

# Phylogeography and biogeography of the lower Central American Neotropics: diversification between two continents and between two seas

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## ABSTRACT

Lower Central America (LCA) provides a geologically complex and dynamic, richly biodiverse model for studying the recent assembly and diversification of a Neotropical biota. Here, we review the growing literature of LCA phylogeography studies and their contribution to understanding the origins, assembly, and diversification of the LCA biota against the backdrop of regional geologic and climatic history, and previous biogeographical inquiry. Studies to date reveal that phylogeographical signal within taxa of differing distributions reflects a diversity of patterns and processes rivalling the complexities of LCA landscapes themselves. Even so, phylogeography is providing novel insights into regional diversification (e.g. cryptic lineage divergences), and general evolutionary patterns are emerging. Congruent multi-taxon phylogeographic breaks are found across the Nicaraguan depression, Chorotega volcanic front, western and central Panama, and the Darién isthmus, indicating that a potentially shared history of responses to regional-scale (e.g. geological) processes has shaped the genetic diversity of LCA communities. By contrast, other species show unique demographic histories in response to overriding historical events, including no phylogeographic structure at all. These low-structure or incongruent patterns provide some evidence for a role of local, ecological factors (e.g. long-distance dispersal and gene flow in plants and bats) in shaping LCA communities. Temporally, comparative phylogeographical structuring reflects Pliocene–Pleistocene dispersal and vicariance events consistent with the timeline of emergence of the LCA isthmus and its major physiographic features, e.g. cordilleras. We emphasise the need to improve biogeographic inferences in LCA through in-depth comparative phylogeography projects capitalising on the latest statistical phylogeographical methods. While meeting the challenges of reconstructing the biogeographical history of this complex region, phylogeographers should also take up the critical service to society of applying their work to the conservation of its fascinating biodiversity.

**Key words:** Central American Isthmus, conservation, Costa Rica, environmental change, geology, historical biogeography, Panama, palaeogeography, phylogeography.

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## I. INTRODUCTION

Large-scale geographical patterns of biodiversity (e.g. hotspots, coldspots, and latitudinal gradients in species richness) are increasingly well documented (Gaston, 2000; Myers *et al.*, 2000). However, understanding the mechanisms underlying global patterns of species richness and community composition remains one of the great challenges of ecology and biogeography (Gaston, 2000; Wiens & Donoghue, 2004; Lomolino *et al.*, 2010). Correlations between ecological factors (e.g. Kreft & Jetz, 2007), and ecological-drift models (Hubbell, 2001), have been shown to predict species richness and abundance accurately. Admirably, the latter approach even links local, deterministic processes (e.g. ecological interactions) and regional, historical processes (*sensu* Ricklefs, 1987). Such models are inadequate, however, to infer the historical origins and assembly of species-rich biotas, or the relative contributions of local- *versus* regional-scale processes towards shaping their diversification (e.g. Pennington, Cronk & Richardson, 2004; Ricklefs, 2006; Simon *et al.*, 2009). Here, historical biogeography (Arbogast & Kenagy, 2001; Posadas, Crisci & Katinas, 2006) is essential because biogeographical processes of dispersal, speciation, and extinction alter regional species pools *and* local community diversity through time (Ricklefs, 1987, 2006; Ricklefs & Schluter, 1993; Schneider, Cunningham & Moritz, 1998; Moritz *et al.*, 2000; Smith & Bermingham, 2005). Unfortunately, elucidating mechanisms underpinning the assembly and diversification of continental biotas has remained elusive because past attempts were limited to distributional data, which are often problematic due to inadequate taxonomic resolution, lack of fossil data, or historical range dynamics (e.g. Losos & Glor, 2003). Also, continental-scale insights into historical community fluctuations from molecular phylogeography have only recently become available for many areas (Bermingham & Avise, 1986; Bermingham & Martin, 1998; Avise, 2000; Beheregaray, 2008). Thus our understanding of the histories by which most biotas assembled and diversified remains limited.

Phylogeography is among the most integrative and fastest growing fields in biology today and is critical to understanding evolutionary diversification (e.g. Riddle *et al.*, 2008; Knowles, 2009; Hickerson *et al.*, 2010). Through illuminating geographical histories of genetic lineages within and among species, phylogeography provides tremendous insight into processes of lineage divergence (speciation) and spread and, therefore, historical biogeographical scenarios (Avise *et al.*, 1987; Avise, 2000; Kidd & Ritchie, 2006). Phylogeography offers an array of methods that, constantly debated and refined (e.g. Bloomquist, Lemey & Suchard, 2010), present exciting alternatives to traditional distribution-based biogeographical analyses. Phylogeography has proven very successful in historical biogeography due to its capacity for uncovering cryptic biodiversity, thus challenging traditional taxonomy (e.g. Avise, 2000; Riddle & Hafner, 2006); deciphering past movements and population dynamics of organisms (e.g. Hewitt, 2000); and integrating statistical frameworks and previously disjunct fields (e.g. Knowles & Maddison, 2002; Hickerson, Dolman & Moritz, 2006a; Hickerson, Stahl & Takebayashi, 2007; Kozak, Graham & Wiens, 2008).

Yet phylogeographic knowledge is markedly uneven with respect to geography. Of interest to the present review, while the Neotropical zone boasts seven of the world's 25 biodiversity hotspots (Mesoamerica, Caribbean, Chocó/Darién/western Ecuador, Tropical Andes, Brazil's Cerrado and Atlantic Forest, and Central Chile; Myers *et al.*, 2000), a recent worldwide survey of 2434 phylogeography publications found that Neotropical studies formed only ~3% (Central America) to 6.3% (South America) of studies (Beheregaray, 2008). Remarkably, this means that the top two areas of vertebrate species richness, endemism and threat—the Tropical Andes and Mesoamerica (Myers *et al.*, 2000)—are largely underrepresented. Such general lack of phylogeographical information on Neotropical biotas limits our ability to gauge biodiversity levels and infer processes of diversification including the relative contributions of local *versus* regional processes (Wiens & Donoghue, 2004; Ricklefs,

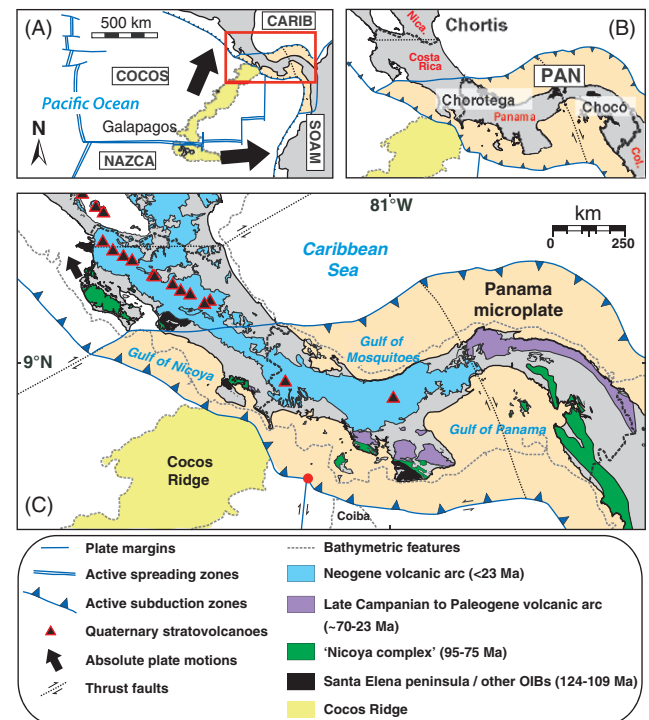
2006; Simon *et al.*, 2009). More phylogeographic studies are clearly needed to understand Neotropical diversification.

Despite phylogeography's crucial role in understanding mechanisms of diversification, it is difficult to determine whether intraspecific phylogeographies represent patterns broadly imprinted across regional biodiversity (Avice, 2000; Castoe *et al.*, 2009). By comparing phylogeographical patterns across multiple lineages codistributed in a region, 'comparative phylogeography' provides a means of testing whether such general evolutionary patterns exist (Bermingham & Avice, 1986; Bermingham & Martin, 1998; Bermingham & Moritz, 1998; Sullivan, Arellano & Rogers, 2000; Arbogast & Kenagy, 2001; Hickerson, Stahl & Lessios, 2006b; Hickerson *et al.*, 2007). Spatially and temporally congruent patterns across multiple, independent lineages indicate a shared history of responses to the same overriding events, e.g. vicariance due to geological processes (Rosen, 1978; Nelson & Platnick, 1981; Ronquist, 1997). Phylogeography also enables inference of the environmental histories of landscapes (e.g. habitats; Crawford, Bermingham & Polania, 2007; Wang, Crawford & Bermingham, 2008), as 'ecological niche conservatism' tends to hold over evolutionary timescales across taxa (Peterson, Soberón & Sánchez-Cordero, 1999; Wiens & Graham, 2005); this can provide additional information on histories of species within a biogeographical region, independent of geological processes. Phylogeography, especially comparative phylogeography, of Neotropical biotas will therefore be most illuminating when applied in geographically and geologically complex areas lacking historical consensus (Arbogast & Kenagy, 2001; Castoe *et al.*, 2009; Daza, Castoe & Parkinson, 2010).

One such area, the lower Central American (LCA) isthmus, presents an exceptional natural laboratory for studying the recent historical assembly and diversification of a Neotropical biota using comparative phylogeography (Fig. 1). Here, we review and critically evaluate LCA phylogeography studies against a backdrop of the geologic and climatic setting, and previous biogeography studies, to provide a framework for subsequent work. We close our review by emphasising the need to improve inferences through in-depth comparative phylogeography analyses using the latest statistical phylogeographical approaches. We also discuss ways that future research can apply phylogeography to jointly refine our understanding of LCA biodiversity and regional conservation.

## II. LOWER CENTRAL AMERICA

We define lower Central America ( $7^{\circ}11' - 11^{\circ}13'N$ ,  $77^{\circ}10' - 85^{\circ}57'W$ ) as the area spanning Costa Rica and Panama, plus nearby islands (e.g. Quepos, Bocas del Toro, Coiba, Las Perlas, Cocos). Part of the Caribbean plate (CARIB; Fig. 1A), LCA is underlain by Mesozoic oceanic basement formed by submarine volcanism > 80 million years ago (Ma; Mann, Rogers & Gahagan, 2007). LCA sits at the intersection of four tectonic plates, but it mostly



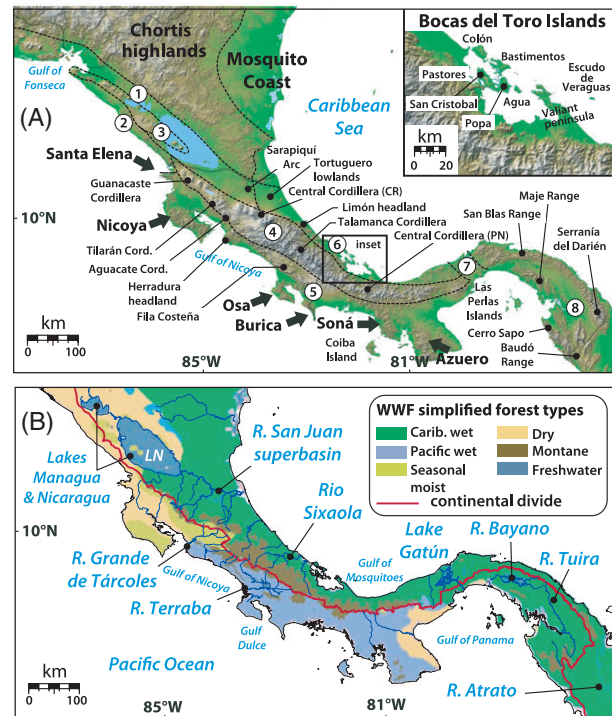
**Fig. 1.** Maps summarising the present-day tectonic setting and geology of lower Central America (LCA) and the Panama microplate (PAN; light orange shading). (A) Plate tectonic overview showing plate boundaries and absolute motions. Plate names are as follows: COCOS, Cocos; NAZCA, Nazca; CARIB, Caribbean; SOAM, South American. The Cocos plate and its prominent Cocos Ridge (yellow shading) subduct beneath CARIB, whereas NAZCA subducts beneath both CARIB and SOAM. Subaerial land is shaded grey. The red box delineates the study area, detailed in (B, C). (B) Basement blocks of the western Caribbean plate: Chortis, Chorotega, and Chocó. The Panama microplate comprises Chorotega (in part) and Chocó blocks. Country names are given in red (Col., Colombia; Nica., Nicaragua). The full extent of Chortis is shown in Fig. 4A. (C) Geological map of LCA showing major rock formations, quaternary stratovolcanoes of the Chorotega volcanic front (CVF), the Cocos–Nazca–Caribbean 'triple junction' (red dot), and major bathymetric features (fine-dotted grey lines) including the 200 m contour and Cocos and Coiba ridges (compiled after Coates & Obando, 1996; Carr *et al.*, 2007; Gazel *et al.*, 2008; Funk *et al.*, 2009; Buchs *et al.*, 2011).

forms the fault-bounded Panama microplate spanning the Chocó (in part) and Chorotega blocks (Fig. 1B). Along LCA's Pacific margin, the Cocos plate converges beneath CARIB at geological lightning speed ( $\sim 85$  mm/year), hindered by flat subduction of the aseismic Cocos Ridge (e.g. Funk *et al.*, 2009). Present-day active plate-boundary tectonics creates a high frequency of volcanic, earthquake, and mudslide hazards (Rose *et al.*, 2006; Sherrod *et al.*, 2007), which have likely contributed to localised population extinction and genetic isolation. LCA also carries risk of environmental damage from hurricanes (Atlantic), tsunamis (Pacific), and catastrophic flooding during wet season rains.



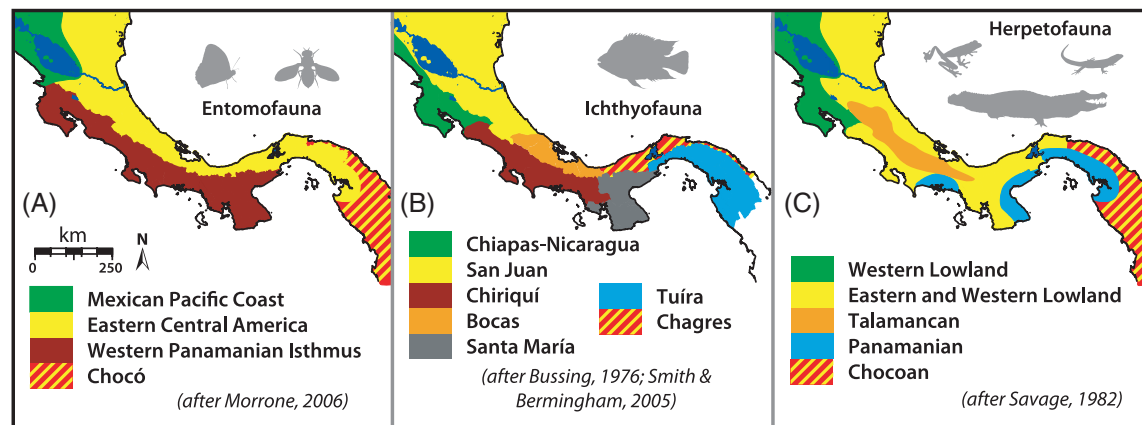
Despite covering only  $\sim 0.09\%$  ( $127050 \text{ km}^2$ ) of earth's land area, only slightly larger than the state of Mississippi, LCA is one of the most physically and biologically complex areas on the planet (Fig. 1). Mainland LCA forms a long ( $\sim 1170 \text{ km}$ ), narrow isthmus tapering from  $\sim 240 \text{ km}$  across Costa Rica to merely  $65 \text{ km}$  at the Panama Canal basin. Physiography is largely defined by NW-trending, volcanic cordilleras intermittently bisected by fertile valley complexes (4 in Fig. 2A). The Chorotega volcanic front provides the most obvious regional geographical barrier including LCA's highest peak  $3820 \text{ m}$  above present sea level (a.s.l.), Cerro Chirripó Grande (Talamanca Cordillera). This and other Talamanca peaks create sky-islands of isolated montane habitat. Mountains of the Fila Costeña (mean  $\sim 1200 \text{ m a.s.l.}$ ; Fig. 2A), 'Nicoya complex' ( $> 600\text{--}900 \text{ m}$ ; Fig. 1C), Limón headland, and Darién (e.g. Cerro Sapo,  $1145 \text{ m}$ ; Serranía del Darién,  $1875 \text{ m}$ ; Fig. 2A) also add notable relief. In the Darién, these produce basin-and-range (e.g. Chucunaque basin–San Blas) topography. Elevations drop below  $200 \text{ m}$  in central Panama and along coastlines, except where steep-faced mountain ranges rise close to the ocean, constricting coastal plains to narrow corridors restricting movement of lowland species at Herradura headland, Bocas del Toro, Gulf of Mosquitoes, Soná peninsula, and Cerro Sapo. While much of LCA ( $36\%$  land area) is tropical forest biome, it encompasses diverse vegetation zones from jungle-shrouded lowland wet and dry forests to mangrove estuaries, rolling savannas and grasslands, and once-pristine montane habitats (Fig. 2B; Marshall, 2007). Sharp climatic-vegetation transitions occur across headlands and the continental divide, which creates a Pacific-coastal rain-shadow effect. The resulting alternating pattern of wet forest, dry forest and savanna habitats along the Pacific versant has long been hypothesised to present climatic filter barriers limiting dispersal (e.g. Savage, 1966). Bocas del Toro, Perlas and Coiba islands are mostly forested and the closest islands ( $\sim 35 \text{ km}$  distance) of any real size to the LCA mainland. In comparison, Costa Rica's Cocos Island lies  $550 \text{ km}$  away. The hydrological network reveals many short incisive rivers; in NE Panama, essentially all rivers are  $< 15 \text{ km}$  long (Birmingham & Martin, 1998). Major watersheds, e.g. Tuira and Chagres rivers, are spaced throughout and two of the largest tropical lakes worldwide, Lakes Managua ( $1042 \text{ km}^2$ ) and Nicaragua ( $8624 \text{ km}^2$ ), connect to the Caribbean through the Rio San Juan superbasin (Fig. 2B).

Despite its small size, LCA has among the highest levels of biodiversity per  $\text{km}^2$  worldwide (Reid & Miller, 1989). Approximately  $4\text{--}10\%$  ( $\sim 500000$  species) of global biodiversity resides in Costa Rica alone, depending on the taxonomic group considered (Obando, 2002), and Panama may be more diverse. Beyond more than  $300000$  insect species, LCA harbours as many or more species of birds ( $> 970$  species) and vascular plants ( $> 19500$  species,  $6.3\text{--}14.5\%$  endemic) per  $10000 \text{ km}^2$  as anywhere worldwide (Hurlbert & Villalobos-Figueroa, 1982; Stotz *et al.*, 1996; Davis *et al.*, 1997; Obando, 2002; Mutke & Barthlott,



**Fig. 2.** Map of present-day physiography and vegetation cover of lower Central America (LCA). (A) Physiographic province boundaries (dashed lines) enclosing distinct LCA landform assemblages, drawn over digital elevation model derived from NASA SRTM image PIA03364 (after Marshall, 2007). Provinces: 1, Nicaraguan depression (ND); 2, Sandino fore arc; 3, Nicaraguan volcanic front (NVF); 4, Chorotega volcanic front (CVF); 5, Chorotega fore arc; 6, Chorotega back arc; 7, Panama Canal Zone (PCZ) lowlands; 8, Darién isthmus. Major peninsulas and headlands (arrows) and mountain ranges mentioned in the text are indicated. Names of major island chains are also given. The inset map describes the Bocas del Toro (BDT) archipelago and mainland. (B) World Wildlife Fund forest ecoregions (modified from Crawford *et al.*, 2007) and major freshwater drainages (LN, Lake Nicaragua) shown in reference to the continental divide (red line).

2005). Its freshwater fishes ( $\sim 170$  species,  $58\%$  endemic), reptiles and amphibians ( $\sim 830$  species,  $10\text{--}15\%$  endemic), and mammals ( $\sim 212$  species in Costa Rica alone,  $< 5\%$  endemic) are also highly species-rich or endemic (Savage, 1982, 2002; Obando, 2002; Smith & Birmingham, 2005; Abell *et al.*, 2008; Bolaños, Savage & Chaves, 2011; Fishbase, <http://www.fishbase.org/>). The Atlantic and Pacific coasts are often distinct biotic assemblages, e.g. for insects (Fig. 3A) and freshwater fishes (Fig. 3B). However, reptiles and amphibians are highly endemic in the Talamanca mountains (Fig. 3C) and herpetofauna, insect and plant areas of endemism overlap both central Panama coasts (Gentry, 1982; Savage, 1982; Morrone, 2006). These biodiversity patterns suggest that factors promoting *in situ* geographical isolation have played an important role in shaping LCA biotas. However, LCA's rich biodiversity is likely attributable to multiple factors including its position within tropical



**Fig. 3.** Examples of biogeographical province boundaries in lower Central America (LCA) representing areas of high species turnover, shown for (A) insects, (B) freshwater fishes and (C) herpetofauna. Provinces (colours) reflect areas of endemism with distinct biotic assemblages. Below each panel, a legend of the province names is provided. Province names are given from their original sources (referenced within each panel).

latitudes, its role as a transition zone between North and South American biotas, its varied physiography and geomorphology, and its rich geologic history (Whitmore & Prance, 1987; Jackson, Budd & Coates, 1996).

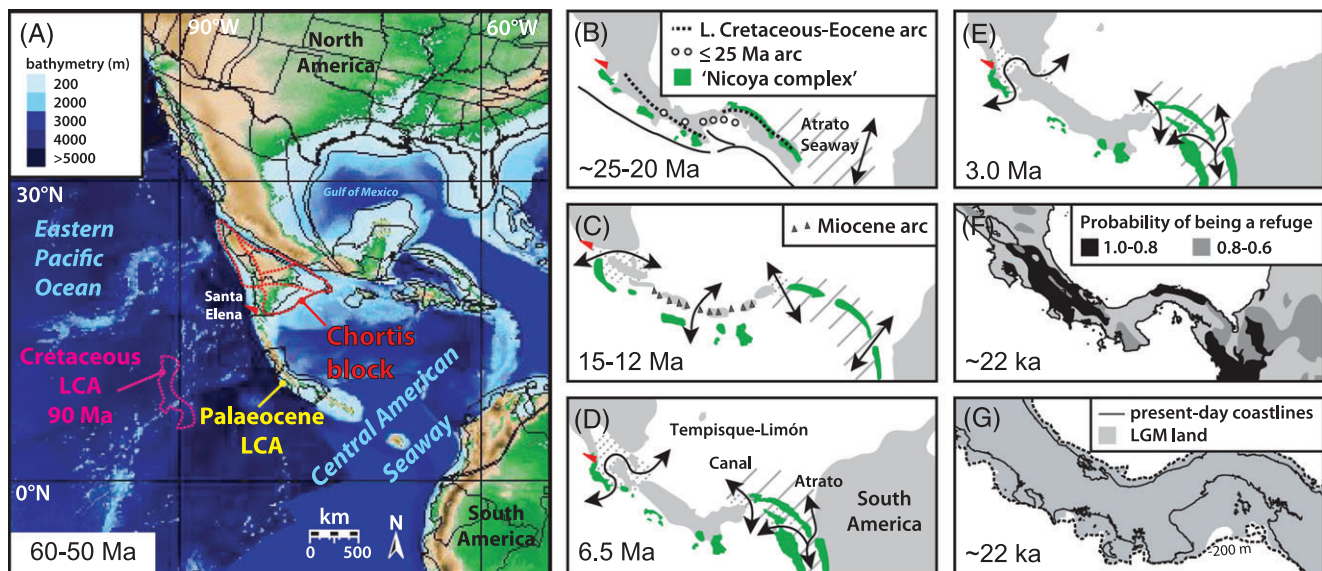
### III. GEOLOGICAL HISTORY

Geodynamic evolution in LCA dates back over 100 Ma, from the Early Cretaceous onset of Santa Elena peninsula formations (124 to 109 Ma; Hauff *et al.*, 2000) and Costa Rica arc volcanism (Gazel *et al.*, 2008), to Holocene isolation of Bocas del Toro islands ~10 to 1 thousand years ago (ka) due to sea-level rise and continental submergence (Anderson & Handley, 2002). This interval witnessed dramatic geographic changes critical to the assembly of LCA landforms and biotas, altering probabilities of dispersal, vicariance, and extinction through time.

In the Late Cretaceous, LCA was incorporated along the western CARIB after fusing to the Chortis block, and the Chocó block (e.g. Baudó Range) was developing *via* submarine oceanic plateau volcanism. Early LCA is an enigma; however, as the dinosaurs were going extinct 65 Ma, Soná peninsula (and possibly Osa peninsula) was subaerial (Hauff *et al.*, 2000; Hoernle *et al.*, 2002). By Palaeocene times LCA was a Pacific island archipelago and dispersal into the region ~60 to 50 Ma must have occurred over an up to ~400 km ocean gap to the north and ~400–1500 km ocean gap(s) to the south, based on plate reconstructions (Fig. 4A; Hauff *et al.*, 2000; Mann *et al.*, 2007; Scotese, 2008). The Baudó terrane remained submerged, but emergent Eocene lands included Nicoya complex terranes (Fig. 1; 95 to 75 Ma; Seyfried *et al.*, 1991; Hauff *et al.*, 2000) and active Azuero peninsula and San Blas arcs separated by ocean connections (Montes *et al.*, 2012). By mid-Eocene ~50 Ma, volcanism increased in western Costa Rica and was peaking in the San Blas Range and part of the Atrato basin, where

it slowed 38 to 15 Ma (Seyfried *et al.*, 1991; Montes *et al.*, 2012). The earliest remnants of *in situ* volcanism surface in Costa Rica–Nicaragua stratigraphic records in the Late Eocene–Miocene, beginning with alkaline Sarapiquí arc (Fig. 2A) eruptions (Abratis & Wörner, 2001; Gazel *et al.*, 2008).

LCA's major morphotectonic features formed largely since the Miocene. The Cocos plate formed ~23 Ma *via* Farallón plate rifting, subducted beneath CARIB, and has since uplifted LCA substantially (Mann *et al.*, 2007; Marshall, 2007). The Baudó terrane surfaced in the Miocene. Yet LCA's overall Miocene configuration remains disputed. One 'peninsula model' (Fig. 4B) posits that a long, narrow peninsula jutting from Chortis ~25 to 16 Ma progressively narrowed the Atrato seaway gap with Colombia. This is supported by land-mammal fossils (Whitmore & Stewart, 1965; Kirby & MacFadden, 2005; Retallack & Kirby, 2007) and stratigraphic dating analyses (Kirby, Jones & MacFadden, 2008). Upgraded Panama geological data and maps implicate that mountain ranges east of the Panama Canal were emergent around Late Eocene and helped form a contiguous peninsula since the Miocene (Montes *et al.*, 2012). The alternative 'island model' based on palaeobathymetric and sedimentary records posits that a Mid-Miocene–Pliocene volcanic archipelago spanning western Costa Rica to Colombia was disconnected from Nicaragua and South America, leaving marine connections open across the nascent isthmus (Fig. 4C–E; Coates & Obando, 1996; Coates *et al.*, 2004). The former model requires over-water dispersal by colonising propagules, followed by movement along contiguous land; the latter would require multiple over-water dispersal bouts between segments. The Early-Mid Miocene saw the accretion of Nicoya complex terranes and other basalts to Panama ~20 to 15 Ma (Hauff *et al.*, 2000; Hoernle *et al.*, 2002). By Mid-Miocene, substantial land was emerging in central-SE Costa Rica: the Talamanca Cordillera began forming



**Fig. 4.** Palaeogeography of lower Central America (LCA). (A) Palaeocene–Eocene plate reconstruction showing the position of LCA, the Chortis block (red-dashed lines), and the Santa Elena peninsula (red triangle) (modified from Scotese, 2008). Note that LCA was an ancient island archipelago at this time, isolated from nearby mainland areas to the north and southeast (shaded green to brown with increasing elevation above sea level) by ocean gaps (blue; see bathymetric legend) including the Central American Seaway. The position of LCA ~90 Ma in the Cretaceous (Mann *et al.*, 2007) is shown in magenta. (B–E) Miocene–Pliocene reconstructions of LCA: light grey, emergent land; grey diagonal lines, abyssal to bathyal (> 2000 m) depths; grey dotting, neritic depths; green shading, exotic oceanic terranes known as the ‘Nicoya complex’; arrows, marine corridors; red triangles, subaerial Santa Elena peninsula. The geography of LCA ~25 to 20 Ma based on the ‘peninsula model’ (B; redrawn after Montes *et al.*, 2012), is contrasted against (C) middle Miocene (15 to 12 Ma), (D) Late Miocene (6.5 Ma, pre-Cocos Ridge), and (E) Pliocene (3 Ma, initial isthmus closure) ‘island model’ reconstructions (after Coates & Obando, 1996; Coates *et al.*, 2004, 2005). Names of marine corridors are given in (B, D). (F, G) LCA environments during the Last Glacial Maximum (LGM) ~22–19 ka. (F) Proposed remnant Pleistocene forests shaded according to their probabilities of being refugia, after Whitmore & Prance (1987). (G) Palaeobathymetry model showing LCA land (grey shading) extending over the continental shelf during the LGM (–110 m sea levels; modified from Smith & Bermingham, 2005) in the context of present-day coastlines and the 200 m contour.

17.5 Ma, and then the Aguacate Cordillera started 11.4 Ma and went extinct ~4.0 Ma (reviewed by Gazel *et al.*, 2008). LCA reached its modern position after a major Mid-Miocene collision with South America 12.8 to 7.1 Ma that created active left-lateral strike-slip faults along the Darién (Coates *et al.*, 2004). Around the same time, extensional forces at LCA’s northern boundary formed the Nicaraguan depression (Fig. 2A), a long, fault-bounded rift valley spanning El Salvador’s Median Trough to the Tortuguero lowlands basin. This depression opened SE–NW ~10 to 0 Ma, especially following Cocos slab break-off 10 to 4 Ma (Mann *et al.*, 2007; Funk *et al.*, 2009).

The most stunning changes occurred over Late Neogene–Quaternary, when gradual emergence of the LCA isthmus cut off the Central American Seaway and permanently linked the Americas for the first time in the Late Pliocene. Key events included: (i) collision and subduction of the Cocos Ridge 5.5 to 3.5 Ma beneath Costa Rica, which rapidly uplifted the Chorotega volcanic front and sparked increased volcanism, forming the Fila Costeña and Talamanca Cordillera (Abratis & Wörner, 2001; Mann *et al.*, 2007); and (ii) deposition of the Limón, Canal Zone, Chucunaque and Darién basins 7 to 0 Ma by

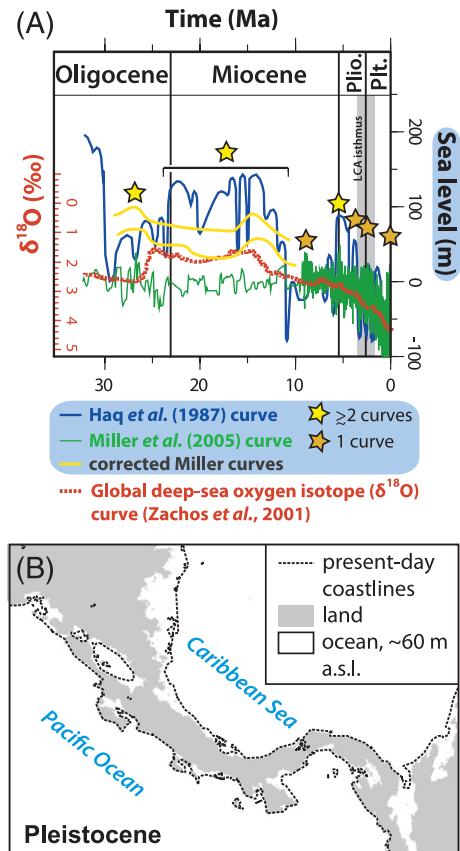
crustal erosion associated with Chorotega and Andean uplift (reviewed by Coates & Obando, 1996). By ~4.6 Ma, ocean currents and ecosystems became reorganised (Keigwin, 1982; Haug & Tiedemann, 1998). The isthmus then became fully closed by at least 3.5 to 3.1 Ma before a permanent Isthmian Link with South America formed 3.1 to 1.8 Ma (Keller, Zenker & Stone, 1989; Duque-Caro, 1990; Coates *et al.*, 1992; Coates & Obando, 1996; Ibaraki, 2002). Combined with the simultaneous and rapid uplift of the Colombian Andes (Gregory-Wodzicki, 2000), development of the LCA isthmus played a role in Miocene–present global climate change by altering patterns of regional oceanic and atmospheric circulation, resulting in more intense Atlantic thermohaline circulation, more high-latitude Northern Hemisphere precipitation, and larger ice sheets (Keigwin, 1982; Schmidt, 2007; Lunt *et al.*, 2008). The last 2.2 to 0 Ma of the Quaternary were marked by activity of Chorotega volcanic front stratovolcanoes, which laid several sizeable debris fans that likely destroyed everything in their paths. The ~1.7 to 1.1 million year (Myr)-old Orotina debris fan (Avalancha formation) overlying the Rio Grande de Tárcoles (Marshall *et al.*, 2003) and Late Pleistocene Barú volcano debris fan (Sherrod *et al.*, 2007) provide good



examples of the latter. Overall, most of the LCA landscape formed since the Neogene. LCA thus provides a remarkable biogeographic experiment where, unlike continents, large subaerial areas are relatively young.

#### IV. CLIMATE AND SEA-LEVEL FLUCTUATIONS

Radical geologic evolution in LCA has been accompanied by climate and sea-level fluctuations altering the spatial and taxonomic habitat composition. Global climate progressively moistened and cooled through the Late Cenozoic, dropping to near present-day temperatures by ~4 to 2 Ma (Fig. 5A). Since at least that time (> 4 Ma), Pacific dry forest habitats of today have essentially been intact (Graham & Dilcher, 1995), although they probably oscillated between forest patches and savannas during the vicissitudes of the Late Pleistocene (Piperno & Pearsall, 1998). Around 39.4 to 28.1 ka during the Late Pleistocene, cold/humid conditions with relatively high seas and lower precipitation prevailed in LCA (González, Urrego & Martínez, 2006). Subsequently, LCA climate became much cooler and sea levels reached their lowest levels 28 to 14.5 ka (González *et al.*, 2006), overlapping the Last Glacial Maximum (LGM) 22 to 19 ka. LGM pollen records and other data show that mean 5–8°C cooling throughout LCA shifted montane forests down in elevation, creating a highland Costa Rica–Panama páramo corridor (Bush *et al.*, 1992; Colinvaux, 1996; Colinvaux *et al.*, 1997; Islebe & Hooghiemstra, 1997). The highest Talamancan peaks were simultaneously covered by small glaciers (< 50 km<sup>2</sup>) that deglaciated ~10 ka (Lachniet, 2004). Whether corridors of savanna habitat existed over wide swathes of Neotropical lowlands during the LGM (or other Pleistocene periods) is intensely debated (e.g. Colinvaux, De Oliveira & Bush, 2000). The ‘Pleistocene refugia hypothesis’ (Haffer, 1969), which provided the impetus to spark this debate, explains terrestrial areas of endemism by predicting that glacial aridity fragmented LCA/Amazonian forests, isolating lowland taxa in persistent upland refugia separated by savannas (Fig. 4F; Haffer, 1969, 1997; Whitmore & Prance, 1987). The alternative ‘disturbance-vicariance’ hypothesis (Colinvaux, 1993, 1996; Colinvaux *et al.*, 1997) posits that LCA/Amazonia never had upland forest refugia fragmented by aridity, or wide savanna corridors (*cf.* Webb & Rancey, 1996). Rather, LCA was a mosaic of Late Pleistocene forest patches caused by glacial cooling cycles, and uplands (> 500 m a.s.l.) carried diverse montane biota without invading lowland species (Bush *et al.*, 1992; Colinvaux, 1993, 1996). Following the LGM, LCA experienced cooling and near present-day warming cycles 14.4 to 11.1 ka, while the ensuing Holocene was characterised by drying, human disturbance, and relative climatic stability (Bush *et al.*, 1992; Bush & Colinvaux, 1994; Leigh, O’Dea & Vermeij, 2014). Modern LCA climate is tropical (daily highs throughout the region range between 23.9 and 32.2°C, year round), and tropical moist forests that typically receive > 2000 mm total annual



**Fig. 5.** Links between global changes in Late Cenozoic climate and sea levels, and their potential impacts on lower Central America (LCA). (A) Mean deep-sea oxygen isotope ( $\delta^{18}\text{O}$ , in parts per thousand) record (dark red dashed line), a temperature proxy positively correlated with global cooling, from Zachos *et al.* (2001). Several eustatic sea-level curves are also given. Dark green trend lines are from Miller *et al.* (2005); yellow trends are Miller *et al.*'s (2005) curves corrected and smoothed by Kominz *et al.* (2008); and the dark blue trendline is from Haq *et al.* (1987). Plio., Pliocene; Plt., Pleistocene. Stars indicate sea-level spikes greater than or equal to ~25 m a.s.l.; yellow stars indicate support from two or more curves; orange stars reflect support from a single curve. These sea-level highstands may have substantially inundated emergent LCA lowlands. (B) Marine inundation of LCA during the Pleistocene, modelled as a hypothetical high-sea stand ~60 m a.s.l. based on present-day digital elevation data (NASA SRTM, 90 m). This model presents a conservative estimate illustrating potential effects of extensive Pleistocene sea-level spikes, e.g. hypothesised by Norez (1999, 2004; see text).

precipitation dominate land cover (Fig. 2B). However, high-elevation zones (e.g. Talamanca Cordillera) experience lower temperatures and have shrub- and grass-dominated páramo habitat; and Pacific environments of Santa Elena, Nicoya and Azuero peninsulas possess dry forests characterised by < 2000 mm total annual precipitation (Fig. 2B).

Long-term eustatic sea-level estimates indicate that the seas have dropped rather continuously since LCA land began to emerge, especially since the Eocene–Oligocene

transition (Fig. 5A). However, multiple high-sea stands have affected LCA biogeography. Sedimentary records show that a marine corridor inundated the Nicaraguan depression until at least Late Pliocene (Coates & Obando, 1996), and this undoubtedly limited LCA–nuclear Central America (Guatemala to Nicaragua) (NCA) dispersals (e.g. of freshwater fishes; Bussing, 1976). Multiple eustatic curves converge on similar Miocene spikes  $\sim 25$  to  $50$  m a.s.l. around 20, 14, and 12 Ma (Kominz *et al.*, 2008; Müller *et al.*, 2008), and these likely created or maintained an LCA archipelago configuration, at least temporarily. Late Miocene–present spikes  $\geq 25$  m a.s.l. were inferred  $\sim 9$  Ma and 5 to 4.5 Ma (Fig. 5A) and sea levels breached the Panama Canal  $\sim 7$  to 6 Ma (Coates *et al.*, 2004). Reliably determined Pleistocene eustatic spikes  $\sim 20$  m a.s.l. occurred 2.4 to 1.8, 1.3 and 0.45 to 0.1 Ma and potentially connected the Atlantic and Pacific oceans (Keller *et al.*, 1989; Hearty *et al.*, 1999; Miller *et al.*, 2005). However, substantial Neotropical diversity is thought to have resulted from  $\sim 100$  m Miocene–Quaternary marine incursions supported by coastline and Amazonian studies (Webb, 1995; Nores, 1999, 2004). While the extent and timing of such incursions outside Amazonia remains controversial because evidence stems from tectonically uplifting areas, other reviews list large, potentially  $+85$  m a.s.l. peaks around the 0.63 Ma interglacial (Mediterranean basin; Emig & Geistdoerfer, 2004). We modelled a slightly lower incursion,  $+60$  m a.s.l., over modern elevations because LCA land approximated modern landmasses around this time [unpublished data, based on a 90 m-resolution NASA Shuttle Radar Topography Mission digital elevation model (<http://www2.jpl.nasa.gov/srtm/>)]. Results indicated that had major sea level highstands occurred during Pleistocene interglacials, these could have widely inundated lowland LCA habitats, altering lowland species distributions and causing genetic isolation (Fig. 5B).

## V. CONSERVATION SIGNIFICANCE

As part of the Mesoamerica biodiversity hotspot, LCA contains exceptional biodiversity and endemism (Section II); unfortunately, hotspot membership is also predicated upon widespread and active human threats and therefore reflects growing recognition that LCA's fascinating biodiversity is in peril (Myers *et al.*, 2000). Land use is a leading proximate cause of global biodiversity loss and human-induced environmental change (Sala *et al.*, 2000), and a major threat to LCA biotas. Habitat destruction is spreading in LCA due to widespread land-clearing for agriculture and cattle ranching, combined with rampant human population growth: less than 40% of virgin forests remained in Central America by the late 1980s (Leonard, 1987), and today only 20% of original primary vegetation extent remains (Myers *et al.*, 2000). Some evidence suggests active restoration efforts in Costa Rica are helping to increase overall forest area back towards pre-1970s levels; however, problems such

as hillside deforestation, forest conversion, and firewood acquisition remain widespread and ongoing. Invasive species, e.g. rainbow trout (*Oncorhynchus mykiss*) introduced to Costa Rica in 1925 (Hildebrand, 1938), and Mozambique tilapia (*Oreochromis mossambicus*) introduced in LCA since 1950 for aquaculture (Welcomme, 1988), threaten the fragile balance of LCA ecosystems. Environmental pollution is an enormous problem seen everywhere. Freshwater ecosystems are widely threatened by introduction of agrochemicals that poison local communities (e.g. localised fish-kills in Costa Rica due to pesticide poisonings), watershed destruction, and increased flooding and sediment loads due to logging and land cultivation (Leonard, 1987; Bussing, 1998). Commercial species of lobsters, shrimps, anchovies, and turtles have long been overexploited (Leonard, 1987). What is more, disease also poses a major threat; particularly alarming is the case of contagious fungal diseases. Well-known cases of amphibian declines in Costa Rica and Panama, which occur suddenly and sometimes result in species extinction, affect possibly up to half of extant amphibian species in the region (e.g. Lips, Reeve & Witters, 2003; Young *et al.*, 2004).

Despite many threats, LCA also is an international model of conservation efforts. This includes preservation of natural areas. Fully 28% of Costa Rica is legally protected land (93 total protected areas), and another 264 228 ha are private nature reserves, while 34.4% of Panama (89 protected areas) is legally protected and 40 000 ha are private reserves (Evans, 1999; Chacón, 2005, 2008; ANAM, 2010). LCA is also part of the United Nations Man and Biosphere Programme and the location of four UNESCO Biosphere Reserves, including two unique Costa Rican reserves (Cordillera Volcánica Central, Agua y Paz), one unique Panama reserve (Darién), and La Amistad reserve, a 'peace park' spanning the Costa Rica–Panama border (UNESCO, 2012a). This program integrates science, education and social programs to promote sustainable development, e.g. involving local communities in ecosystem management. An area of incredible cultural diversity due to its 'frontier' anthropological history, LCA is also multicultural, boasting  $> 80$  different dialects; thus cultural and linguistic diversity will need to be maintained along with nature. Due to consideration as having outstanding universal value, seven LCA areas are designated UNESCO World Heritage Sites, including La Amistad Reserve, Cocos Island National Park, and the Area de Conservación Guanacaste in Costa Rica, as well as four unique Panamanian sites —Fortifications on the Caribbean Side of Panama: Portobelo-San Lorenzo (endangered due to lack of management and urban development), Darien National Park, La Amistad, the Archaeological Site of Panamá Viejo and Historic District of Panamá, and Coiba National Park and protected marine zone (UNESCO, 2012b). LCA countries also participate in a World Bank-funded regional partnership, the Mesoamerican Biological Corridor project (<http://www.biomeso.net/>), aimed at conserving ecological connectivity and promoting environmentally sustainable development through linking  $> 321\,000$  km<sup>2</sup> of protected



areas from southern Mexico to Panama (IEG, 2011). However, despite multi-million dollar investments, conservation resources allocated to fresh waters lag well behind those committed to terrestrial and marine ecosystems.

## VI. A BRIEF HISTORY OF LOWER CENTRAL AMERICAN BIOGEOGRAPHY

### (1) A rare land bridge

LCA is earth's sole interoceanic and intercontinental landmass and most prominent land bridge. Land bridges are important in historical biogeography because they cut off marine connectivity, isolating communities on either side, and facilitate convergence of continental biotic components through inland dispersal (Lomolino *et al.*, 2010). Not surprisingly, the importance of LCA in shaping New World biogeography has long been recognised. Charles Darwin and other 19th Century naturalists thought that LCA served as a refuge where temperate North American and tropical American vegetation mixed, surviving the glacial stages (Darwin, 1859, pp. 338–340). Both Darwin and Alfred Russel Wallace cited work by Günther (1861) on marine fish communities, which, owing to considerable similarity in community composition on either side of the isthmus, indicated previous linkage(s) between the Pacific and Atlantic oceans (Darwin, 1859, p. 317; Wallace, 1876, p. 40). Based on the fish data and his familiarity with fossilised marine gastropods, Wallace (1876) explicitly hypothesised that the area where modern LCA resides became inundated during the Miocene. It was also Wallace (1876) who first articulated the importance of this 'small and insignificant' sliver of land as a driver of biotic convergence and interchange between North and South American biotas. Wallace considered LCA more effective in facilitating inland dispersals than other isthmuses, such as the desert Isthmus of Suez between Africa and Asia:

'The Isthmus of Panama is a more effectual line of union [biotic convergence], since it is hilly, well-watered, and covered with luxuriant vegetation; and we accordingly find that the main features of South American zoology are continued into Central America and Mexico' (Wallace, 1876, p. 38; our clarification in brackets).

However, Darwin and Wallace could not have known how right they were on these latter points. Like other 19th to mid-20th Century biogeographers, their approach to historical biogeography was limited to a vague understanding of phylogeny derived from morphology-based taxonomic lists and Charles Lyell's geologic model of continental and oceanic 'stasis', or permanence.

### (2) The Great American Biotic Interchange and beyond

When the Isthmian Link emerged ~3 Ma in the Late Pliocene, a 'Great American Biotic Interchange' (GABI) of terrestrial and freshwater species ensued overland,

yielding increased species turnover and filling of open niches, and range expansions, speciation, and extinctions across the Americas (Stehli & Webb, 1985). By elucidating the sequence of this incredible natural experiment, 20th Century biogeographers made LCA famous worldwide as an example of the influence of continental convergence and land-bridge formation in shaping biotas. Wallace (1876, p. 131) had hypothesised that South American mammals invaded North America before the ice ages. However, it was not until classic studies by George Gaylord Simpson that detailed GABI histories of many lineages became fully known. Simpson (1940, 1950) recognised three 'strata' of South American land-mammalian fossils and derived an ecological and biogeographical explanation for their movements between North and South America before and after LCA isthmus emergence (reviewed by Stehli & Webb, 1985; Riddle & Hafner, 2010). Simpson showed that lineages moved predominantly southward across LCA to invade South America over Late Miocene–recent, more than had done so at previous times; however, interamerican dispersals had started before then and were bidirectional. For example, South American 'herald taxa' suddenly appeared in the Mid-Miocene mammal record of North America *via* (over-water) waif dispersals northward, or 'island hopping' (Simpson, 1950; Webb, 2006). A host of large-scale, distribution-based biogeography studies followed Simpson, including studies of Neotropical plants (Raven & Axelrod, 1974; Gentry, 1982; Gómez, 1986), insects (Halffter, 1987; McCafferty, 1998), freshwater fishes (Miller, 1966; Myers, 1966; Rosen, 1975; Bussing, 1976, 1985; Smith & Bermingham, 2005) and tetrapod amphibians and reptiles (Savage, 1966, 1982, 2002; Campbell, 1999), birds (Karr, 1990), and mammals (Marshall, 1979; Marshall *et al.*, 1979; Kirby & MacFadden, 2005). Drawing on improved 1960s–1970s field museum collections, plate tectonics theory, and geological mapping, these studies inferred historical scenarios, including GABI sequences, and heavily influenced LCA historical biogeography. Work through the early 1980s culminated in a synthesis of GABI histories of many organismal groups, and geological models, led by S. David Webb, Larry Marshall, and colleagues (Stehli & Webb, 1985). Over the 1990s to present, this synthesis has been updated by large-scale analyses of fossil and extant species records (e.g. Vermeij, 1991; Cadle & Greene, 1993; Webb & Rancey, 1996; Webb, 1997, 2006; Burnham & Graham, 1999; Leigh *et al.*, 2014). In contrast to land-mammalian patterns, the above studies demonstrated that rainforest plants, mayflies, freshwater fishes, herpetofauna, and rainforest birds dispersed predominantly northward from South America (despite bidirectional GABI movements) to become established in Central America, and beyond, since the Neogene.

The broad-scale studies mentioned above proposed numerous testable hypotheses of biogeographic provinces (e.g. based on areas of endemism) and elements, plus dates of Mesozoic–recent dispersals into LCA from outlying areas and *in situ* diversification or extinction of clades.

In particular, Savage (1966, 1982) proposed four Central American herpetofaunal elements — ‘South American’, ‘Middle American’, ‘Old Northern’ and ‘Young Northern’. Savage hypothesised that the older extant lineages of these elements dispersed into LCA and NCA during the Late Cretaceous, went extinct in LCA over Eocene–Miocene, then reinvaded the isthmus during Miocene–Pliocene times (Savage, 1966, 1982). Bussing (1976) proposed three biogeographic elements of freshwater fishes and concluded, similarly to Savage, that South American fish lineages colonised NCA during the Cretaceous–Palaeogene *via* a temporary interamerican land bridge (that later disappeared), diversified in NCA and South America, and then invaded LCA in a second Miocene–Pliocene wave. Although LCA was never a Cretaceous land bridge, these models reconcile with current tectonic models: the proto-Greater Antilles arc passed through the ocean gap between North and South America over the Cretaceous–Paleogene (e.g. Hauff *et al.*, 2000; Hoernle *et al.*, 2002; Mann *et al.*, 2007). In a later work, Savage (2002) hypothesised that LCA highland herpetofaunal diversity originated as a result of Plio–Pleistocene climatic fluctuations (similar to refuge theory) as montane habitats shifted down in elevation during glacials, then up (being isolated again) during interglacials. Raven & Axelrod (1974) identified many northern-continent plant families thought to have migrated from South America during the Cenozoic. Likewise, Gentry (1982) hypothesised the presence of two floristic elements in LCA, ‘Gondwanan’ and ‘Laurasian’, and inferred that their biogeographic history was dominated by asymmetrical northward dispersals of South American lineages (lianas, canopy trees) into lowland plant communities following LCA isthmus emergence. While many biogeographical hypotheses from the above studies can be tested using phylogeography, their claims remain seldom tested by phylogeography studies today (but see, for example, Dick, Abdul-Salim & Bermingham, 2003; Castoe *et al.*, 2009; Streicher, Crawford & Edwards, 2009).

### (3) Biogeographical paradigms

The 20th Century witnessed confrontations between several major biogeographical paradigms. In the 1960s, plate tectonics became accepted then superseded ‘land-bridge biogeography’ and ‘oceanic dispersal’ as the dominant theory explaining intercontinental biogeography (Raven & Axelrod, 1974; Lomolino *et al.*, 2010). MacArthur & Wilson’s (1967) Equilibrium Theory of Island Biogeography (ETIB) revolutionised ‘static’ biogeographical thinking by modelling species diversity as the outcome of a dynamic balance between migration and extinction. Much subsequent debate in historical biogeography sought to establish the primacy of dispersal *versus* vicariance in explaining large-scale biogeographical patterns (Lomolino *et al.*, 2010). While vicariance (or ‘cladistic’) biogeography (e.g. Nelson & Platnick, 1981), which aligned plate tectonics and phylogenetics, came to dominate explanations of continental biogeography, island biogeography remained best explained by dispersal and related processes (Lomolino *et al.*, 2010).

Land-bridge/oceanic-dispersal theories were generally abandoned in favour of vicariance; in LCA, however, available evidence supported land-bridge and oceanic-dispersal scenarios well before such debates emerged. Even as vicariance biogeography bloomed, biogeographers easily maintained the classic view that dispersal along an evolving land bridge, combined with vicariance and extinction events, explained LCA biogeography, e.g. species emplacement and diversification (Simpson, 1940, 1950; Savage, 1966, 1982; Raven & Axelrod, 1974; Marshall *et al.*, 1979; Gentry, 1982; Bussing, 1985). Geological evidence firmly supports a Pacific LCA origin, meaning no truly vicariant divergences (taxa) could even exist between LCA and outlying continental lineages, *sensu* Gondwanan vicariance; and fossils irrefutably show that taxa colonised LCA *via* oceanic dispersal. Thus the question in LCA biogeography is not whether vicariance and dispersal (oceanic or inland) occur, but what has been the sequence, effects, and relative importance of these events? Today, island biogeography is undergoing a paradigm shift setting aside the ETIB and vicariance biogeography (Heaney, 2007). Biogeographical data increasingly show that these models are inadequate to explain island life, and a new island biogeography paradigm is emerging combining elements of both ecological and evolutionary dynamics of relevant processes (reviewed by Heaney, 2007; Lomolino *et al.*, 2010). Species diversity patterns analysed in light of modern geography typically upheld ETIB predictions, whereas historical perspectives from phylogeography have repeatedly challenged this model [e.g. demonstrating very ancient island lineages (falsifying predicted high turnover rates), island–island migration, and intra-island speciation; Brown & Lomolino, 2000]. The eco-evolutionary shift also appears directed at remedying the well-known poor fit between the ETIB and systems and processes operating over geological timescales (i.e. that the model *sensu stricto* was limited to ecological timescales, assuming equivalent dispersal abilities/probabilities among species and no speciation; Heaney, 2007). Given its numerous land-bridge islands (Figs 1 and 2), LCA phylogeography is primed to contribute to the present period of testing and reshaping island biogeography theory, although few studies exist so far (but see below).

### (4) The advent of molecular biogeography

Molecular data and analytical tools have assumed enormous importance in biogeography. Since the 1980s–1990s, advances in DNA sequencing technologies (e.g. polymerase chain reaction, automated sequencing, next generation sequencing) and molecular phylogenetic methods, and the exploding phylogeographic literature and toolkit, have fuelled an era of rejuvenated interest and growth in historical biogeography (Riddle *et al.*, 2008; Knowles, 2009; Hickerson *et al.*, 2010). Compared with traditional area-based inference (reviewed by Posadas *et al.*, 2006; Ebach & Tangney, 2007), DNA-based biogeography provides critical improvements such as molecular estimates of lineage divergence dates. Aside from dating species origins, molecular dating

permits empirically testing hypotheses (e.g. vicariance dates), thereby elucidating the timing *and* mechanisms underlying biogeographical patterns. Among their many advantages, molecular analyses provide billions more DNA characters than morphology/distribution-based approaches; explicitly model nucleotide substitution and other processes; accommodate evolutionary rate heterogeneity (e.g. relaxed clocks); permit splitting DNA matrices into separately modelled data partitions (e.g. by gene; no comparably sophisticated models exist for morphological evolution); and estimating lineage divergence times ( $T$ ), with or without fossil information [best if rates or calibration points are well established, e.g. by taxonomic group or geological event (Lomolino *et al.*, 2010)]. With appropriate outgroup sampling, phylogeographical methods permit testing a variety of hypotheses, e.g. population demographic models and topological models, to infer the historical sequence of dispersal, vicariance, extinction and recolonisation events by which lineages arrived and diversified in LCA (Bermingham & Martin, 1998; Crawford *et al.*, 2007). Also, while area-based inference relies heavily on endemism (Nelson & Platnick, 1981), phylogeography infers historical events or processes (e.g. population expansion) even when spatial-genetic endemism is absent (Zink, 2002; Garrick, Caccone & Sunnucks, 2010). As noted above, phylogeography is also highly synthetic: by the 1990s, improved palaeogeographic models for LCA (Coates & Obando, 1996) and eustatic sea-level curves (Haq, Hardenbol & Vail, 1987) became available, and early studies showed that these could be used in conjunction with inferred phylogeographical relationships among populations to derive historical scenarios and test geological models (Bermingham & Martin, 1998). The advent of molecular biogeography has also provided impetus for refining GABI sequences, mainly using higher-level phylogenies (e.g. Weir, Bermingham & Schluter, 2009; Cody *et al.*, 2010), and sparked trans-isthmian marine studies developing LCA as a classical model of allopatric speciation in the oceans (e.g. Bermingham, McCafferty & Martin, 1997; Lessios, 2008).

## VII. PHYLOGEOGRAPHICAL PATTERNS EMERGING FROM LOWER CENTRAL AMERICA

Here, we summarise (with select examples) major patterns emerging from phylogeographical studies of LCA taxa. Multi-taxon phylogeographical breaks and evidence for general patterns of dispersal, vicariance and other processes impacting the assembly and diversification of LCA biotas are emphasised. Our review draws on a database of 58 phylogeography studies, including 57 studies consistent with our goals published between 1996 and 2012, in addition to one of our own unpublished studies of three freshwater fish species (see online supporting information, Appendix S1). Studies to date represent ~94 nominal taxa sampled from multiple sites throughout their ranges, including LCA and surrounding areas. Mapping sampling localities from 66%

of studies reveals that phylogeographers have sampled LCA widely, producing extensive geographical coverage (Fig. 6A). LCA's complex earth history and ecological heterogeneity predicts that generally complex patterns of phylogeographic congruence and incongruence are likely to be recovered within and among lineages. Consistent with this prediction, LCA taxa showcase a diversity of phylogeographical patterns rivaling the complexity of LCA landscapes (Fig. 6; Tables S1–S3). Apart from landscape diversity and history, this probably also reflects the diverse distributions of species sampled to date (Table S1).

### (1) Phylogeographic structuring is common within LCA taxa and reveals cryptic biodiversity

Most (63.4%) LCA lineages show genetic structuring in the form of phylogeographic breaks (phylogenetic splits between mostly distinct geographical lineages). In total, LCA lineages support 31 major phylogeographic breaks, shown in Fig. 6B (with further details in Tables S1–S3), most of which have been recovered from mitochondrial DNA markers (see online Appendix S2). Apparently, long-term mechanisms of genetic isolation (physical, reproductive, etc.) have been at play in many species. Although phylogeographical studies have recovered clues to some species GABI histories (e.g. freshwater fishes, Bermingham & Martin, 1998; Reeves & Bermingham, 2006), these results suggest that isthmian

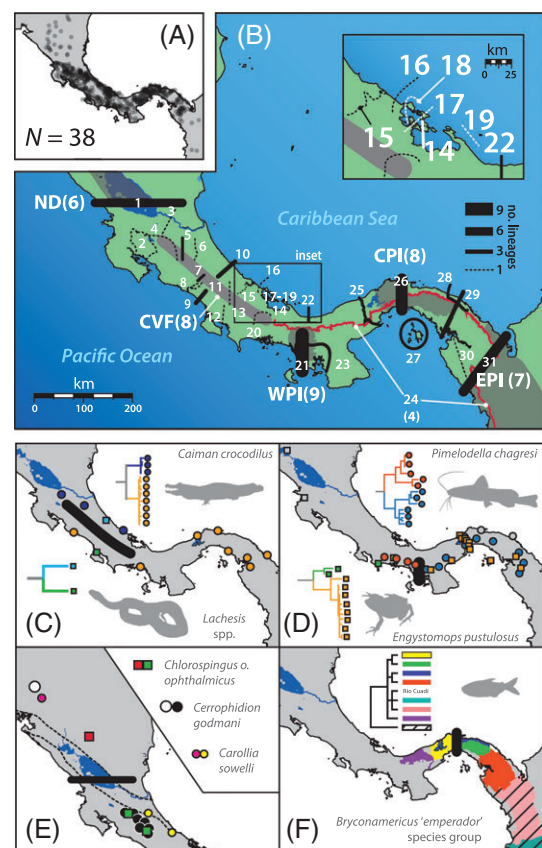


Fig. 6. Legend on next page.



environments, not just dispersal into or out of the region, have contributed significantly to within-LCA diversification. Results also underscore the point that LCA is more than a mere biogeographic crossroads between continents, but harbours unique genetic endemism (Wang *et al.*, 2008). Data from a synthesis of phylogeographical patterns from eastern North America show that ~78% of organisms investigated exhibited clear phylogeographical structuring based mainly on organellar DNA markers (Soltis *et al.*, 2006; excluding taxa not analogous to those considered herein, e.g. marine organisms). Thus, LCA organisms exhibit just slightly less prevalent phylogeographical structuring than that of a much older and larger, truly continental area.

In a similar vein, LCA provides a classic, subcontinental-scale showcase of phylogeography's ability to make discoveries that might otherwise go unnoticed, principally

**Fig. 6.** Sampling and phylogeographical breaks emerging from lower Central American (LCA) phylogeography studies. (A) Map summarising geographical coverage of sampling localities, which were available from most (66%) studies in this review (see online Appendix S1). (B) Map of phylogeographical breaks (different coloured lines) discussed in the text, with abbreviations given for the five major breaks. Breaks (numbers of nominal taxa/lineages split across each break): 1, ND = Nicaraguan depression ( $N=6$ ); 2, BEB = Rio Bebedero ( $N=1$ ); 3, SJ1 = San Juan break 1 ( $N=1$ ); 4, SJ2 = San Juan break 2 ( $N=1$ ); 5, CC = Central Cordillera ( $N=2$ ); 6, SJ3 = San Juan break 3 ( $N=1$ ); 7, TCMF1 = Talamanca Cordillera montane forest break 1 ( $N=2$ ); 8, SAV = Rio Savegre break ( $N=1$ ); 9, FILA = Fila Costeña ( $N=3$ ); 10, LI = Limón ( $N=3$ ); 11, CVF = Chorotega volcanic front ( $N=8$ ); 12, PB = Piedras Blancas ( $N=1$ ); 13, TCMF2 = Talamanca Cordillera montane forest break 2 ( $N=1$ ); 14, POPA = Popa Island–mainland ( $N=2$ ); 15, SIXA = Sixaola–Changuinola ( $N=1$ ); 16, BDT1 = Bocas del Toro break 1 ( $N=1$ ); 17, BDT2 = Bocas del Toro break 2 ( $N=1$ ); 18, BDT3 = Bocas del Toro break 3 ( $N=1$ ); 19, ESCU = Escudo de Veraguas Island–mainland ( $N=1$ ); 20, BARU = Barú volcano ( $N=1$ ); 21, WPI = western Panama isthmus ( $N=9$ ); 22, MOSQ = Mosquito Gulf ( $N=2$ ); 23, AZUE = Azuero peninsula ( $N=2$ ); 24, PNSA = Panama–northern South America continental divide ( $N=4$ ); 25, VALLE = El Valle volcano ( $N=2$ ); 26, CPI = central Panama isthmus ( $N=8$ ); 27, PERL = Las Perlas Islands ( $N=2$ ); 28, CHIC = Rio Playón Chico basin ( $N=2$ ); 29, BT = Bayano–Tuira ( $N=3$ ); 30, SAPO = Sapó range ( $N=1$ ); 31, EPI = eastern Panama isthmus ( $N=7$ ). (C–F) Typical spatial-genetic splits recovered within different species, each contributing to major multi-taxon phylogeographic breaks shown in (B); examples show the (C) CVF break in *Caiman crocodilus* crocodiles (Venegas-Anaya *et al.*, 2008) and *Lachesis* spp. bushmasters (Zamudio & Greene, 1997); (D) WPI break in *Pimelodella chagresi* catfishes (e.g. Bermingham & Martin, 1998) and *Engystomops pustulosus* frogs (Weigt *et al.*, 2005); (E) ND break in *Chlorospingus ophthalmicus* birds (e.g. Weir *et al.*, 2008), *Cerrophidion godmani* pit-vipers (e.g. Castoe *et al.*, 2009), and *Carollia sowelli* bats (Hoffmann & Baker, 2003); and (F) CPI break in the *Bryconamericus* 'emperor' species group (Reeves & Bermingham, 2006).

cryptic lineage divergences. Overall, approximately 197 genetically distinct evolutionary lineages are recovered within 94 nominal taxa sampled to date, amounting to, on average, 2.1 lineages per taxon (Table S1). These patterns vary widely among taxa and have various biogeographical and taxonomic implications; however, amphibians and freshwater fishes harbour particularly exceptional cryptic diversity that appears informative for testing geological hypotheses. For example, a study of four nominal freshwater fish species uncovered ~12–22 novel lineages (~3–5 cryptic lineages/taxon; Bermingham & Martin, 1998). Their comparative phylogeographical inferences led Bermingham & Martin (1998) to propose a new model (B/M model) of landscape evolution for the LCA region. Also, one poison-dart frog species, *Oophaga pumilio*, apparently contains from several to up to 18–19 unique genetic lineages, depending how you count them (Wang & Shaffer, 2008). Venegas-Anaya *et al.* (2008) upheld genetic and geographical distinctiveness of *Caiman* crocodile subspecies but also discovered a novel cryptic lineage representing a new taxon. Several other studies have also identified cryptic lineages representing putative new species, or operational taxonomic unit-level biodiversity (Table S1; e.g. Martin & Bermingham, 2000; Reeves & Bermingham, 2006; Jones & Johnson, 2009; Vázquez-Miranda, Navarro-Sigüenza & Omland, 2009).

## (2) Multi-taxon spatial structuring suggests general evolutionary patterns and highlights importance of regional processes shaping diversification

'To do science is to search for general patterns, not simply to accumulate facts...' (MacArthur, 1972, p. 1).

Many ( $N=17$ ; 54.8%) of the phylogeographical breaks recovered in LCA to date are spatially congruent across multiple taxa (Fig. 6B; Table S3), over small to regional scales. This supports the existence of generalised evolutionary patterns in LCA. Furthermore, congruence among taxonomically and ecologically divergent but codistributed lineages indicates historical associations of genotypes possibly due to shared biogeographic history in the same local communities (Arbogast & Kenagy, 2001; Zink, 2002). Notably, multi-taxon breaks are recovered across the Chorotega volcanic front (CVF, Fig. 6B, C); western Panamanian Isthmus (WPI, Fig. 6B, D); Nicaraguan depression (ND, Fig. 6B, E; representing LCA–NCA divergences); central Panama at or east of the Panama Canal Zone (CPI, Fig. 6B, F); and eastern Panama (EPI, Fig. 6B; representing LCA–South America divergences directly within or in the vicinity of the Darién isthmus). The striking correlation between these breaks and physiography, particularly major geographical barriers (Section III), suggests that regional processes (e.g. orogeny, oceanic terrane accretion and uplift, and other geological processes) have played a major role in shaping intraspecific diversification across LCA biodiversity, by promoting and maintaining long-term zoogeographical barriers.

### (3) Low phylogeographic structuring and incongruent patterns highlight roles of chance, ecological differences, and local processes shaping LCA communities

In contrast to the above patterns, a considerable proportion of LCA lineages ( $N = 34$ , or 36.6%; representing 22 studies) exhibit zero to limited phylogeographic structure (Table S1). Around a third of these studies conducted inadequate spatial or numerical sampling (e.g. coarse sampling grain or density) of widely distributed taxa (e.g. *Uroderma bilobatum* bats; Hoffmann, Owen & Baker, 2003). In such cases, determining the degree to which the observed lack of structuring is attributable to actual evolutionary genetic patterns (e.g. 'phylogeographic category V'; Avise *et al.*, 1987) versus sampling artifacts (e.g. inadequate phylogenetic signal or poor marker selection leading to unresolved phylogenetic topologies) is problematic. However, species may exhibit low intraspecific structuring due to high gene flow (e.g. migration-drift non-equilibrium), hybridisation, large historical effective population sizes ( $N_e$ ; e.g. making equilibrium and complete lineage sorting hard to attain), or recent colonisation (e.g. founder events) combined with low mutation rates (Avise, 2000; Wakeley, 2002). Processes contributing to lack of phylogeographical structuring within these species are therefore likely to vary and may reflect ecological differences.

At a comparative level, phylogeographic incongruence can arise from historical differences among species at the same parameters surrounding the evolutionary circumstances of zero–low intraspecific phylogeographic structuring discussed above. However, in comparative phylogeography, spatial incongruence indicates potentially independent responses of species to the series of geologic and palaeoclimatic changes that have occurred within an area (Avise, 2000; Arbogast & Kenagy, 2001; Zink, 2002). With that said, cases of low phylogeographic structuring in LCA (Table S1) are incongruent relative to the multi-taxon patterns described above, suggesting that species may have experienced different responses to historical events within shared distributions. Phylogeographic incongruence is commonly inferred from comparative LCA studies. Phylogeographical comparisons of codistributed LCA bat (Hoffmann & Baker, 2003; Martins *et al.*, 2009), frog (Crawford *et al.*, 2007), snake (Castoe *et al.*, 2009) and freshwater fish species (Bermingham & Martin, 1998; Reeves & Bermingham, 2006; J. C. Bagley & J. B. Johnson, unpublished data)—in many cases, focal taxa that combined range throughout much or all of LCA or Central America—reveal idiosyncratic patterns of area relationships and gene flow patterns, up to regional scales. This also supports a potential lack of shared biogeographic history. Common processes may not have influenced diversification of some ecological communities at broader spatial scales, leading to different historical responses by habitat, within and among taxonomic groups. However, chance, including stochastic differences in the timing of LCA colonisation among lineages, might partly account for this. Differential dispersals into LCA could reflect the influence of extrinsic

ecological factors (e.g. presence of available suitable habitat in the target area) or intrinsic ecological differences of lineages (e.g. dispersal abilities) in shaping biodiversity distributions (Bermingham & Martin, 1998; Arbogast & Kenagy, 2001; Zink, 2002).

### (4) Deep phylogenetic subdivisions within plants appear rare in LCA: truth or illusion?

Taxonomic sampling biases have favoured animals over plant taxa at a 9:1 ratio, precluding robust comparisons between plant and animal phylogeographies (see online Appendix S2). Strikingly, however, available data reveal that no plant species possess deep phylogeographic breaks or contribute to multi-taxon breaks within LCA. Yet is this a representative portrait of the evolutionary history of LCA plant species, or an illusion? It would be tempting to conclude from these data that LCA plant species share a congruent lack of phylogeographic structure, suggesting that they have been largely unaffected by historical barriers and processes shaping genetic isolation in animal taxa. However, the observed lack of phylogeographical structure in plants more likely reflects a combination of (i) low genetic marker resolution and (ii) higher relative dispersal potential of plant species studied to date, facilitated by intrinsic and extrinsic ecological factors promoting dispersal to and establishment in new areas. For example, most plant studies have relied on chloroplast DNA (cpDNA), which may evolve 10–100 times more slowly than animal mtDNA, limiting the ability of this marker to detect phylogeographic structure (see Avise, 2000, and references therein). Moreover, regarding dispersal, most LCA plants studied to date have been large tree species that by their nature are more dispersive than other plant types, a situation which lends itself to less genetic structuring in these species (Petit & Hampe, 2006). Despite such potential biases, previous studies have concluded that Neotropical plant species are more dispersal-prone than animals based on fossil pollen and molecular phylogenetic data showing that multiple plant lineages reached LCA before many vertebrate GABI participants (Raven & Axelrod, 1974; Cody *et al.*, 2010). Indeed, over-water dispersal apparently has played a more important role in shaping LCA plant distributions than anticipated (Cody *et al.*, 2010). Taking one species as an example, despite water-intolerant seeds, phylogeographical analyses demonstrate that *Symphonia globulifera* trees reached LCA from South America before Late Pliocene isthmus completion, via long-distance oceanic dispersal (Dick *et al.*, 2003; Dick & Heuertz, 2008). However, while *S. globulifera* demonstrates that over-water dispersal is a mechanism that has operated during the assembly of the LCA flora, it is important to note that populations are differentiated based on genetic data from DNA sequences and microsatellites (Dick & Heuertz, 2008); therefore, despite containing no deep phylogeographical structuring, this species apparently experiences dispersal limitation after it colonises new areas. This example illustrates the importance of factoring in the peculiarities of plant species genetics and ecologies when conducting phylogeographic analyses and highlights how

incorporating more rapidly evolving markers (e.g. nDNA or cpDNA microsatellites) could provide better avenues to geographical inference in future studies of LCA plants.

### (5) Other dispersal-demography connections

The previous sections highlight a strength of phylogeography—its ability to link ecology and demography to broader macroevolutionary and biogeographical patterns (Avice *et al.*, 1987). Limited phylogeographical structuring is expected in superior-dispersing and -colonising species in the absence of strong physical barriers to dispersal/gene flow, whereas progressively monophyletic gene tree lineages are expected across strong environmental gene flow barriers through time (Avice *et al.*, 1987; Avice, 2000). Phylogeographic structure should therefore correlate inversely with behavioural preference and physiological capacity for dispersal (e.g. high rates, over large distances). Aside from some of the plant patterns (but see caveats and discussion in Section VII.4), patterns from other taxa also support this prediction. For example, widely distributed *Atta* leafcutter ants (Solomon *et al.*, 2008) and bees capable of long-distance dispersal (Dick *et al.*, 2004) show limited genetic structuring. Conversely, dispersal-limited montane salamanders and frogs show substantial Tertiary–Quaternary diversification (García-París *et al.*, 2000; Streicher *et al.*, 2009). Congruent with expectations, livebearing ‘secondary’ freshwater fishes with presumed salt tolerance (Myers, 1938) lack isolation in Atlantic-coast drainage basins (J.C. Bagley & J.B. Johnson, unpublished data). Unexpectedly, however, salt-intolerant ‘primary’ freshwater fishes, considered to have relatively lower dispersal potential (Myers, 1938), display evidence for rapid deployment across the landscape, recent clades, and sometimes no phylogeographical signal at all (e.g. *Cyphocharax magdalenae*, Reeves & Bermingham, 2006).

### (6) Filter barriers: biogeographic province boundaries and other features are permeable barriers to dispersal

Whereas Wallace (1876) thought that the LCA isthmus allowed relatively unimpeded dispersal through the region (Section VI.1), Simpson (1950) viewed the LCA isthmus as a historical ‘filter barrier’ reducing, without eliminating, inland movements of species. Simpson’s view has since become widely accepted, and it is supported by phylogeographic patterns, particularly across biogeographic province boundaries (e.g. Fig. 3). Province boundaries are thought to explain species turnover and reflect localised vicariant barriers historically limiting gene flow and species distributions (Avice *et al.*, 1987; Ronquist, 1997). Therefore, historical processes should have promoted LCA lineage divergence at province boundaries (Lee & Johnson, 2009); however, evidence for this prediction is mixed. On the one hand, multi-taxon breaks span province boundaries (Fig. 3), e.g. the Chorotega volcanic front (Fig. 6B, C; Table S3). On the other hand, gene flow, or a mixed phylogeographical structuring, has been inferred across this and other province boundaries. Freshwater fish

communities have mixed genetically across the Chorotega front (Jones & Johnson, 2009; Lee & Johnson, 2009) and the eastern-central Panamanian Isthmus (Reeves & Bermingham, 2006), aided by headwater river capture events. Gene flow has probably also occurred across the West Panama portion of the CVF in pseudoscorpions (Zeh, Zeh & Bonilla, 2003bb). Additionally, bird data indicate that *Chlorospingus ophthalmicus* bush-tanagers possibly exchanged genes across montane areas of bird endemism (Guatemalan *versus* Talamancan; Weir, 2009) separated by the Nicaraguan depression (Bonaccorso *et al.*, 2008), while *Glyphorynchus spirurus* woodcreepers apparently experienced long-distance dispersal/gene flow across the Colombian Andes (Marks, Hackett & Capparella, 2002), or EPI break area (Fig. 6B). Assuming these cases represent actual gene-flow events (not incomplete lineage sorting), then (i) patterns of LCA vicariance, dispersal and gene flow vary not only across spatial scales (Smith & Bermingham, 2005), but also according to physiographic barrier (province boundary) considered; (ii) vicariant barriers have had mixed impacts on community formation and species distributions; and (iii) the above examples support the interpretation that the corresponding province boundaries represent filter barriers. Building on the third of these points, a growing list of studies reveals phylogeographic breaks broadly correlated to Bocas del Toro, Panama (BDT; Fig. 2A) environments, and this indicates that this area presented a historically important filter barrier in LCA. East of BDT, phylogenetic splits across the Caribbean Gulf of Mosquitoes break (MOSQ; 22 in Fig. 6B; Tables S1, S3) are supported by mtDNA lineages of *Caiman crocodilus* crocodiles (Venegas-Anaya *et al.*, 2008) and *Pristimantis ridens* frogs (Wang *et al.*, 2008). Phylogeographic breaks correlated with the BDT region are also recovered in mtDNA variation in catfishes (Perdices *et al.*, 2002) and frogs (Crawford *et al.*, 2007; Robertson, Duryea & Zamudio, 2009) and differentiated nuclear ribosomal spacer sequences in trees (Dick & Heuertz, 2008). Interestingly, these patterns have arisen despite a lack of obvious geographical barriers (e.g. contiguous Caribbean wet and mangrove forests dominate the coastline, Fig. 2B). This illustrates the ability of phylogeography to derive and test new biogeographical explanations as required when phylogeographic breaks fit no known historical events (Riddle, 1996; Gascon *et al.*, 2000). This area is low in elevation and forms a young, contiguous Limón–Bocas del Toro coast exposing Neogene sediment and rock formations (Marshall, 2007). The BDT embayment and mainland were also partly inundated after a nearby 1991 earthquake (Marshall *et al.*, 2003), and our sea level model (Fig. 5B) suggests that this area could have been extensively affected by Pleistocene seas. Thus, isolation caused by marine incursions presents an alternative to tectonic uplift (Venegas-Anaya *et al.*, 2008) and restricted coastal dispersal corridors (Crawford *et al.*, 2007) as a potential explanation for this filter barrier.

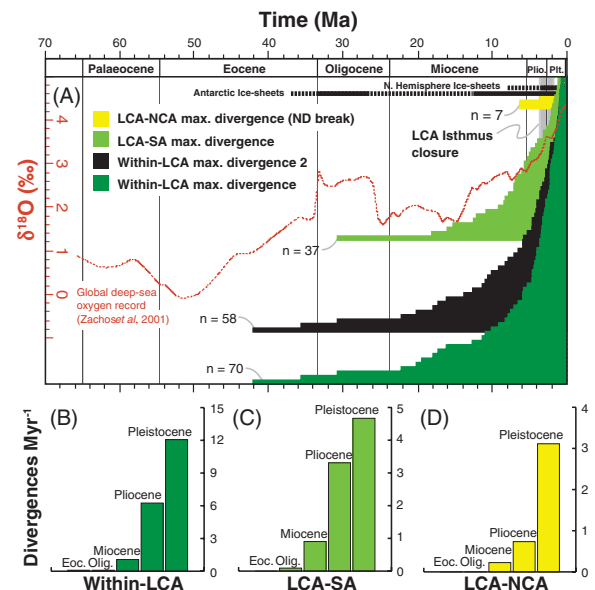


## (7) Phylogeography and island biogeography theory in LCA

Traditional island biogeography theory (Section VI.3) makes several predictions germane to LCA, including that (i) islands have likely been colonised from nearby mainland source-pools; (ii) due to rapid turnover, island species should be young; and (iii) larger, more distant islands should harbour older, more genetically divergent lineages due to lower extinction (remnants of former radiations persist). From coastal geology (Section III; Coates & Obando, 1996), bathymetry (e.g. Fig. 4G), and sea level dynamics (Figs 4G and 5A; Fleming *et al.*, 1998), we also predict (iv) land-bridge islands located over the LCA continental shelf originally had species similar to mainland communities (due to colonisation during low seas, when exposed shelf habitat created mainland connections; e.g. as shown in Fig. 4G for the Bocas del Toro archipelago) whose populations recently became isolated (during high seas) from mainland populations. Phylogeographic datasets from several LCA taxa support the above predictions. For example, poison-dart frog phylogeography does not fit a vicariance model (sequential mainland–island isolation events) at Bocas del Toro; these frogs apparently originated from nearby Costa Rican mainland frogs and achieved their present distributions through multiple mainland–island, island–island, and island–mainland dispersal events (Wang & Shaffer, 2008). These poison-dart frog lineages are also predictably shallow, or recently isolated (see below). However, island biogeography prediction ii above is rejected: extinction has apparently not been strong enough to remove many novel insular lineages, e.g. the poison-dart frog radiation persists and various other frogs, birds, and freshwater fishes exhibit mainland– or island–island phylogeographical breaks, e.g. BDT1–3, ESCU, PERL (Fig. 6B; Tables S1–S3). The data suggest that different taxa/lineages have colonised LCA islands at vastly different times and persisted, forming endemic lineages through genetic drift. The most striking example is the ancient Las Perlas Islands lineage of salt-tolerant *Synbranchus marmoratus* swamp-eels, which possibly colonised the islands > 50 Ma via oceanic dispersal (Perdices, Doadrio & Bermingham, 2005; PERL break, Fig. 6B). These data corroborate the prediction from ‘new’ island biogeography theory that island biotas are typified by persistence, rather than extinction (Heaney, 2007).

## (8) Temporal patterns suggest a mainly Pliocene–Pleistocene timeframe for biotic diversification in LCA

The largely Late Neogene–recent timing of landscape evolution (Section III) and interamerican biotic exchange (e.g. GABI; Section VI.2) in LCA predicts that biotic assembly and diversification in LCA, and between LCA clades and sister clades in outlying continental areas, should coincide with this interval. A meta-analysis (see online Appendix S1) of divergence times inferred from



**Fig. 7.** (A) Time ranges of initial within-lower Central America (LCA), LCA–Nuclear Central America (NCA), and LCA–South America (SA) lineage divergence events estimated for LCA lineages studied to date. Thin horizontal bars span the time in millions of years ago (Ma) since the initial speciation or divergence event for each clade to the present and are plotted in increasing chronological order by geographical class (colours). Within-LCA diversification time ranges are shown for clades confined to the study area (within-LCA max. divergence), and for splits including clades containing samples from outlying areas (within-LCA max. divergence 2; see text, and Appendix S1 and Table S2 for the raw data). Time-range data are presented over major earth history parameters/events: dashed red line, mean deep-sea oxygen isotope ( $\delta^{18}\text{O}$ ) curve, a temperature proxy mostly controlled by changes in continental ice-sheet volume (thick black horizontal bars, permanent ice sheets; thick dashes, times with partial or melting ice sheets; modified from Zachos *et al.*, 2001); vertical grey bar, timeframe of LCA isthmus closure (Section III). (B–D) Exponential increases in speciation/lineage divergence rates, or possibly declining extinction rates, within LCA (by geological epoch) over Eocene–Pleistocene, inferred based on divergence time distributions in (A) (with corresponding colours).

time-calibrated molecular phylogenetic divergences from studies reviewed herein supports this prediction. Divergence dates for stem and crown nodes recovered in LCA phylogeography studies (summarised in Table S2) exhibit an over 40 Myr range, from 42.1 Ma (max. crown age, *Craugastor podiciferus* frogs; Streicher *et al.*, 2009) to a mere 235 ka (LCA–SA divergence within *Anopheles albimanus* mosquitoes; Loaiza *et al.*, 2010a). However, most lineage divergence can be constrained to less than 20 Ma, and a broadly exponential pattern of lineage diversification since ~14 Ma is evident in the time ranges of estimated initial lineage diversification events (Fig. 7A). Most lineage divergences, including 69% of within-LCA divergences and 57% of LCA–SA divergences, are constrained to Pliocene–recent, with maximum divergence dates ranging no later than Early

Pliocene (5.3 Ma). These results imply potentially higher speciation rates since the Pliocene, a suspicion corroborated by rate calculations. Crudely estimating lineage divergence rates, which presumably reflect speciation rates, shows a likewise exponential pattern of increase across estimates over Oligocene–Pleistocene (Fig. 7B–D). This might reflect marginally higher divergence rates due to redundant samples in our time-range plots but is unlikely to be due to variation in sampling, given the large number of lineages we sampled and that we observed the highest speciation rates more recently (whereas unsampled lineages are expected to cause declines in recent speciation rates). Another potential explanation for the pattern of higher speciation rates since the Pliocene is the likely extinction of older lineages. Nonetheless, the observed period of exponentially increasing diversification rates is synchronous with or just follows Early Pliocene high-sea stands that, combined with East Panama microplate vertical positioning, maintained a partially drowned Panama Isthmus  $\sim 7$  to 3.7 Ma (Duque-Caro, 1990; Coates *et al.*, 2004). Subsequent divergences in our compilation overlap global cooling, LCA land bridge emergence, GABI exchanges, and Quaternary intensification of glacio-eustatic cycles. Mirroring similar meta-analyses based on recent molecular phylogenetic evidence from Neotropical taxa, these results suggest that Neogene–recent geological and palaeogeographic events *and* Quaternary glacio-eustatic cycles are likely to have been important drivers of biotic diversification in LCA and surrounding Neotropical areas (Cody *et al.*, 2010; Rull, 2011, and references therein).

### VIII. CHALLENGES: IMPROVING METHODS AND INFERENCES IN LCA PHYLOGEOGRAPHY

The field of LCA phylogeography must face several challenges to ensure continued progress and improved historical biogeographical inferences. First, more phylogeography studies using better data are needed to elucidate further the historical origins, assembly, and diversification of LCA biotas. Conducting phylogeographical analyses of LCA organisms can be difficult due to landscape complexity and logistical issues. Still, meeting this challenge through amassing more single-species datasets will enhance our knowledge of the processes underlying genetic variation within LCA species. In turn, increasing the number of codistributed species datasets will permit expanded comparative analyses needed to test further the generality of the emerging phylogeographical patterns herein. However, future studies should proactively work to improve finer-scale sampling and counteract existing geographical and taxonomic sampling biases. In particular, more studies sampling plants and taxa with premontane to montane distributions are needed (Section VII.4; online Appendix S2), e.g. in the under-sampled Talamancan Cordillera (Fig. 6A). Indeed, while few comparative analyses of highland taxa have been conducted (e.g. Castoe *et al.*, 2009), filling this gap will likely continue unveiling distinct lineages that are new to science along with insights

into how highland diversity is maintained (e.g. García-París *et al.*, 2000; Streicher *et al.*, 2009). On the related issue of gene sampling, workers have relied principally on single-locus analyses of mtDNA and cpDNA (see online Appendix S2); however, the maturation of the field will require development of nuclear phylogeography perspectives. Although mtDNA is highly informative and a robust indicator of population history and species limits (Avice, 2000; Zink & Barrowclough, 2008), single gene trees have both historical and random components and can be discordant topologically with one another as well as ‘true’ species/population trees, e.g. due to incomplete lineage sorting (Maddison, 1997). Thus, sequence data from multiple unlinked loci are needed to overcome noisy historical gene tree signals and correctly infer phylogenetic relationships in a species tree framework (e.g. Liu & Pearl, 2007; Kubatko *et al.*, 2009), and multi-locus data also provide a robust framework for accurately estimating divergence times and demographic parameters (e.g. migration rates) to infer phylogeography (Edwards & Beerli, 2000; Hey & Machado, 2003). To accelerate nDNA marker development, we recommend new methods identifying exon-primed intron-crossing markers and anonymous nuclear loci based on genome-enabled approaches (reviewed by Thomson, Wang & Johnson, 2010). However, we note that comparative phylogeography (Arbogast & Kenagy, 2001; Riddle *et al.*, 2008) accounts for the gene tree variance problem by testing for replicated population divergences across taxa, indicating common historical events in a region (though inferences are most reliable when congruence is demonstrated across many taxa).

Developing a more hypothesis-driven and statistically rigorous research program capitalising on novel advances in statistical population genetics and geospatial analysis presents a second, arguably more formidable challenge. Building ‘just-so’ stories or *ad hoc* explanations from observed genetic patterns has been commonplace in LCA studies, and this is not all bad: exploratory analyses cover ‘scenario space’ and often yield unexpected discoveries (Garrick *et al.*, 2010) such as the cryptic divergences discussed above. And, aside from our review, this is supported by previous syntheses of phylogeographical data from Amazonia (e.g. Patton, Da Silva & Malcolm, 1994) and the southeastern US Coastal Plain (Avice *et al.*, 1987; Avice, 2000) that also highlight cryptic genetic breaks useful for interpreting regional historical biogeography. However, reliance on pattern discovery and matching is nonstatistical and embodies the major criticisms of phylogeography (references in Edwards & Beerli, 2000; Arbogast & Kenagy, 2001; Knowles & Maddison, 2002; Posadas *et al.*, 2006; Hickerson *et al.*, 2010). By contrast, ‘statistical phylogeography’ (Knowles & Maddison, 2002; Knowles, 2009; Garrick *et al.*, 2010) provides more objective and statistically rigorous methods to infer demographic history while taking geography and stochastic population genetic processes into account. Drawing on coalescent theory (Wakeley, 2002) and probabilistic simulations, these sophisticated model-based methods can estimate population parameters (e.g. Kuhner, 2009) and statistically discriminate

among *a priori* demographic and biogeographic models while accounting for coalescent variance (e.g. Knowles & Carstens, 2007). Statistical phylogeographical approaches naturally lend themselves to developing and testing *a priori* hypotheses (e.g. modeling explicit historical scenarios, with varying population sizes, divergence times, and migration rates), thus their application will be essential for developing a more hypothesis-driven focus. And this will also benefit comparative analyses: as larger comparative datasets are assembled, approximate Bayesian computation methods will permit tests of co-dispersal, co-vicariance, or other patterns of shared demographic histories (*versus* multiple divergences) using highly parameterised statistical phylogeographical models (Hickerson *et al.*, 2006a,b, 2007, 2010; Knowles, 2009; Huang *et al.*, 2011). Perspectives from other underutilised tools such as geospatial modelling (e.g. ecological niche models; Kozak *et al.*, 2008) and phylclimatic modelling (Yesson & Culham, 2006) should also be developed and used to enhance phylogeographical inferences. For example, geospatial-modelling applications can be used to predict the impacts of historical environments on species palaeodistributions (e.g. range dynamics), and this information can subsequently aid the generation and testing of *a priori* models/hypotheses using statistical phylogeography (e.g. Kidd & Ritchie, 2006; Richards, Carstens & Knowles, 2007; Chan, Brown & Yoder, 2011).

A third, more general future challenge for LCA phylogeography will be integrating insights into organismal evolutionary history with theory and methods from other disciplines including ecology, other historical biogeographical techniques (Posadas *et al.*, 2006), comparative phylogenetics, palaeontology and the geosciences. The general trend of fragmentation between historical biogeography and ecology, and among the various sub-fields of historical biogeography, is widely recognised (Wiens & Donoghue, 2004; Ebach & Tangney, 2007; Sanmartín, 2010). However, methodological integration with other fields will be increasingly critical as LCA workers address more interdisciplinary questions, including those surrounding spatial-genetic analyses of selection, adaptation, functional trait evolution, community assembly and more. Virtually no studies link LCA phylogeography and adaptation; yet which came first, environmental adaptations or phylogeographical lineage divergences? Also, which lineages more likely diversified during Pleistocene climatic fluctuations—physiologically plastic ones or those with higher genotypic diversity (limited plastic adaptations)? In addition, contributions of adaptive and phenotypic differences to phylogeographical patterning are poorly explored; however, if addressed from a genomic perspective, such questions may also yield insight into the origins of adaptive and functional diversity.

## IX. PHYLOGEOGRAPHY AND LCA CONSERVATION

Phylogeography stands to make several critical contributions to conservation in lower Central America, in light of the region's threatened status. First, as illustrated in Section VII.1, phylogeography is poised to provide the unique service of uncovering cryptic lineage divergence and speciation patterns in LCA. This can aid conservation efforts in several ways. Knowledge of cryptic speciation patterns aids identifying and refining species limits and therefore regional species diversity patterns, which may highlight the need to alter conservation plans (e.g. if today's most species-rich areas are not the hottest regional hotspots tomorrow). The challenges for, and impacts on, systematics and taxonomy are obvious: it will be critical to formally describe novel biodiversity as it is revealed, and to determine its place in the tree of life. Also, conservation strategies typically prioritise species with various extinction-risk correlates, including small geographic ranges, low abundances, and specialised life histories or feeding phenotypes; however, phylogeographers often discover cryptic lineages by studying common, widespread species. Detecting natural species with smaller ranges contained within widespread, non-target 'species' may identify 'new' species at greater risk of extinction, thus warranting conservation resources. Second, where comparative phylogeography uncovers replicated cryptic divergences, areas of diversity and endemism can be better identified—areas where processes generating biodiversity have acted and presumably still are acting across multiple taxa to maintain biodiversity (Moritz, 2002). Sub-areas spanning environmental gradients within those areas can then be selected to preserve adaptive differences (Moritz, 2002), and highly threatened sub-areas can be pinpointed. If multi-taxon breaks are found to occur over distinct geographical barriers that limit gene flow between areas, and one area or the other is most susceptible to climate change, this may determine primacy of areas due to increased likelihood of future extirpation or extinctions. Thirdly, expounding on this latter theme, it will be important for LCA conservation that phylogeographical inferences are integrated with predictive niche-based models of the past, present, and future distributions of lineages. As illustrated by work on Brazil's Atlantic Forest by Ana Carnaval, Craig Moritz, and colleagues identifying areas of high genetic diversity and environmental stability, integrative phylogeographical approaches can highlight areas that have contributed to local endemism and that are most likely to withstand climate change over the coming centuries (Carnaval & Moritz, 2008; Carnaval *et al.*, 2009). A similar approach combining geographic information systems (GIS)-based modelling and statistical phylogeography seems to hold promise for predicting, and explaining, patterns of LCA biodiversity as well (Chan *et al.*, 2011). Undoubtedly, the unique physiography and complex earth history of lower Central America will continue to provide a fascinating backdrop for addressing integrative questions relevant



to Neotropical biogeography and diversification, through phylogeography. However, the above steps may help us not only understand, but also conserve, the patterns and processes of diversification in this unique Neotropical region.

## X. CONCLUSIONS

(1) Despite covering only  $\sim 0.09\%$  of earth's land area, lower Central America is among the most physically and biologically complex areas worldwide. LCA boasts distinct landform (Fig. 2A) and biotic assemblages (Fig. 3), each reflecting unique histories of landscape *versus* organic evolution. Indeed, levels of physiographic variation in LCA are usually only attained at whole-continental scales (Marshall *et al.*, 2003; Marshall, 2007).

(2) Throughout the past 100 Myr, LCA has experienced diverse geographical changes (particularly since the Miocene) that altered probabilities of biogeographical processes (e.g. dispersal) and earth surface processes (orogeny and sea-level and climatic fluctuations, plus major earth history events e.g. formation of the Isthmus of Panama). These undoubtedly figured prominently in structuring modern Neotropical biogeography patterns. Combined with the observation that LCA landscapes are mostly geologically young (many major physiographic features formed Neogene–recent), which should limit the complexity of biogeographical patterns, this makes LCA particularly attractive for phylogeography.

(3) Whereas the extent of Plio-Pleistocene sea-level rise and fall remains debated, elevation data and consensus from sea-level curves suggest that sea-level change may have significantly impacted LCA biodiversity over Neogene–recent. However, phylogeographical data have rarely been used explicitly to address sea-level events as drivers of LCA diversification (but see Jones & Johnson, 2009). Whether and to what extent marine incursions have influenced broad-to-fine-scale diversification of LCA biota should be tested further, and geologically correlated.

(4) As part of the Mesoamerica biodiversity hotspot, LCA is of great conservation significance; however, despite landmark-scale conservation efforts, its biodiversity remains highly threatened by anthropogenic factors. More conservation efforts are essential to ensure the persistence of LCA biota; certain habitats including fresh waters warrant more recognition and conservation resources.

(5) LCA presents a rare intercontinental and interoceanic land bridge that facilitated massive interamerican exchanges of species since  $\sim 3$  Ma, the 'Great American Biotic Interchange' (Stehli & Webb, 1985). GABI histories of taxa have been a primary focus of historical biogeographical research in LCA; however, these and other key biogeographical hypotheses (scenarios) proposed for Central America, e.g. Savage's (2002) Pleistocene model,

warrant more testing. Overemphasising species GABI histories has left finer-scale patterns of colonisation and post-colonisation diversification lesser known, and more phylogeographical inquiry is essential to overcome this knowledge gap.

(6) Most LCA taxa show phylogeographical breaks indicating that LCA environments apparently have contributed to within-LCA diversification. Therefore, LCA is more than a mere biogeographic crossroads between continents, but harbours unique genetic endemism.

(7) LCA provides a classic showcase of phylogeography's ability to make otherwise unnoticed discoveries, especially cryptic lineage divergences. Amphibians and freshwater fishes harbour particularly exceptional cryptic diversity and appear informative for testing geological hypotheses. Given the prevalence of cryptic divergences, LCA would be ideal for studying population divergence/speciation by comparing multiple diverged lineage pairs; this could provide robust tests for 'suture zones' (Remington, 1968), which have not been rigorously evaluated.

(8) Comparative phylogeographical patterns reveal at least 17 multi-taxon phylogeographical breaks in LCA, highlighting the importance of regional processes in shaping genetic diversity and composition of LCA biotic communities. Yet more work is needed (*i*) to test the evolutionary generality of these breaks across biodiversity (e.g. through comparisons with new datasets from other species), and (*ii*) to evaluate temporal congruence (e.g. simultaneous divergence) *versus* other patterns, e.g. pseudocongruence (identical area relationships caused by different underlying events; Cunningham & Collins, 1994), and to test more rigorously for underlying causal factors.

(9) A surprisingly large proportion of LCA taxa exhibit little or no phylogeographical structuring, particularly plants. Although such patterns could reflect a diversity of alternative mechanisms, they indicate a role for chance, ecological differences (e.g. dispersal potential) and local processes (e.g. ecological interactions) in shaping regional patterns of biotic assembly and diversification. However, using more rapidly evolving genetic markers will likely recover greater levels of genetic structure in LCA plant species.

(10) Phylogeographic data agree with the long-held view that LCA, and areas of the subcontinent (e.g. coastal headlands, Bocas del Toro), presents biological filter barriers (e.g. Simpson, 1950; Savage, 1966; Crawford *et al.*, 2007). More study will be instructive, however, in determining (*i*) which filter barriers have figured most prominently in shaping LCA biogeographical patterns; (*ii*) why LCA environments filter dispersal/gene flow in some taxa, but not close relatives; and (*iii*) whether filter barriers are also areas of secondary contact (creating suture zones, as per above).

(11) A new metamorphosis of theory is brewing in the field of island biogeography, resulting in the setting aside of classic theories (ETIB, vicariance biogeography) in explaining patterns of island life (e.g. Heaney, 2007;

Lomolino *et al.*, 2010). LCA contains land-bridge islands, and inland habitat 'islands' (e.g. Talamanca sky-islands), that can be used to test island biogeography predictions. Phylogeographical data from LCA taxa support some predictions of the traditional models, but suggest that inter- and intra-island patterns of dispersal, diversification (e.g. radiation), and persistence deserve more attention (e.g. Wang & Shaffer, 2008).

(12) Phylogeographical studies recover historical patterns of dispersal and population divergence coincident with formation of LCA's Isthmus and other major physiographic features, especially since the Pliocene. Quantitatively summarising the timeline of diversification inferred from studies to date suggests that both Neogene and Quaternary events have driven LCA diversification, with an exponential Pliocene–recent increase in rates of diversification.

(13) Although LCA phylogeography studies are uncovering many novel insights into the assembly and diversification of this recent Neotropical biota, more phylogeography studies using (i) better data, including larger numbers of unlinked molecular markers; (ii) geographically and taxonomically expanded, comparative sampling strategies; (iii) more hypothesis-driven approaches; and (iv) the latest statistical phylogeographical methods accounting for coalescent stochasticity and other potentially confounding processes, are needed. Adopting these approaches should greatly improve biogeographical inferences in the region; however, given the long-recognised state of fragmentation in historical biogeography, future work should also (v) integrate phylogeographical inferences with data and methods from disjunct fields of biogeography (e.g. ecological biogeography) and other disciplines, e.g. ecology and geospatial modelling.

(14) Phylogeography is poised to make critical contributions to conservation biology in LCA, including the way we view and prioritize areas and species for conservation resources. We encourage phylogeographers to apply their work to conservation; here, inferences into cryptic intraspecific diversification, genetic endemism, and predicting past-to-future species persistence and environmental stability across multiple taxa and areas seem particularly promising.

## XI. ACKNOWLEDGEMENTS

We thank M. F. Breitman, B. J. Adams, and two anonymous reviewers for very helpful comments on earlier drafts of this manuscript. J.C.B. was funded by research and teaching assistantships from the Brigham Young University (BYU) Department of Biology, a Graduate Research Fellowship from BYU Graduate Studies, and a BYU Mentoring Environment Grant (to J.B.J.). J.C.B.'s PhD research received additional funding from an NSF Doctoral Dissertation Improvement Grant (DEB-1210883), and Idea Wild (<http://www.ideawild.org/>).

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### XIII. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Table S1. Summary of patterns emerging from lower Central American (LCA) phylogeography studies ( $N = 58$ ), including phylogeographical breaks.

Table S2. Summary of molecular dating methods and divergence dates for major lineages recovered in lower Central American phylogeography studies.

Table S3. Summary of species contributions to phylogeographic breaks recovered in LCA.

Appendix S1. Materials and methods.

Appendix S2. Literature search results.

(Received 23 December 2012; revised 29 November 2013; accepted 3 December 2013; published online 3 February 2014)