGMA: not given	Reeb & Awise (1990)
<i>Crepidula convexa</i>	marine gastropod	mtDNA seq	Atlantic Coast–Gulf Coast (Atlantic break is central Florida)	parsimony network, 100% for Atlantic; 90% for Gulf	Collin (2001)
<i>Spisula solidissima</i>	surfclam	mtDNA seq	Atlantic Coast–Gulf Coast	parsimony, 100% for each clade	Hare & Weinberg (2005)
<i>Lampsilis</i> sp.	freshwater mussel	mtDNA seq	Mobile Basin–rivers to the east	parsimony, 90% for Mobile Basin, 80% for clade of other rivers	Roe <i>et al.</i> (2001)

Table 2 Continued

Taxon	Common name	Markers	Pattern	Method of analysis/Support	References
CRUSTACEAN					
<i>Limulus polyphemus</i>	horseshoe crab	mtDNA res. sites	Atlantic Coast–Gulf Coast (Atlantic break is central Florida)	parsimony network, not given	Saunders <i>et al.</i> (1986)
<i>Pagurus pollicaris</i>	hermit crab	mtDNA seq; allozymes; morphology	Atlantic Coast–Gulf Coast	UPGMA; parsimony; maximum likelihood; not given	Young <i>et al.</i> (2002)
<i>Pagurus longicarpus</i>	hermit crab	mtDNA seq; allozymes; morphology	Atlantic Coast–Gulf Coast	UPGMA; parsimony; maximum likelihood; 100% Atlantic clade; 68% for most of the Gulf clade (< 50% for entire Gulf clade)	Young <i>et al.</i> (2002)
<i>Sesarma reticulatum</i>	grapsid crab	allozymes	Atlantic Coast–Gulf Coast	UPGMA: not given	Felder & Staton (1994)
<i>Uca minax</i>	ocypodid crab	allozymes	Atlantic Coast–Gulf Coast	UPGMA: not given	Felder & Staton (1994)
<i>Emerita talpoida</i>	mole crab	mtDNA seq	Atlantic Coast–Gulf Coast	parsimony; maximum likelihood; neighbour joining; 100% Atlantic clade; 1 sample from Gulf	Tam <i>et al.</i> (1996)
<i>Litopenaeus setiferus</i>	white shrimp	mtDNA seq; microsats	Atlantic & eastern Gulf–western Gulf (with some sympatry of lineages)	minimum spanning tree; NJ, not given	McMillen-Jackson & Bert (2003)
<i>Farfantepenaeus aztecus</i>	brown shrimp	mtDNA seq	no structure	minimum spanning tree; NJ, not given	McMillen-Jackson & Bert (2003)
<i>Gammarus tigrinus</i>	amphipod	mtDNA seq	N–S Atlantic Coast	parsimony; neighbour joining; 96% NJ, 80% MP (north); 76% NJ, 95% MP (south)	Kelly <i>et al.</i> (2006)
<i>Dahnia obtuse</i>	Daphnia	mtDNA seq; microsats	'NA1' clade has four subclades: western USA – two clades with considerable overlap in central USA – a small clade in Illinois	Bayesian; NJ, 78% western, 57% and 78% for two clades in central USA; 71% for Illinois	Penton <i>et al.</i> (2004)
BRYOZOAN					
<i>Bugula neritina</i>	bryozoan	mtDNA seq	North Atlantic (Delaware & north) – South Atlantic and Gulf (North Carolina & South)	neighbour-joining; 100% for each clade	McGovern & Hellberg (2003)
HYDROZOAN					
<i>Hydractinia</i> sp.	athecate hydroid; symbiont on <i>Pagurus</i> (hermit crab)	DNA-DNA hybridization	Atlantic Coast–Gulf Coast	UPGMA	Cunningham <i>et al.</i> (1991)

Table 2 Continued

Taxon	Common name	Markers	Pattern	Method of analysis/Support	References
INSECT					
<i>Cicindella dorsalis</i>	tiger beetle	mtDNA res. sites; ITS	Atlantic Coast–Gulf Coast	parsimony; not given	Vogler & DeSalle (1993) Vogler <i>et al.</i> (1994)
<i>Ophraella communa</i>	leaf beetle	mtDNA seq; allozymes: morphology	no regional localization of haplotypes	maximum likelihood	Knowles <i>et al.</i> (1999)
<i>Rhagoletis pomonella</i>	fruit fly	mtDNA & nuclear seq	no structure in E.N.A.	parsimony	Feder <i>et al.</i> (2003)
<i>Nigronia serricornis</i>	saw-combed fishfly	mtDNA seq	6 major geographically structured clades in E.N.A.; three northward migrations proposed after glaciation	Bayesian; nested clade, pp > .95 for many clades	Heilveil & Berlocher (2006)
FUNGUS					
<i>Serpula himantoides</i>	dry rot fungus	ITS & nuclear seq	some differentiation in eastern North America (but limited sampling)	neighbour-joining; parsimony, low support, 72% for Pennsylvania clade	Kauserud <i>et al.</i> (2004)
<i>Schizophyllum commune</i>	common mushroom	IGS seq & restriction sites	significant differentiation between a population from Miami, Florida and those from North Carolina and Georgia	genetic distance	James & Vilgalys (2001), James <i>et al.</i> (2001)
<i>Xerula furfacea</i>	macrofungus	ITS seq	little variation, differentiation (but limited sampling)	parsimony; support < 50% at populational level	Mueller <i>et al.</i> (2001)
RED ALGA					
<i>Gracilaria tikvahiae</i>	red alga	cpDNA & ITS seq	4 lineages, Canada, NE USA; SE Florida; E Gulf Coast; W Gulf Coast	network; maximum likelihood, 64% SE Florida; 63% W Gulf Coast	Gurgel <i>et al.</i> (2004)
GREEN ALGA					
<i>Trebouxia</i>	green algal photobionts associated with lichen fungus	ITS seq	strong differences between southern coastal plain (Florida, South Carolina, Georgia and 1 North Carolina site) – inland (North Carolina, Virginia, Pennsylvania, Ozarks)	Gene diversity; Bayesian, southern clade pp > .95	Yahr <i>et al.</i> (2004, in press)
<i>Bryopsis</i> sp.	siphonous seaweed	cpDNA seq	differences between Atlantic coast populations; two clades with break at Virginia; a third clade is widespread	parsimony; 100% for each clade	Krellwitz <i>et al.</i> (2001)
MOSS					
<i>Sphagnum bartlettianum</i> / <i>S. rubellum</i>	sphagnum	cpDNA & nuclear seq	little variation and differentiation (but limited sampling)	Bayesian, not given	Shaw <i>et al.</i> (2004, 2005)
<i>Fontinalis</i> sp.	Moss	ITS & cpDNA seq	little variation and differentiation (but limited sampling)	parsimony; support < 50% at populational level	Shaw and Allen (2000)

Table 2 Continued

Taxon	Common name	Markers	Pattern	Method of analysis/Support	References
GYMNOSPERM					
<i>Pinus virginia</i>	Virginia pine	allozymes	NW Appalachians–SW Appalachians	UPGMA: not given	Parker <i>et al.</i> (1997)
<i>Pinus palustris</i>	longleaf pine	allozymes	more variation in populations west of Mississippi River; little structure	allozymes; multivariate	Schmidtling & Hipkins (1998)
<i>Pinus clausa</i>	sand pine	allozymes	E–W Apalachicola	UPGMA; not given	Parker <i>et al.</i> (1997)
<i>Pinus taeda</i>	loblolly pine	microsats	E–W Mississippi River	PCA	Al-Rabab'ah & Williams (2002)
<i>Chaemaecyparis thuyoides</i>	white cedar	allozymes	E–W Apalachicola	UPGMA; none given	Mylecraine <i>et al.</i> (2004)
ANGIOSPERM					
<i>Sagittaria latifolia</i>	arrowhead	cpDNA RFLP	greatest diversity in SE USA	minimum spanning tree; not given	Dorken & Barrett (2004)
<i>Liquidambar styraciflua</i>	sweetgum	plastid seq	complex; no clear geographical clades	parsimony	Morris <i>et al.</i> (in prep.)
<i>Liriodendron tulipifera</i>	tulip tree	cpDNA res. sites	E–W Apalachicola (peninsular Florida–rest of range) E–W Apalachicola; (peninsular Florida–rest of range, the latter with two subgroups	parsimony; not given	Sewell <i>et al.</i> (1996)
		allozymes		PCA	Parks <i>et al.</i> (1994)
<i>Piriiqueta caroliniana</i>	pitted stripe seed	cpDNA res. sites	Northwest Florida & Georgia – Central and South Florida	nested clade: not given	Templeton <i>et al.</i> (2000)
<i>Apios americana</i>	groundnut	nuclear seq	E–W Appalachians	parsimony network, not given	Maskas & Cruzan (2000)
<i>Trillium grandifolium</i>	Trillium	cpDNA seq; allozymes	E–W Appalachians	UPGMA; nested clade, not given	Joly & Bruneau (2004)
<i>Polygonella gracilis</i> / <i>P. macrophylla</i>	Polygonella	allozymes	genetic differentiation between members of this sister pair occurring E–W Apalachicola	gene diversity	Griffin & Barrett (2004)
<i>Sarracenia purpurea</i>	pitcher plant	allozymes, morphology	W Apalachicola (Florida panhandle & Mississippi) – Georgia & North Carolina plus Minnesota & Wisconsin	not given	Lewis & Crawford (1995)
<i>Dicerandra linearifolia</i>	coastal plain balm	ITS & cpDNA seq	Atlantic Coast–Gulf Coast drainages (E–W of Apalachicola)	parsimony; maximum likelihood	Godt & Hamrick (1998), Ellison <i>et al.</i> (2004)
<i>Prunus species</i>	plum	cpDNA seq	no structure	parsimony	Oliveira <i>et al.</i> (in press)
<i>Acer rubrum</i>	red maple	cpDNA seq	colonization from northern populations; southern populations distinct	parsimony network	Shaw & Small (2005)
<i>Fagus grandifolia</i>	beech	cpDNA seq	colonization from northern populations; southern populations no structure	parsimony network	McLachlan <i>et al.</i> (2005)
<i>Juglans nigra</i>	black walnut	cpDNA seq	E–W Mississippi River	parsimony network	McLachlan <i>et al.</i> (unpublished)
<i>Quercus rubra</i>	red oak	cpDNA res. sites	latitudinal trend in differentiation; populations survived close to glacial margin	parsimony network, not given	Magni <i>et al.</i> (2005)
<i>Arabidopsis thaliana</i>	mouseear cress	AFLP	no regional structure in eastern North America (this is an introduced species from Europe)	neighbour-joining, not given	Jorgensen & Mauricio (2004)
					Schmid <i>et al.</i> (2006)

Analyses with spatial models

We tested the hypothesis that major phylogeographical breaks between diverse taxa are spatially congruent by examining the geographical distribution of a random sample of the 148 studies in Table 2. The best tests of phylogeographical congruence involve testing both phylogenetic and geographical patterns (cf. Carstens *et al.* 2005a; Kozak *et al.* 2006). We could not conduct similar tests with data from the literature because data quantifying genetic divergence among populations were often not accessible. However, if we accept the major phylogenetic divisions presented in individual studies, we can test whether they are distributed in a geographically coherent pattern.

From Table 2, we picked those studies from which we could readily identify population location. We excluded taxa with coastal distributions and limited geographical range (54 taxa) because we were looking for congruent patterns across the entire study region. We likewise excluded the 24 studies that did not identify a phylogeographical pattern because we mapped large phylogeographical breaks. Excluding these studies actually biases our results towards finding congruent patterns.

From this subset of the literature survey (50 taxa), we randomly selected 10 studies (*Apalone mutica*, *Liriodendron tulipifera*, *Fundulus catenatus*, *Chrysemys picta*, *Elaphe obsoleta*, *Erimystax dissimilis*, *Percina eoides*, *Eurycea bislineata*, *Ambystoma talipoideum*, and *Fagus grandifolia*) and identified the geographical location of the largest phylogenetic break in each taxon using Monmonier's distance algorithm (cf. Manel *et al.* 2003). Briefly, neighbouring samples were identified using Delaunay triangulation, genetic distances were calculated between neighbouring samples (based on a binary variable identifying each sample as a member of one of the two most divergent clades), and Monmonier (1973) maximum difference algorithm was used to identify the two most genetically distinct geographically coherent groupings across the dataset. Analysis was carried out using the program ALLELES IN SPACE (Miller 2005). The density of phylogeographical breaks was estimated on a two-degree-by-two-degree grid using the LINES DENSITY tool in ARCMAP (a component of ARCVIEW; ARCGIS version 9.0, ESRI).

If at least some of the phylogeographical breaks across taxa were spatially congruent, we would expect the breaks we calculated using Monmonier's algorithm to be spatially clumped. If the biogeographical barriers noted above were generally important across taxa, we would expect phylogeographical breaks to map onto those boundaries. If the distribution of phylogeographical breaks were species-specific, we would expect their density to be highest in the centre of the study area. Species-specific breaks would not be uniformly distributed because the range sizes of taxa examined in this study are large relative to the study area, and phylogeographical breaks are consequently long. A

random distribution of long breaks would overlap more commonly in the centre of the range than at the periphery.

We conducted a permutation test to learn where in our study area the concentration of phylogeographical breaks was different from the pattern expected under a random spatial distribution of such breaks. In each permutation, each of the 10 phylogeographical breaks was randomly rotated and spatially shifted within the area bounded by the original data (a rectangle bounded by 100°W and 76°W longitude and 28°N and 46°N latitude). Thus, the shape and length of phylogeographical boundaries was preserved but their location and orientation was randomized within the study area. The density of 20 of these networks of 'pseudophylogeographical breaks' was calculated as above. Note that the density of pseudobreaks under this null model of spatial randomization is higher in the centre of the study area rather than uniformly distributed because long linear features were constrained to fall within a set area. Long lines tend to cross in the centre rather than along the periphery.

We noted the distribution of grid cells in the data that had higher or lower densities of phylogeographical breaks than found in any of the 20 random permutations. Such grid cells are not necessarily statistically significant, because testing each of the grid cells separately inflates the probability of type I error (a multiple testing problem). However, cells whose densities of phylogeographical breaks are within the range of the random permutations are consistent with the null hypothesis.

Results and discussion

Survey of the literature

Our recent Web of Science survey of the literature from 2000 to 2005 identified 396 articles (excluding reviews) that involved analyses of 'phylogeography'. Of those, 331 (83.5%) focused on animals, with 45 (11.4%) on plants, and the remaining 20 (5%) on fungi and protists. In 1998, using the same keyword, Avise (2000) identified just over 100 articles. His survey further found that roughly 70% of all articles published between 1987 and 1998 that used 'phylogeography' or 'phylogeographic' as a key term focused on animals. Our recent survey also shows that despite a dramatic increase in the total number of phylogeographical articles, over 80% of those articles remain focused on animals.

This disparity in the number of phylogeographical studies of plants and animals is due in part to the degree of resolution afforded to intraspecific studies by the rapidly evolving animal mitochondrial genome. The mitochondrial DNA (mtDNA) gene cytochrome *b* is routinely sequenced in such analyses. In contrast, the more slowly evolving chloroplast genome typically does not provide the variation

needed to infer organellar phylogenies within species (Schaal & Olsen 2000; but see Soltis *et al.* 1997). Although technological advances now permit the sequencing of numerous base pairs with relative ease and at only moderate expense, the sequencing of 5000 or more base pairs of fast-evolving chloroplast DNA (cpDNA) spacer regions may still yield very little variation within species. For example, in witch hazel, *Hamamelis*, only a few variable sites were discovered among species despite the sequencing of more than 4200 bp of cpDNA (Morris *et al.*, unpublished). However, higher levels of intraspecific cpDNA variation (relative to traditional interspecific approaches) have been observed in other woody taxa (Soltis *et al.* 1997; Brunsfeld *et al.* 2001; Manos, unpublished).

This problem in plants is being rectified to some degree via the use of single-copy nuclear genes (Olsen & Schaal 1999; Hare 2001; Gaskin & Schaal 2002; Sang 2002; Caicedo & Schaal 2004) and relatively fast-evolving cpDNA spacer regions (e.g. Shaw *et al.* 2005), making it possible to target and survey larger portions of the cpDNA genome. However, recent work suggests that purported trends in the phylogenetic utility of cpDNA regions across angiosperms (Shaw *et al.* 2005) may not be consistent at the population level (Morris *et al.*, unpublished). Therefore, while studies of animal phylogeography may rely on one or a few mtDNA genes, researchers involved in plant phylogeographical studies will likely need to screen many regions (cpDNA or nuclear DNA) to find suitable levels of variation to detect historical patterns.

Through our survey, we added numerous new examples of phylogeographical studies from unglaciated eastern North America (post 2000, the year of publication of 'Phylogeography', by Avise) (Table 2). Whereas some taxonomic groups, such as birds, amphibians, reptiles, fish, and crustaceans, now appear well represented in phylogeographical studies from this region, other groups remain poorly studied or unrepresented. Considering vertebrates, mammals are underrepresented and most studies of reptiles involve turtles. There have been only a few studies on insects, and this group remains grossly underrepresented. Few studies have involved fungi or microbes (Lomolino & Heaney 2004; Dolan 2006). Several broad geographical studies of fungi have included multiple samples from eastern North America (although sampling was generally small) and revealed either no clear evidence of genetic differentiation or weak differentiation among samples (e.g. Mueller *et al.* 2001; Kauseud *et al.* 2004). However, genetic structure was evident in eastern North America in the mushroom *Schizophyllum commune* (James & Vilgalys 2001; James *et al.* 2001).

Although phylogeographical studies of plants from eastern North America are increasing, most are of angiosperms; few analyses involve algae, bryophytes, lycophytes, ferns, or gymnosperms. Phylogeographical studies in eastern

North America have involved both red and green algae (e.g. Gurgel *et al.* 2004; Yahr *et al.* 2004, in press). A phylogeographical analysis of *Grimmia* from western North America (Fernandez *et al.* 2006) illustrates the potential of phylogeographical analyses of bryophytes. Several other phylogenetic studies of bryophytes have been conducted on a broad geographical scale and have included limited sampling from eastern North America (e.g. Shaw & Allen 2000; Vanderpoorten *et al.* 2003; Shaw *et al.* 2005) (Table 2). No phylogeographical analyses of ferns have been conducted in eastern North America (Wolf *et al.* 2001; P. Wolf, personal communication).

Major phylogeographical patterns in unglaciated eastern North America

We observed a number of different patterns in our survey of the literature — some appear simple, others very complex, and some taxa show no phylogeographical structure (Figs 1–6; Table 2; see also Avise 2000). Importantly, the patterns initially described by Avise and co-workers extend to a more diverse array of organisms (Table 2). We summarize the most common of the patterns below. In Figs 1–6, we illustrate particular phylogeographical profiles using organisms with representative patterns; for each pattern, a plant example was also included, if available. Although certain, comparable signals emerge from many of these studies, the strength of those signals varies with levels of divergence, or with extent of species distributions. Therefore, considerable variation may be present around each general theme, in some cases melding one pattern into another. Furthermore, these major patterns are not the only ones observed. Therefore, while the patterns presented here are repeated many times, there are variations on these themes. Finally, ~17% of the organisms (both plants and animals) that have been investigated from unglaciated eastern North America exhibit no clear phylogeographical structure with the markers employed. Examples of such organisms (Table 2) include a number of highly mobile organisms (e.g. birds; see also Avise 2000).

Maritime — Atlantic Coast/Gulf Coast discontinuity

Groups that share this pattern exhibit distinct Atlantic and Gulf Coast lineages, with the break occurring at various points along the southern Florida peninsula (Fig. 1). Avise's (2000) review of this pattern covered several vertebrates and invertebrates, including the horseshoe crab (*Limulus polyphemus*) (Fig. 1b), seaside sparrow (*Ammodramus maritimus*) (Fig. 1c), black sea bass (*Centropristis striata*), diamondback terrapin (*Malaclemys terrapin*), and the beach tiger beetle (*Cicindela dorsalis*). Recent studies have revealed this general pattern in many additional diverse organisms (over 25 examples; see Table 2), including the hermit crab

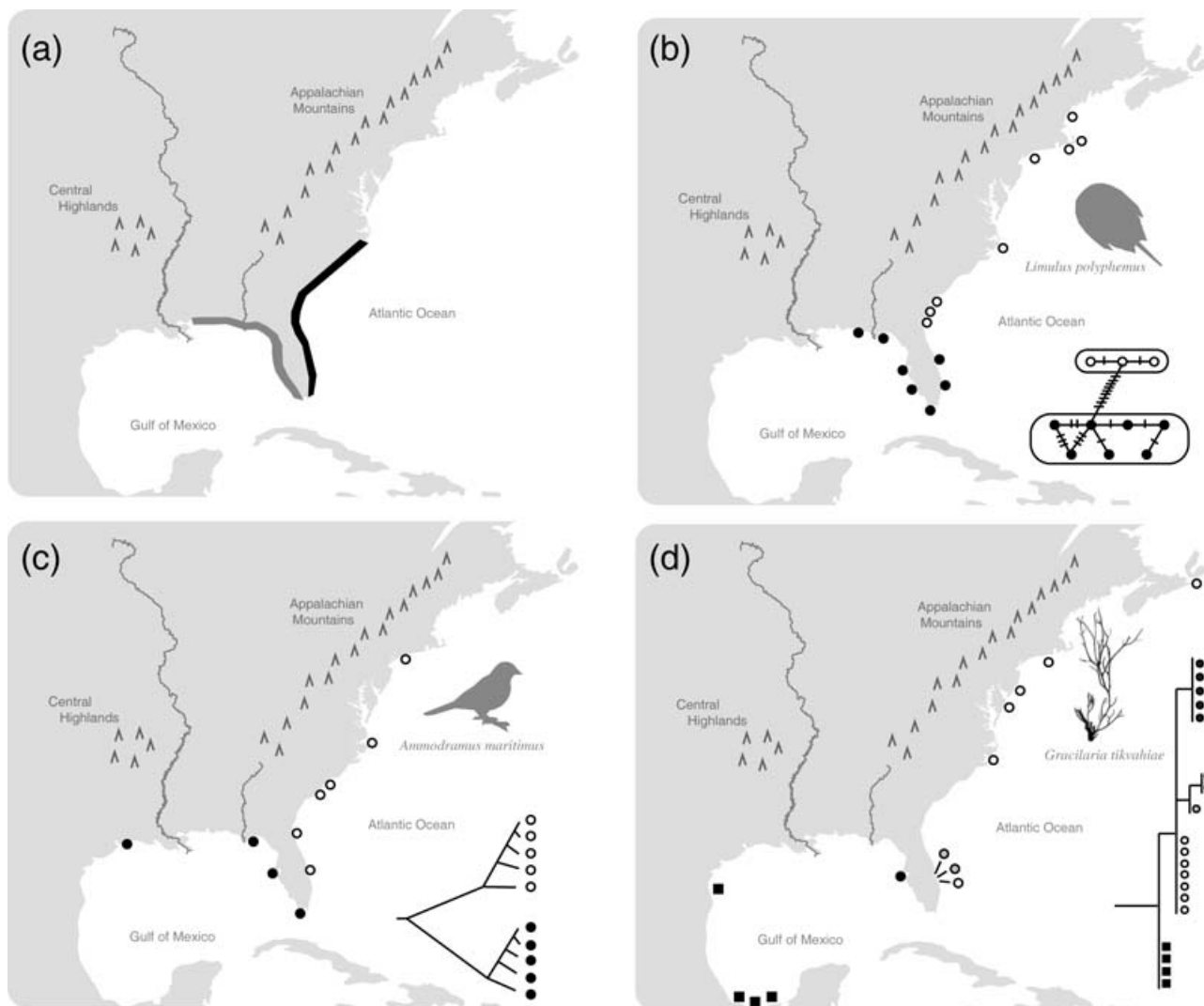


Fig. 1 The maritime Atlantic Coast vs. Gulf Coast discontinuity. Many plants and animals share this pattern, with a major phylogeographical break typically occurring at various points along the Atlantic Coast of the Florida peninsula. (a) General pattern of molecular divergence; (b) the horseshoe crab, *Limulus polyphemus* (redrawn from Saunders *et al.* 1986); (c) the dusky seaside sparrow, *Ammodramus maritimus* (redrawn from Avise & Nelson 1989); (d) the red alga, *Gracilaria tikvahiae* (redrawn from Gurgel *et al.* 2004).

(*Pagurus longicarpus*) (Young *et al.* 2002), blacktip shark (*Carcharhinus limbatus*) (Keeney *et al.* 2005), sinistral whelk (*Busycon* spp.) (Wise *et al.* 2004), long squid (*Loligo pealei*) (Herke & Foltz 2002), and surfclam (*Spisula solidissima*) (Hare & Weinberg 2005).

Some organisms exhibit molecular patterns having additional complexity compared to those taxa described initially by Avise and co-workers. The scorched mussel, (Fig. 1) *Brachidontes exustus*, exhibits Gulf vs. Atlantic groups (Lee & Foighil 2004). However, two other clades were recovered: (i) a Key Biscayne clade, restricted to southeastern Florida, and (ii) a clade restricted to the Bahamas and the southern tip of Florida.

The red alga *Gracilaria tikvahiae* (Gurgel *et al.* 2004) also exhibits the maritime Atlantic-Gulf phylogeographical

pattern. However, like the scorched mussel, *Gracilaria* is also geographically widespread and also exhibits additional phylogeographical complexity. Four distinct cpDNA lineages were detected (Fig. 1d) (i) a Canadian–northeast US lineage; (ii) an Atlantic Coast Florida lineage; (iii) an eastern Gulf of Mexico lineage; and (iv) a western Gulf of Mexico lineage (Table 2).

Not all marine species investigated exhibiting an Atlantic-Gulf Coast distribution exhibit genetic differentiation between the two regions [e.g. Spanish mackerel (*Scomberomorus maculatus*), scamp (*Mycteroperca phenax*); Table 2]. Alternatively, in the case of red drum (*Sciaenops ocellatus*), an initial allozyme analysis did not reveal a clear Atlantic-Gulf pattern of differentiation (Bohlmeyer & Gold 1991); red drum was therefore considered an example of a fish

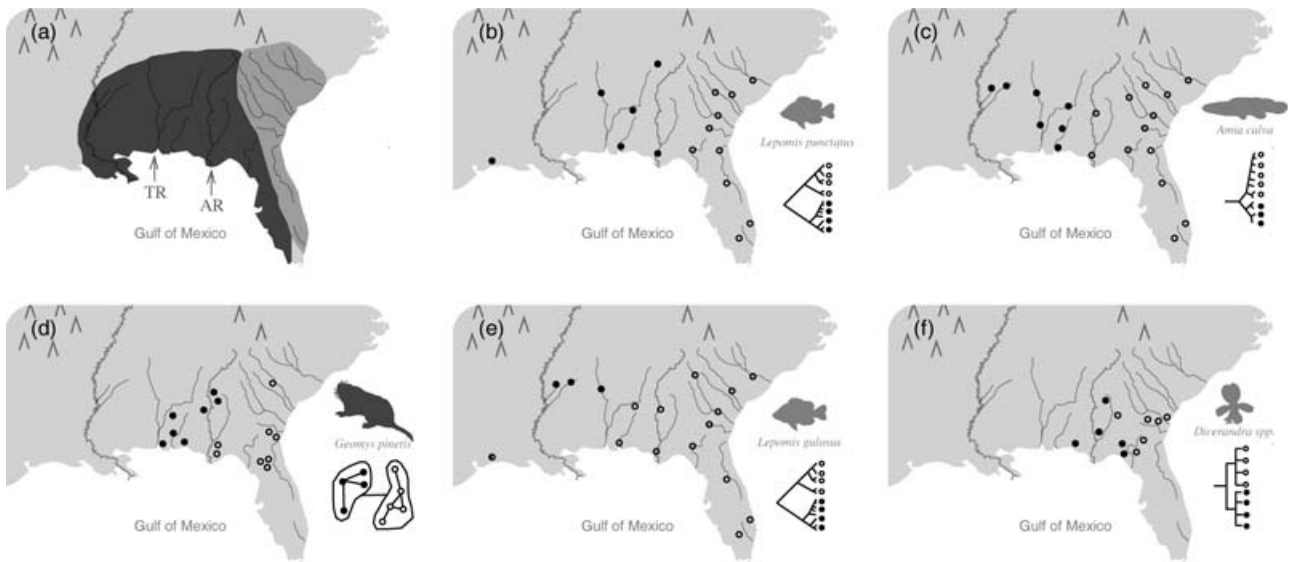


Fig. 2 The Apalachicola River (a, b, c, d, f) and Tombigbee River (e) discontinuities. (a) General patterns of molecular divergence; dark and light shading indicates distinction between rivers that flow into the Atlantic Ocean (light grey) vs. the Gulf of Mexico (dark grey); AR, Apalachicola River; TR, Tombigbee River. (b) The spotted sunfish, *Lepomis punctatus* (redrawn from Birmingham & Avise 1986). (c) The bowfin, *Amia calva* (redrawn from Birmingham & Avise 1986). (d) The pocket gopher, *Geomys pinetis* (redrawn from Avise *et al.* 1979). (e) The warmouth sunfish, *Lepomis punctatus* (redrawn from Birmingham & Avise 1986). (f) The coastal plain balm, *Dicerandra* (redrawn from Oliveira *et al.* in press).



Fig. 3 The Appalachian Mountain discontinuity. A number of plants and animals exhibit a phylogeographical break east vs. west of the Appalachian Mountains; the Apalachicola/Chattahoochee River drainage is indicated by the black arrow. (a) Hypothesized patterns of refugial migrations (other patterns have been proposed); (b) the spotted salamander, *Ambystoma maculatum* (redrawn from Church *et al.* 2003); (c) Atlantic white cedar, *Chamaecyparis thuyoides* (redrawn from Mylecraine *et al.* 2004).

species from this region with no genetic structure (Avise 2000). Subsequent analyses, however, did reveal significant mtDNA, as well as otolith chemical, differentiation between populations from the Atlantic and Gulf Coasts (Gold *et al.* 1999; Patterson *et al.* 2004) (Table 2). Thus, even in those cases when initial or early studies have not revealed genetic structure, subsequent studies with other markers may reveal phylogeographical structuring.

The break point between Atlantic and Gulf haplotypes is in very different locations depending on the organism (compare Fig. 1b, c). For some species, haplotypes come

into contact at the southern tip of Florida, whereas for others, the division occurs along the east coast of Florida, to as far north as Jacksonville (Avise 2000). Adding to the complexity, the bryozoan *Bugula neritina* exhibits an approximate break between 'Atlantic' and 'Gulf' clades in North Carolina (McGovern & Hellberg 2003). Avise (2000) suggested that the Gulf Stream may promote 'leakage' of Gulf haplotypes into the Atlantic Coast of Florida, but questions remain: Are the causal factors the same in these various cases? Is this one pattern or multiple, similar patterns (see pseudocongruence)?

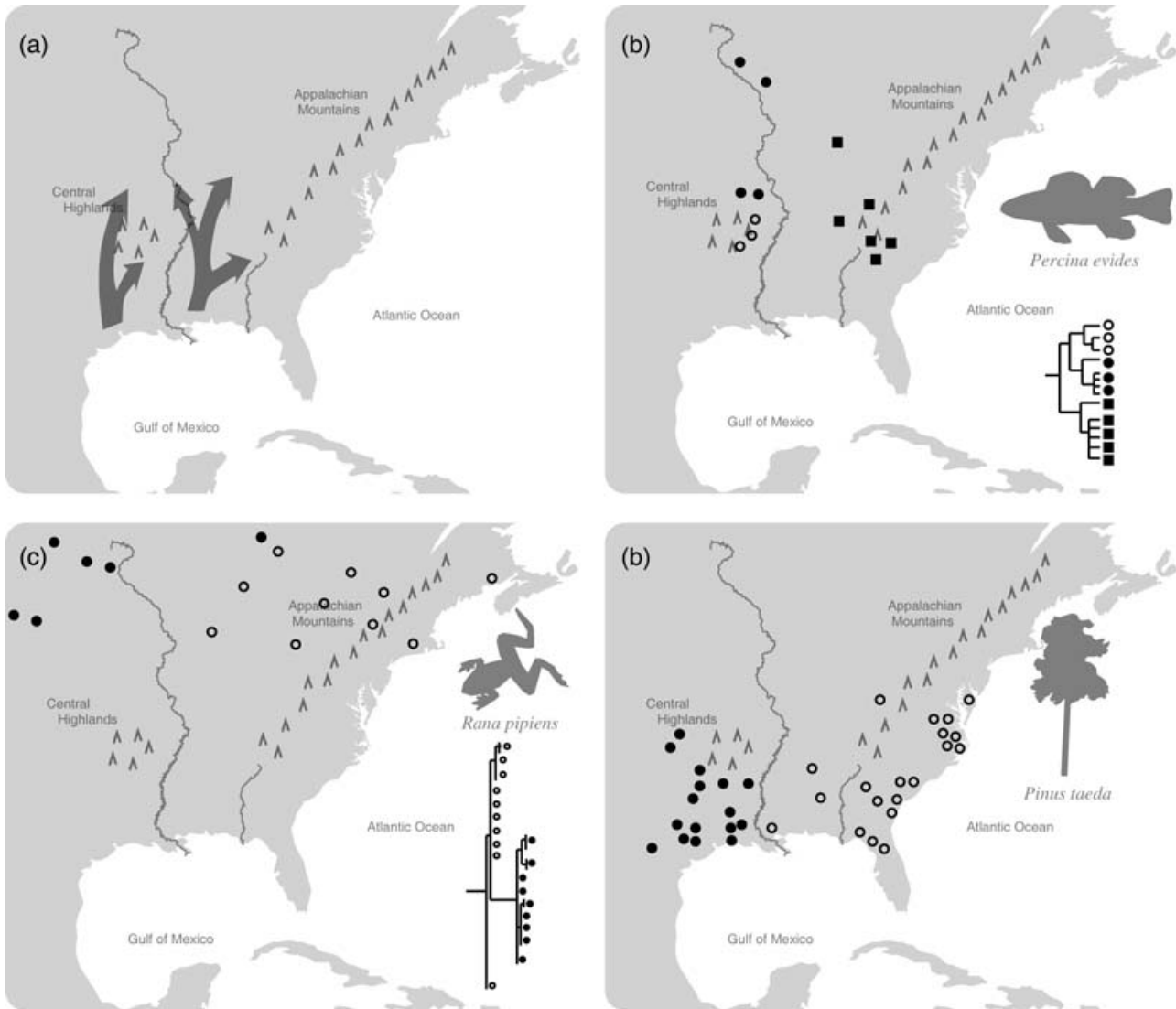


Fig. 4 The Mississippi River discontinuity. This pattern has been documented in both plants and animals. Major clades are separated by the Mississippi River. (a) Hypothesized patterns of refugial migrations (other patterns have been proposed); (b) the gilt darter, *Percina evides* (redrawn from Near *et al.* 2001). (c) The northern leopard frog, *Rana pipiens* (redrawn from Hoffman & Blouin 2004), showing a distribution north of the Pleistocene glacial boundary; (d) loblolly pine, *Pinus taeda* (redrawn from Al-Rabab'ah & Williams 2002).

Causal factors underlying the Atlantic vs. Gulf Coast pattern were proposed by Wise *et al.* (2004): 'the combination of subtropical climate, carbonate sediments, mangrove-dominated ecosystems, and adverse currents encountered along the eastern Florida coast seems to have blocked migration between the Atlantic Ocean and the Gulf of Mexico entirely' (p. 1167). Because most of these mechanisms are specific to marine systems, we would not expect this pattern to be common in terrestrial animals or plants. However, some coastally distributed animals (e.g. the dusky seaside sparrow, *Avise & Nelson 1989*) do exhibit this pattern. Additional coastally distributed animals and plants should be investigated.

Terrestrial and riverine discontinuities in the southeastern USA

In the southeastern USA, several topographic features may have resulted in genetic discontinuities in both terrestrial and freshwater species. The first described terrestrial discontinuity from the southeast was the Atlantic vs. Gulf drainage pattern (*Avise 2000, 2004*); it is also commonly referred to as 'east vs. west of the Apalachicola River', which empties into the Gulf of Mexico after it transects the panhandle of Florida. A variant on this general east-west theme is a genetic discontinuity in several animals that coincides with the Tombigbee River in Alabama (*Fig. 2c*).

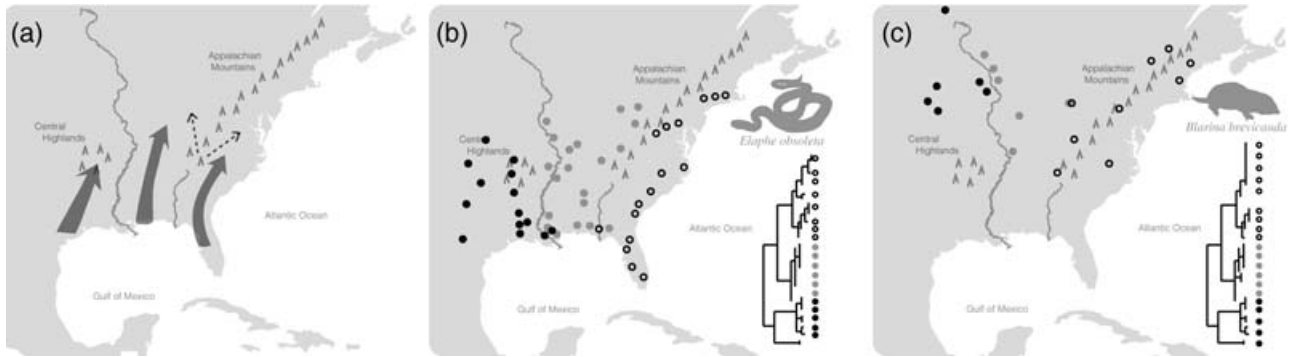


Fig. 5 The Mississippi River and Apalachicola River discontinuities. This pattern has only documented in animals so far and is inferred to reflect multiple Gulf Coast refugia. (a) Hypothesized patterns of refugial migrations (other patterns have been proposed, as indicated by dotted lines); (b) the black rat snake, *Elaphe obsolete* (redrawn from Burbrink *et al.* 2000); (c) the short-tailed shrew, *Blarina brevicauda* (redrawn from Brant & Ortí 2003).



Fig. 6 Northern refugia. Recent studies identify postglacial spread from refugia farther north than previously assumed. (a) Some of the documented migration patterns; (b) In American beech, *Fagus grandifolia*, most cpDNA haplotypes in formerly glaciated terrain derive from populations just south of the former ice margin. Haplotype diversity is higher at the northern range limit of this species than in its southern range. (c) Populations of red maple, *Acer rubrum*, occurring north of the glacial limit generally descended from populations in the Southern Appalachians, north of the Coastal Plain.

There appear to be diverse, overlapping phylogeographical patterns in the southeastern USA, and it may be inappropriate to consider all of these east–west patterns to be the result of the same causal factors. By lumping all organisms into the same pattern (e.g. east vs. west of the Apalachicola), we may be obscuring patterns of phylogeographical diversity (see pseudocongruence). To facilitate future investigation we are therefore making an effort to distinguish among the Apalachicola River discontinuity, the Tombigbee River discontinuity, and the Appalachian Mountains discontinuity.

The Apalachicola River Basin discontinuity. A number of fish and turtle species exhibit phylogeographically structured haplotypes that adhere to Atlantic vs. Gulf drainages to varying degrees (Fig. 2) (Table 2; Walker & Avise 1998; Avise 2000, 2004). The Atlantic sturgeon (*Acipenser oxyrinchus*) (Wirgin *et al.* 2002) exhibits a genetic continuity that exactly coincides with Atlantic vs. Gulf drainages. However, the Atlantic–Gulf haplotype division is not clean; in most

aquatic organisms, samples from one or more Gulf drainages possess the Atlantic, rather than Gulf, haplotype (Fig. 2b, c, d). For example, *Lepomis punctatus* corresponds closely to a Gulf–Atlantic drainage pattern, but samples from the Suwannee River, which drains into the Gulf of Mexico, have the Atlantic haplotype (Fig. 2b). *Amia calva* (bowfin) is similarly considered to have the Atlantic–Gulf drainage pattern, but two Gulf Coast populations have the Atlantic haplotype (Fig. 2c). Thus, in many organisms the Apalachicola River serves as the primary geographical marker of the break (Fig. 2). Recent studies have revealed additional cases of this east–west pattern (there are ~20 examples, Table 2), including the American alligator (*Alligator mississippiensis*) (Davis *et al.* 2002).

A pattern similar to that above for aquatic organisms also occurs in terrestrial animals not confined to river drainages. In fact, the general pattern of differentiation east and west of the Apalachicola was first seen in one of the first organisms to be investigated for what would later be

termed 'phylogeographical pattern', the pocket gopher (*Geomys pinetis*; Fig. 2d) (Avice *et al.* 1979). Surprisingly, some highly mobile animals, including the white-tail deer (*Odocoileus virginianus*), also display this general pattern (Table 2) (Ellsworth *et al.* 1994). Similar patterns are also seen in some plants, including the coastal plain balm (*Dicerandra linearifolia* complex) (Oliveira *et al.* in press) (Fig. 2f) and sand pine (*Pinus clausa*) (Parker *et al.* 1997). Other possible plant examples include the pitted stripe-seed (*Piriqueta caroliniana*) (Maskas & Cruzan 2000) and species of the mint genus *Conradina* (Edwards *et al.*, unpublished).

Additional support for the importance of this general east–west pattern emerged from an analysis of contact zones, hybrid zones, and phylogeographical breaks. Swenson & Howard (2005) detected the co-occurrence of many contact zones in Alabama, which they interpreted to be the result of contact between closely related species or populations emerging from refugia located in Florida and eastern Texas/western Louisiana.

This east vs. west pattern has been attributed to an insular history of Florida related to fluctuating sea level throughout the Pliocene and Pleistocene (Scott & Upchurch 1982; Riggs 1983; Hayes & Harrison 1992; Ellsworth *et al.* 1994), which suggests repeated fragmentation and isolation of populations from this region. Botanical endemism around Apalachicola has long been considered evidence of a climatically determined glacial refugium (Harper 1911). Delcourt & Delcourt (reviewed in 1984) posited stable refugia for mesic temperate species on isolated bluffs associated with alluvial valleys along the Gulf Coast. However, it is possible that members of relictual forests were present in that same area as early as the Miocene and are not the result of Pleistocene retreat (Platt & Schwartz 1990).

However, the causal factors for fish having this pattern may be different from those for terrestrial organisms. Fish and other primarily aquatic organisms, such as freshwater turtles, are likely to show phylogeographical breaks along this boundary due to the physical isolation of drainages, which would probably not function as barriers to gene flow in most terrestrial plants and more mobile terrestrial animals. The major genetic break east and west of the Apalachicola seen in many aquatic organisms may trace to the Pliocene interglacial (Bermingham & Avice 1986) when many southeastern drainages were well isolated. It is also difficult to use the same causal argument to explain the Apalachicola discontinuity in marine species such as the arrow squid (*Loligo plei*) (Table 2).

The Tombigbee River discontinuity. In several organisms, a phylogeographical split corresponds closely with the Tombigbee River in Alabama, rather than with the Apalachicola River in Florida. Examples include a sunfish (*Lepomis gulosus*) (Fig. 2e) (Bermingham & Avice 1986), water

snakes (*Nerodia rhombifera* and *Nerodia taxispilota*) (Lawson 1987), and the Carolina chickadee (*Parus carolinensis*) (Gill *et al.* 1993) (Table 2). This genetic discontinuity has been attributed to the same Pliocene vicariance event referred to above for aquatic organisms exhibiting the Apalachicola discontinuity. Bermingham & Avice (1986) suggest that not all haplotype boundaries are concordant in fish species from this region either because of differential dispersal after the separation event and/or different locations of refugia. But has the same underlying causal factor promoted a similar genetic discontinuity in a bird, the Carolina chickadee (Gill *et al.* 1993)? Gill *et al.* (1993) estimated the divergence event between the east and west chickadees to be about 1 million years, which would agree with the general timeframe suggested for fish having this same pattern. Although typically considered within the general Apalachicola River discontinuity, the Tombigbee River discontinuity may be distinct, with separate causes, and requires additional study.

The Appalachian Mountain discontinuity. For many of the species considered to exhibit an Apalachicola discontinuity, it seems more appropriate to refer to the pattern as east vs. west of the Appalachians (Fig. 3). However, there is not always a clear distinction between east–west of the Appalachians and east–west of the Apalachicola; there are intergradations between the two (e.g. Fig 3c). Animal examples of the Appalachian Mountain discontinuity include salamanders (*Ambystoma tigrinum tigrinum*, Church *et al.* 2003; Fig. 3b; *Ambystoma maculatum*, Donovan *et al.* 2000; Zamudio & Savage 2003) and turtles [e.g. *Sternotherus odouratus*, *S. minor*, *Trachemys scripta* (Walker & Avice 1998); Table 2].

Several plant species also exhibit an Appalachian Mountain discontinuity, including Atlantic white cedar (*Chamaecyparis thyoides*) (Mylecraine *et al.* 2004) (Fig. 3c), yellow poplar or tulip tree (*Liriodendron tulipifera*) (Parks *et al.* 1994; Sewell *et al.* 1996), and the groundnut (*Apios americana*) (Joly & Bruneau 2004). Other possible examples include pitcher plant (*Sarracenia purpurea* species complex) and Virginia pine (*Pinus virginiana*) (Table 2).

This pattern may be the result of different (or partially overlapping) causal factors compared to those responsible for the Apalachicola discontinuity — this topic certainly merits more investigation. This general pattern is typically attributed to survival in two distinct refugia on opposite sides of the Appalachians. For example, in the tiger salamander (*A. t. tigrinum*), survival in refugia east and west of Apalachicola is proposed (Church *et al.* 2003). The distribution of triploid clones in the angiosperm *A. americana* indicate long-term isolation and that colonization after glacial retreat employed separate migration routes on each side of the Appalachian Mountains (Joly & Bruneau 2004). Refugial areas for this pattern remain hypothetical. Eastern

haplotypes of plants and animals may have persisted in the Ocala Highlands region of peninsular Florida, which existed as an island separated from the mainland during the Pliocene (Stanley 1986).

Mississippi River discontinuity

Lowland forests along the Mississippi River currently create a major biogeographical break between areas east and west of the river (Braun 1950). Hence, it is perhaps not surprising that a number of animal taxa exhibit distinct clades of haplotypes on either side of the river. In some cases, there is a discontinuity between populations east and west of the Mississippi with no significant substructuring within these subclades; the data suggest two refugia, one on each side of the Mississippi River (Fig. 4).

The North American bullfrog (*Rana catesbiana*) and the northern leopard frog (*Rana pipiens*) (Fig. 4b) exhibit the Mississippi River discontinuity with no additional substructuring (Austin *et al.* 2004; Hoffman & Blouin 2004). In *R. catesbiana*, southern refugia are suggested (Gulf Coast and southeastern USA; Austin *et al.* 2004). However, for *R. pipiens*, the Mississippi River discontinuity is north of the Pleistocene glacial boundary (Hoffman & Blouin 2004) (Fig. 4c). Other taxa similarly exhibit clades structured east vs. west of the Mississippi River, but are distributed well north of glacial boundaries (Brown *et al.* 1996; Wilson & Herbert 1996; Runck & Cook 2005). The data suggest more northern refugia for some taxa, with subsequent migration resulting in a distribution north of proposed Pleistocene refugia (Fig. 4c).

Genetically well-differentiated eastern and western clades separated by the Mississippi River are also found in a number of fish species, including the darter *Percina evides* (Fig. 4b) (Near *et al.* 2001) and northern hogsucker (*Hypentelium nigricans*) (Berendzen *et al.* 2003). However, these fish appear to be examples of pseudocongruence with similar patterns resulting from different causal factors at different times (see below).

Genetic differentiation between populations east and west of the Mississippi has also been reported in some plants, such as loblolly pine (*Pinus taeda*) (Fig. 4d), which may have had separate Pleistocene refugia east and west of the Mississippi River (Al-Rabab'ah & Williams 2002). Chloroplast DNA variation in black walnut (*Juglans nigra*) shows a similar phylogeographical split corresponding to the Mississippi River Valley (McLachlan *et al.*, unpublished).

Mississippi River and Apalachicola River discontinuities

Several animal species, but no plants, exhibit eastern and western clades that are separated by the Mississippi River, but with substructuring in the east that suggests three refugia (Fig. 5). One of the best examples is the rat snake, *Elaphe obsoleta* (Burbrink *et al.* 2000) (Fig. 5b). 'Eastern' and

'central' haplotype clades are sister groups and are distributed east of the Mississippi. The eastern haplotype occurs in peninsular Florida, east of the Apalachicola River, northward along the Atlantic Coast into Connecticut and Rhode Island. The central haplotype occurs west of Apalachicola and the Appalachian Mountains and east of the Mississippi. The 'western' haplotype of *E. obsoleta* is distributed west of the Mississippi River. This mtDNA pattern was attributed to isolation during Pleistocene glaciation and suggests three glacial refugia: one in peninsular Florida, a second near the Apalachicola River, and a third in southern Texas or adjacent Mexico (Fig. 5a). A strikingly similar pattern is also seen in the eastern fence lizard, *Sceloporus undulatus* (Leache & Reeder 2002), and was initially proposed for the spring peeper, *Pseudacris crucifer* (Austin *et al.* 2002). Each species is thought to have recolonized from multiple Gulf Coast refugia, with patterns of recolonization similar to those suggested for the rat snake (compare Fig. 6 of Austin *et al.* 2002 with Fig. 5 of Burbrink *et al.* 2000). However, more recent work on *Pseudacris crucifer* (Austin *et al.* 2004) suggests a more complex pattern for this species; it contains numerous divergent lineages, including one west of the Mississippi and multiple eastern lineages that appear to have expanded from several southern Appalachian refugia.

The northern short-tail shrew, *Blarina brevicauda* (Fig. 5c), shows a similar pattern. It exhibits distinct eastern and western clades separated by the Mississippi River, and shows additional structure within the eastern clade that suggests multiple eastern refugia. Brant & Ortí (2003) proposed three glacial refugia, one west of the Mississippi and two refugia in the southern Appalachians (see 'other patterns' below). However, it is unclear as to locations of the two eastern refugia; they may have been north of the refugia proposed for the rat snake (Fig. 5c; see dotted lines).

Other patterns and evolutionary processes

Many studies seeking the location of long-term refugia for temperate species focus along the Gulf Coast, but increasing evidence suggests that some temperate species survived glacial cooling farther north (Fig. 6). Our interpretation of the physiographic history of unglaciated eastern North America has been informed greatly by the record of fossilized pollen. Tree species leave a continuous record of their presence in sedimentary pollen assemblages, a distinct advantage over most other taxa for understanding past population fluctuations. However, reconstructions of historical range dynamics (e.g. Davis 1981; Delcourt & Delcourt 1981) are hampered by the fact that pollen is a poor sensor of small populations (McLachlan & Clark 2004). The most recent review of eastern tree distributions at the last glacial maximum (21 500 calendar years BP) concludes that the occurrence of most temperate hardwoods

is difficult to document using the fossil record, except for the Lower Mississippi Valley sites (Jackson *et al.* 2000).

Although we cannot accurately identify the distribution of late-glacial tree populations with existing fossil data, the low pollen abundance of many temperate (Fig. 6) species throughout the continent suggests that whatever populations existed were small or of low density. Small populations often produce the genetic bottlenecks that contribute to phylogeographical structure, but only if they are persistent. Rowe *et al.* (2004) used mtDNA variation to show that eastern chipmunks (*Tamias striatus*) survived glaciation close to the Laurentide Ice Sheet. The eastern chipmunk is associated with deciduous forests, and recent cpDNA surveys from temperate deciduous species also suggest that these species persisted near the ice during glacial times (McLachlan *et al.* 2005).

Chloroplast DNA sequence data for red maple (*Acer rubrum*) support, to some degree, its possible persistence in refugial areas as revealed for other diverse taxa (McLachlan *et al.* 2005). For example, Florida red maples have a separate history from other populations, and distinctive populations in Arkansas may have survived in another glacial refugium, in agreement with earlier suggestions (e.g. Davis 1981; Delcourt & Delcourt 1987). Refugia in Florida and the Ozarks have been suggested for other plant and animal species. However, these haplotypes apparently made only a small contribution to the subsequent migration of red maple into northern, once-glaciated regions. Chloroplast DNA sequence data suggest instead that red maple persisted during glaciation as low-density populations in close proximity (within 500 km) of the Laurentide Ice Sheet in the Appalachian Mountains or in interior refugia (Fig. 6b).

A similar pattern is suggested for American beech (*Fagus grandifolia*) (McLachlan *et al.* 2005). Beech haplotypes common in deglaciated territory are generally derived from populations immediately south of the former ice limit. In particular, the upper Midwest seems to have been colonized by populations west of the Appalachian Mountains and just south of the ice sheet. Along the Gulf Coast, a single widespread cpDNA haplotype dominates beech populations. Beech may have been present south of 35° North latitude during glacial periods, but it was not isolated in the sort of long-term refugia that result in strong phylogeographical structure in other species (Fig. 6c).

Many haplotypes in other temperate deciduous trees, such as sugar maple (*Acer saccharum*), shagbark hickory (*Carya ovata*), and yellow birch (*Betula allegheniensis*) are found exclusively in the northern parts of their ranges (McLachlan *et al.*, in preparation). Many species therefore apparently had populations farther north during glacial periods than has been previously assumed (Delcourt & Delcourt 1987; Davis 1989). These populations must have been small or diffuse, because none of these taxa is recorded abundantly in late glacial pollen assemblages.

Increasing evidence is emerging for one or more refugia in the southern Appalachians. Possible examples include the northern short-tail shrew (*B. brevicauda*) (Brant & Ortí 2003), the eastern tiger salamander (*Ambystoma tigrinum tigrinum*) (Church *et al.* 2003), and the spring peeper (*Pseudacris crucifer*) (Austin *et al.* 2004).

Genetic diversity in some eastern North American taxa has been shaped by hybridization. In some cases, divergent populations from separate refugia have hybridized (e.g. *Liriodendron*; Parks *et al.* 1994) or formed suture zones (Remington 1968; Swenson & Howard 2005). Hybridization may also have occurred within a single refugium. False rosemary (*Conradina*, Lamiaceae) consists of six largely allopatric species endemic to the southeastern USA. It is part of a clade of genera referred to as the southeast scrub mint clade (Edwards *et al.* 2006). Evidence from morphology and internal transcribed spacer (ITS) sequences strongly supports the monophyly of *Conradina* (Edwards *et al.* 2006). In contrast, cpDNA sequence data do not support a monophyletic *Conradina*, but instead similar cpDNA haplotypes are shared by species in different genera of the southeast scrub mint clade, including *Clinopodium*, *Stachydeoma*, and *Piloblephis* (Edwards *et al.* 2006). The cpDNA results could be explained by ancestral polymorphism, but they are also consistent with ancient intergeneric hybridization that may have occurred during the Pleistocene when these taxa were forced into close proximity in a single refugium such as peninsula Florida.

Spatial analysis

Panel A of Fig. 7 shows the distribution of phylogeographical breaks from a random selection of studies in Table 2. As expected, some of these breaks correspond to biogeographical barriers and others do not. However, no clear spatial pattern is apparent based on this analysis of only 10 species; our results agree with the hypothesis that phylogeographical structure in diverse temperate taxa is complex and was not shaped by only a few barriers (Table 1).

The orientation of phylogeographical breaks in this random sample of studies was not predominantly longitudinal. In reference to hypothesis II in Table 1, this finding suggests that, while longitudinally orientated barriers to dispersal may be important for some taxa, they do not explain the phylogeographical patterns of many others.

In Fig. 7(b), we see that the highest concentration of phylogeographical breaks does not coincide with any of the biogeographical barriers that seem to strongly affect individual taxa. In fact, the highest density of breaks occurs in the centre of the study area, away from hypothesized geographical boundaries, a pattern consistent with a random distribution of breaks across the study area. This does not necessarily imply that phylogeographical breaks in eastern

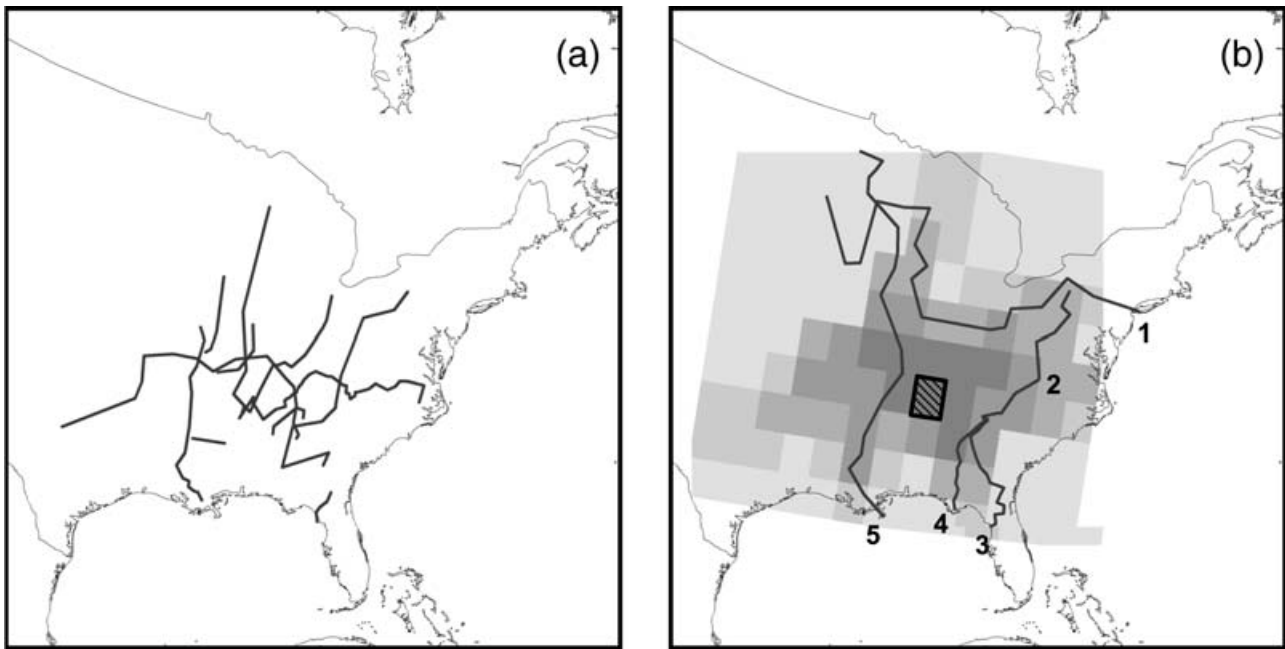


Fig. 7 Distribution of a selection of phylogeographical breaks in unglaciated eastern North America and results of analyses based on Monmonier's algorithm (1973; see text). (a) Proposed phylogeographical breaks of 10 species (randomly chosen from broadly distributed species) as reported in published papers (see text and Table 2). (b) Shaded grid is the density of breaks from panel A as measured using the 'Lines Density' tool in ArcMap; the single hatched gridcell had a density of breaks more extreme than expected under the null hypothesis that breaks were distributed at random across the study area. Lines are hypothesized biogeographical/physiographic boundaries: (1) Laurentide Ice Sheet; (2) Appalachian Mountains; (3) Gulf vs. Atlantic drainages; (4) Apalachicola River; (5) Mississippi River.

North American taxa were not influenced by physiographic factors; instead, responses were complex, with little overarching pattern.

A single grid cell in Fig. 7(b) (hatched) had a density of phylogeographical breaks more extreme than the 20 sets of randomly relocated breaks in our permutation test. Although the concentration of phylogeographical breaks in this area of central Tennessee is slightly higher than in any of the 20 data permutations, multiple testing issues stemming from the testing of all grid cells indicates that the density of breaks there is not significantly different from random at an $\alpha = 0.05$. We also note that this grid cell does not correspond to any of our proposed biogeographical barriers. Throughout the rest of the study area, the observed distribution of phylogeographical breaks is not different from what we would expect had they been randomly sprinkled across eastern North America.

Congruence vs. pseudocongruence

Are similar phylogeographical patterns for different organisms truly congruent? That is, do the modern patterns reflect the same underlying causal factors occurring at the same point in time, or did they arise via different processes at very different times? The latter phenomenon, now referred to as pseudocongruence (Cunningham & Collins

1994), was early recognized as a source of concern. Twenty years ago, Bermingham & Avise (1986) stated, 'can all of these genetic and distributional data be integrated into a reasonable set of zoogeographical hypotheses for the fish fauna of the southeastern USA? Uncertainty regarding both regional geology and the absolute rates of mtDNA divergence in fishes cautions against overzealous interpretation of the data.' Molecular clocks have been used to date phylogenetic splits for correlation with the known timing of major geological events. Although molecular dating is susceptible to many sources of error, we here accept the dates provided by the original papers for purposes of discussion, with the caveat that these dates may be incorrect due to biological and/or analytical factors.

Pseudocongruence has been shown to be important in other studies of biogeography and phylogeography. For example, a number of plants share similar disjunct distributions in eastern North America, western North America, and eastern Asia. Although long assumed to be the result of a common series of events, recent investigations, including the use of molecular data, indicate that different plant genera achieved these disjunct distributions at very different times (Xiang *et al.* 2000; Donoghue *et al.* 2001; Xiang & Soltis 2001; Donoghue & Moore 2003).

Phylogeographical studies focused on eastern North America often cite Pleistocene barriers to gene flow as the

primary driver for the observed patterns, but rarely is there external evidence to support this hypothesis. In fact, some geographical barriers (e.g. the Suwanee Straits) often attributed to the Pleistocene actually occurred much earlier, between the late Cretaceous and Middle Miocene (Randazzo 1997). Furthermore, eastern North America experienced numerous glacial cycles, each of which could have left its signal in modern populations. Progress in the field of phylogeography will require new focus on the temporal element (as emphasized by Donoghue & Moore 2003) by integrating fossils where possible and by applying new analytical approaches to test possible alternative hypotheses (see Carstens *et al.* 2005a, b).

For both the maritime Atlantic vs. Gulf discontinuity and the Apalachicola discontinuity, taxa exhibit very different degrees of mtDNA differentiation (reviewed in Avise 2000). For example, the fish and turtle species found east and west of the Apalachicola River differ considerably (sometimes by more than an order of magnitude) in the amount of mtDNA differentiation observed between the two clades. These differences could either reflect differences in rates of molecular evolution or different divergence times (i.e. pseudocongruence). For example, the Atlantic-Gulf clades in the scorched mussel exhibit a much higher level of mtDNA divergence (12.7%; Lee & Foighil 2004) than do the horseshoe crab (*L. polyphemus*; 2% divergence; Saunders *et al.* 1986) and the American oyster (*Crassostrea virginica*; 2.5% divergence; Reeb & Avise 1990). Using a lineage-specific or calibrated molecular clock approach for the mtDNA sequence data, Lee & Foighil (2004) estimated that the Atlantic-Gulf split for the scorched mussel (*Brachidontes exustus*) occurred during the Pliocene. This date is earlier than that estimated for the split (Pleistocene) in the other maritime taxa.

Even in those maritime taxa in which the pattern has been inferred to have arisen during the Pleistocene, pseudocongruence may have been involved (Avise 2000). There were several episodes of glacial advance and retreat during the Pleistocene, each impacting sea level and altering estuarine habitats. It is possible therefore that convergent phylogeographical patterns arose at different points in time during the Pleistocene. This issue is difficult to tease apart with current divergence time estimates, particularly given the narrow historical window and the error inherent in divergence time estimation.

The Mississippi River discontinuity may have been achieved at very different times and via different mechanisms. In the American bullfrog, this pattern is inferred to date to the mid- to early Pleistocene, suggesting isolation in Pleistocene glacial refugia east and west of the Mississippi (Austin *et al.* 2004). In contrast, although some fish species from the Central Highlands and eastern North America also have an mtDNA discontinuity east and west of the Mississippi, the underlying phylogeographical history is

complex and differs from that for the American bullfrog and other taxa. Phylogeographical studies of some fish with ranges that include the Central Highlands and eastern North America (Strange & Burr 1997; Near *et al.* 2001; Berendzen *et al.* 2003) suggest a genetic divergence that may be Miocene or Pliocene in origin. Recently, Near & Keck (2005) used fossil data and identified two distinct vicariance events for fish within the Central Highlands geographical region, resulting in pseudocongruent patterns. One event dates to between the mid-Miocene to the mid-Pliocene, while the second event dates to the Pleistocene. Thus, the mtDNA patterning in some fish existed prior to the onset of Pleistocene glaciation (as originally proposed by Mayden 1988). These fish are part of the Teays fauna (Wiley & Mayden 1985; Burr & Page 1993). The Teays River system flowed northward from West Virginia and Kentucky into central Ohio and from there into the Erie lowlands. In some fish species, well-differentiated eastern and western clades apparently were present during the existence of the Teays, prior to the establishment of the modern Mississippi River drainage pattern. Thus, whereas many of the animals and plants exhibiting a genetic discontinuity east and west of the Mississippi River may be the result of Pleistocene glaciation, in other groups (e.g. some fish) this discontinuity occurred much earlier (e.g. Pliocene).

Perhaps one aspect of pseudocongruence that is underappreciated is actually researcher-mediated. That is, as a direct result of the efforts of researchers to categorize patterns visually, patterns that are subtly distinct may be lumped together — similar patterns may, in fact, not fully coincide, and inferring agreement may obscure actual patterns and lead to erroneous conclusions. We offer several possible examples of this phenomenon that merit more attention. The pattern initially referred to as Gulf vs. Atlantic (or west vs. east) drainages in the southeastern USA may be the best example. This category includes organisms with discontinuities east–west of the Apalachicola River, east–west of the Tombigbee River, and east–west of the Appalachian Mountains. Another example may be provided by the maritime Atlantic vs. Gulf break. In some species, the break is clearly near the southern tip of Florida, whereas in other cases, the break occurs along the Atlantic Coast in mid- or northern Florida to as far north as North Carolina.

Applications of comparative regional phylogeography to issues in ecology

The forces affecting population abundance and distribution are dynamic at all spatial and temporal scales (Webb 2000). This review emphasizes the peculiar situations when persistent, isolated populations have strong subsequent influence on population structure across the range of a species. This happens when isolation, mutation, and drift

create distinctive genetic compositions in several populations, and descendents of these populations expand to fill more or less discrete geographical regions.

The distribution of terrestrial plants is largely determined by climate, which is why fossil pollen assemblages can be used to reconstruct past climate (Wright 1993). Historically, ecologists working in eastern North America have suggested that ice age climates would restrict the ranges of most mesic temperate species to isolated southern refugia (Deevey 1949; Braun 1950). Such a scenario would likely produce generally congruent phylogeographical patterns across a broad array of taxa, as apparently occurred in Europe and the Pacific Northwest of North America. Glacial climates in northern Europe were especially cold and dry, restricting temperate mammals, insects, and plants to isolated Mediterranean refugia in the Iberian Peninsula, Italy, and the Balkans. Subsequent postglacial population expansion across restricted mountain passes resulted in congruent phylogeographical structure among many diverse taxa (Hewitt 1999; Petit *et al.* 2002).

Several eastern North American plant taxa share phylogeographical patterns previously identified for terrestrial and aquatic animals along the Gulf Coast and illustrate the common biogeographical framework affecting all terrestrial organisms (such as the inundation of much of Florida during the Pliocene). However, glacial climates were extremely variable, and terrestrial organisms respond to climate individually (Huntley & Webb 1989). As phylogeographical studies continue to develop, we expect to see more examples that reveal still additional complexity and that do not fit exactly into any current pattern. For example, Walter & Epperson (2001) found patterns of genetic diversity in red pine (*Pinus resinosa*) suggesting that the centre of genetic diversity was north of the former ice sheet margin. The causal factors in red pine likely include multiple refugia, complex migration routes, and postglacial isolation and genetic drift among shrinking populations in the southern range of the species.

Debate about the effect of climate change on plant distributions has been strongly influenced by reconstructions of the ranges of eastern North American species after the last ice age. These reconstructions are largely based on the network of sediment cores containing fossil pollen and plant macrofossils. Phylogeographers are only beginning to augment this data set with studies of molecular variation. A robust inference from palaeoecological data is the observation that the geographical response of individual species to changing environments is idiosyncratic (Cushing 1965; Davis 1976; Webb 1988). Species such as American beech and eastern hemlock have similar distributions today, but palaeoecological data show that this is a recent phenomenon, emerging only in the mid-Holocene (Davis 1981). The impermanence of species associations is so ubiquitous in the fossil record that much of eastern North America was

at some time dominated by plant communities so different from modern assemblages that they are difficult for ecologists to describe (Jackson & Williams 2004).

On the other hand, palaeoecological reconstructions of eastern trees do suggest testable geographical hypotheses. Influential reconstructions of postglacial tree distributions from the 1980s suggest that many temperate species were restricted to southern latitudes during the last ice age and rapidly spread northward following glacial warming (Davis 1981; Delcourt & Delcourt 1987). Alternative scenarios for postglacial spread suggest that temperate species were present in low densities across much of the continent, even during the most severe glacial periods (Bennett 1985).

Resolving this debate with fossil data is difficult because palaeoecological data poorly identify the distributions of species when they are not abundant (McLachlan & Clark 2004). The controversy is important to resolve, however, because inferences about how plants accommodate glacial/interglacial cycles have implications for the conservation of species facing global warming: rapid range expansion implies an important role for the establishment and growth of peripheral populations and poses a challenge to landscape planners north of a species' current range (Pitelka *et al.* 1997). If southern ranges erode as the climate warms, genetic diversity harboured in former glacial refugia may be lost (Hampe & Petit 2005).

Phylogeographical data have the potential to help clarify how plant populations accommodated Quaternary climate swings. Phylogeographical studies of European taxa support palaeoecological evidence for isolated, genetically distinct southern refugia. Migrants from these genetically distinct populations mixed along common routes of expansion, creating 'melting pots' of high genetic diversity, which thin at more northern latitudes (Petit *et al.* 2003). North American species may have persisted at low densities farther north than inferred from pollen data, allowing higher levels of genetic diversity to reach northern range limits and obviating the need for rapid postglacial colonization (McLachlan *et al.* 2005).

Bringing hypothesis testing into comparative phylogeography

Although visual comparison of phylogenetic trees or phylogeographical networks of co-distributed species has been used to develop hypotheses of regional phylogeography (e.g. Soltis *et al.* 1997; Avise 2000; Petit *et al.* 2002), phylogeographical inference has been hampered by a lack of statistical rigor (Bermingham & Moritz 1998; Bossart & Powell 1998; Knowles & Maddison 2002). Similar patterns may not fully coincide, and inferring agreement may mask important dissimilarities and lead to erroneous conclusions — another form of 'pseudocongruence' beyond the case of identical patterns having arisen at different times. Many

factors may contribute to mistaken inferences of congruence among trees or networks. The underlying tree/network will likely have a degree of uncertainty associated with its nodes, but a strict visual comparison among trees/networks will not take this uncertainty into account. A lack of historical signal for one or more species may also lead to erroneous inferences of congruence; however, the absence of distinct differences is not evidence of congruence. Alternatively, a small portion of the tree/network may differ between species, but given large-scale congruence between the trees/networks, the differences may be considered minor and possibly unimportant when they, in fact, may be significant.

Apparent phylogeographical discontinuities can also arise in the absence of true geographical barriers to gene flow (Neigel & Avise 1993; Irwin 2002). Using simulation studies, Irwin (2002) showed that phylogeographical breaks can occur in continuously distributed species when dispersal distances and/or population size are low, as a consequence of uniparental organellar inheritance and isolation by distance. In fact, those markers most often used to demonstrate geographical barriers to gene flow (i.e. mtDNA and cpDNA) are precisely the same markers that are most prone 'to show evidence of barriers that never existed' (Irwin 2002). The lack of correspondence of genetic breaks with geographical barriers in at least some species of the eastern USA is therefore to be expected. Thus, the phylogeographies of some species will not match those of others simply because species-specific attributes of dispersal and population size may differ between the species.

Given the many sources of potential incongruence — including true incongruence — objective approaches for comparing trees or networks for co-distributed species are needed (e.g. Hickerson *et al.* 2006). However, such approaches have rarely been used in comparative phylogeography. Instead, visual comparisons have focused on the major phylogeographical patterns, discounting differences among trees as well as the fact that sampling artifacts may make it dangerous to draw inferences from visual inspection (Templeton 2004). As a result, there are no 'confidence levels' for phylogeographical patterns that have been described, whether in the Pacific Northwest of North America or in Europe. Although debate continues on how best to test phylogeographical hypotheses (Knowles & Maddison 2002; Templeton 2004), we suggest here, briefly, a number of methods that bring hypothesis testing, including the application of confidence intervals and likelihood ratio tests (e.g. Beerli & Felsenstein 1999; Bahlo & Griffiths 2000), among other approaches, into comparative phylogeography. For example, it would be possible to consider processes, such as movements in response to glacial advance and retreat, to model specific phylogeographical patterns. Then, using these patterns, simulated data sets could be derived to develop a distribution of trees, against

which the empirical trees for various species could be compared (see Brunfeldt *et al.* 2001). This approach therefore provides both a specific hypothesis test and a statistical framework for tree comparison. An alternative approach is to borrow methods from studies of cospeciation (e.g. Page 1993, 1994, 2003) to compare trees of different species either directly with each other or to compare trees of each species singly against an area cladogram that represents the hypothesized phylogeographical pattern. A third approach is to use Bayesian methods (e.g. Carstens *et al.* 2005a) to evaluate uncertainty in the patterns and incorporate this into the comparison. Finally, coalescent theory provides a statistical framework for testing a wide range of explicit historical models that do not assume genetic equilibrium (Hudson 1990; Griffiths & Tavare 1994; Bahlo & Griffiths 2000). For example, analyses of mtDNA using coalescent methods have demonstrated that some invertebrate taxa from rocky intertidal habitats of eastern North America recently colonized these areas from Europe, after local extinction from Pleistocene glaciation; in contrast, certain combinations of life-history traits allowed other invertebrate taxa to survive glaciation and recolonize these habitats (Wares & Cunningham 2001). This approach promises the possibility of inferring the evolutionary processes that generated phylogeographical patterns.

Unfortunately, devising methods for statistical comparisons is much easier than implementing them, especially on a regional scale. For example, using data compiled from published papers is not feasible for many reasons, unless the actual data sets are available, for example from TREEBASE, to estimate parameter values for models for simulating data. Although the cospeciation method would not require the original data, this method requires more areas or terminals than are typically present in phylogeographical studies (e.g. two in the Pacific Northwest, three in Europe, typically three in the southeastern USA) to have sufficient power to reject alternative hypotheses. Finally, published papers have not used the same methods; some are based on restriction sites, others on DNA sequences, and still others on microsatellite variation.

Conclusions and future prospects

A diverse array of animal species from unglaciated eastern North America has been the subject of molecular phylogeographical study. The past 5 years have seen a series of phylogeographical analyses of plants from this same general region, although plant studies are still far less numerous than those of animals. Unglaciated eastern North America is a large, geologically and topographically complex area, with the plants and animals examined having similar, yet diverse, distributions: some taxa are broadly distributed, whereas others are restricted in distribution (e.g. the southeastern USA). Thus, it should be expected that phylogeographical

generalizations would be difficult and that numerous patterns would be evident (Table 1, hypothesis I; see Table 2). Nonetheless, some recurrent patterns emerge (Table 1, hypothesis II), including: (i) maritime – Atlantic vs. Gulf Coast; (ii) Apalachicola River discontinuity; (iii) Tombigbee River discontinuity; (iv) Appalachian Mountain discontinuity; (v) Mississippi River discontinuity; and (vi) discontinuities associated with both the Mississippi and Apalachicola Rivers. Although these patterns were initially documented in molecular analyses of animals, most of these patterns are also apparent in plants (Table 1, hypothesis III). Hence, regional phylogeographical patterns are apparent in eastern North America, and many of these patterns are attributable to isolation and differentiation during Pleistocene glaciation (Table 1, hypothesis IV).

However, even taxa having generally congruent patterns and similar phylogeographical histories may show important differences. In some taxa, the Mississippi River has acted as an important barrier, but it has not been a continuous barrier in others (e.g. *Ambystoma maculata*). Similarly, the Appalachian Mountains have been an important barrier in many animals and plants, but not all (e.g. the northern short-tail shrew, *Blarina*; Brant & Ortí 2003).

As important as the generalizations are, other patterns are also clear. For example, similar phylogeographical patterns can result from different underlying causal factors at different times. In some fish, a pronounced east–west discontinuity associated with the Mississippi River occurred well before the Pleistocene and hence is older than that observed in other animals and plants. Similarly, the maritime Atlantic–Gulf discontinuity may have occurred in different lineages at different times. Molecular studies of animals as well as plants suggest patterns that often agree with longstanding hypotheses of glacial refugia (see also Swenson & Howard 2005). In addition, recent data also suggest other possible refugial areas (Table 1, hypothesis IV), most notably in the Appalachian Mountains. Importantly, both plants and animals may have also survived during Pleistocene glaciation in close proximity to the Laurentide Ice Sheet. Proposed refugial areas should be considered with caution; these are hypotheses requiring still additional examination.

A general concordance among phylogeographical patterns in taxa from eastern North America appears to be related to longitude (e.g. Austin *et al.* 2004), but the overriding message appears to be one of complexity. Although generalizations can be made and congruence is observed, every organism represents a new case study.

Finally, based on the current phylogeographical literature for unglaciated eastern North America, general patterns can be compared, but the data cannot be analysed in comparable ways, making rigorous hypothesis testing impossible. We therefore encourage future phylogeographical studies to use DNA sequence data, when possible, and to

deposit the data and trees in public databases, thus facilitating the next generation of phylogeographical meta-analyses of this region.

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