Historical biogeography of the Isthmus of Panama

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ABSTRACT

About 3 million years ago (Ma), the Isthmus of Panama joined the Americas, forming a land bridge over which inhabitants of each America invaded the other—the Great American Biotic Interchange. These invasions transformed land ecosystems in South and Middle America. Humans invading from Asia over 12000 years ago killed most mammals over 44 kg, again transforming tropical American ecosystems. As a sea barrier, the isthmus induced divergent environmental change off its two coasts—creating contrasting ecosystems through differential extinction and diversification.

Approximately 65 Ma invading marsupials and ungulates of North American ancestry, and xenarthrans of uncertain provenance replaced nearly all South America's non-volant mammals. There is no geological evidence for a land bridge at that time. Together with rodents and primates crossing from Africa 42 to 30 Ma, South America's mammals evolved in isolation until the interchange's first heralds less than 10 Ma. Its carnivores were ineffective marsupials. Meanwhile, North America was invaded by more competitive Eurasian mammals. The Americas had comparable expanses of tropical forest 55 Ma; later, climate change confined North American tropical forest to a far smaller area. When the isthmus formed, North American carnivores replaced their marsupial counterparts. Although invaders crossed in both directions, North American mammals spread widely, diversified greatly, and steadily replaced South American open-country counterparts, unused to effective predators. Invading South American mammals were less successful. South America's birds, bats, and smaller rainforest mammals, equally isolated, mostly survived invasion. Its vegetation, enriched by many overseas invaders, remained intact. This vegetation resists herbivory effectively. When climate permitted, South America's rainforest, with its bats, birds and mammals, spread to Mexico. Present-day tropical American vegetation is largely zoned by trade-offs between exploiting well-watered settings versus surviving droughts, exploiting fertile versus coping with poor soil, and exploiting lowland warmth versus coping with cooler altitudes.

At the start of the Miocene, a common marine biota extended from Trinidad to Ecuador and western Mexico, which evolved in isolation from the Indo-Pacific until the Pleistocene. The seaway between the Americas began shoaling over 12 Ma. About 10 Ma the land bridge was briefly near-complete, allowing some interchange of land mammals between the continents. By 7 Ma, the rising sill had split deeper-water populations. Sea temperature, salinity and sedimentary carbon content had begun to increase in the Southern Caribbean, but not the Pacific. By 4 Ma, the seaway's narrowing began to extinguish Caribbean upwellings. By 2 Ma, upwellings remained only along Venezuela; Caribbean plankton, suspension-feeding molluscs and their predators had declined sharply, largely replaced by bottom-dwelling corals and calcareous algae and magnificent coral reefs. Closing the seaway extinguished the Eastern Pacific's reef corals (successors recolonized from the Indo-Pacific 6000 years ago), whereas many molluscs of productive waters that once thrived in the Caribbean now survive only in the Eastern Pacific. The present-day productive Eastern Pacific, with few, small coral reefs and a plankton-based ecosystem contrasts with the Caribbean, whose clear water favours expansive coral reefs and bottom-dwelling primary producers. These ecosystems reflect the trade-off between fast growth and effective defence with attendant longevity. Overfishing with new technologies during the last few centuries, however, has caused population crashes of ever-smaller marine animals, devastating Caribbean ecosystems.

Key words: land bridge, invasions, predation, herbivory, extinction, diversification, trade-offs, vegetation zones, sea barriers, environmental change, plankton productivity, coral reefs.

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I. INTRODUCTION

To explain a region's biogeography one must answer two questions. First, what factors shaped a region's biota, its species pool, diversity, intensity of competition and predation, and resistance to disruptive invasion? Second, how does this biota vary over different parts of the region in relation to geographic barriers and different soils and climates, and why? What fundamental trade-offs, and what accidents of history, shape this variation?

Two major events shaped the biota of Central America and its environs. First, 3 million years ago (Ma), an isthmus connected South America, an island continent isolated from most of the rest of the world for over 50 million years (myr), to North America, a larger continent intermittently connected to Eurasia (Simpson, 1965; Collins, Budd & Coates, 1996a; Coates, 1997; MacFadden, 2006a). As a land bridge, the isthmus opened each continent to invasions from the other, triggering the Great American Biotic Interchange (Marshall *et al.*, 1982; Webb, 1991; MacFadden, 2006a). These invasions transformed terrestrial ecosystems in tropical America. The isthmus was also a sea barrier that divided the Caribbean from the tropical Pacific (Woodring, 1966; Vermeij, 1978). This sea barrier induced divergent environmental change on its two sides, creating local biotic crises that caused extinctions within different groups on the two shores. The end result was an upwelling-driven, plankton-based ecosystem on the Pacific side and a coral-reef-based, clear-water ecosystem in the Caribbean (Glynn, 1982; Jones & Hasson, 1985; Vermeij & Petuch, 1986; Vermeij, 1997; O'Dea *et al.*, 2007, 2012). Second, humans, who had crossed from Siberia to Alaska less than 20000 years ago, began settling in Panama roughly 12000 years ago (Cooke, 1997, 2005) as they spread to the tip of South America. Soon thereafter, they had wiped out most mammals weighing over 44 kg (Martin, 1984). As a

result, an array of indigenous South American mammals as magnificent as East Africa's disappeared. Later, human agriculture transformed the landscape, and the recent wave of deforestation threatens widespread extinction. Before European colonization, human impacts on marine biotas were lower, but still significant (Hardt, 2009); during the last few centuries these impacts have accelerated to catastrophic proportions (Jackson, 1997, 2008; Jackson *et al.*, 2001; Knowlton & Jackson, 2008). In short, Central America's terrestrial biota was shaped by a series of invasions and their consequences, whereas until recently the marine biota primarily reflected differential extinctions imposed by divergent environmental change.

First, we consider the terrestrial biota. How was it affected by invasions over the newly formed land bridge, and the far more recent human invasion? What factors drove the regional and altitudinal differentiation of this biota? Correspondingly, we consider how the new sea barrier shaped the marine biotas flanking the two sides of the isthmus; how human, especially European, colonization affected these biotas, and habitat differentiation within these biotas.

II. THE TERRESTRIAL BIOTA

(1) The impact of invaders heralding or using the new land bridge

(a) Background: factors affecting the two Americas' relative resistance to invaders

The impact of the land bridge reflected the history of the two Americas' biotas before the isthmus formed. South America was a long-isolated island continent. It separated from Africa over 100 Ma (Hay *et al.*, 1999) and from Antarctica, and therefore Australia, between 41 (Scher & Martin, 2006)

and 31 Ma (Lawver & Gahagan, 2003). Very diverse, ever-wet, frost-free early (52 Ma) and middle (47.5 Ma) Eocene forests in Patagonia (mean annual temperature 17°C, mean annual rainfall > 1.7 m), had many plant genera, such as *Papuacedrus* (Cupressaceae), *Agathis* (Araucariaceae), *Acmopyle*, *Dacrycarpus* and *Retrophyllum* (Podocarpaceae), *Gymnostoma* (Casuarinaceae) and *Eucalyptus* (Myrtaceae) now restricted to Australia, New Guinea, New Zealand, New Caledonia, Fiji and/or Southeast Asia (Zamaloa *et al.*, 2006; Wilf *et al.*, 2009; Gandolfo *et al.*, 2011). Accordingly, a moist, frost-free corridor through Antarctica must have connected Australia and South America, perhaps during the Palaeocene-Eocene thermal maximum, as is suggested by early Cenozoic fossils near the Antarctic peninsula (Reguero, Marenssi & Santillana, 2002).

Different South American taxa had very different histories. Our mammal story begins near the end of the Cretaceous. At this time South America's mammals included a variety of dryolestoids, whose ancestors reached South America over 100 Ma, presumably from Africa, gondwanatheres, which appeared in India, Madagascar and South America in the late Cretaceous, bearing witness—along with some dinosaurs and crocodiles—to late Cretaceous land connections via Antarctica among these regions, and platypus (Ornithorhynchidae) which originated in Australia more than 110 Ma and subsequently entered South America via Antarctica (Kielan-Jaworowska, Cifelli & Luo, 2004; Krause *et al.*, 2006; Wilson, Das Sarma & Anantharaman, 2007; Rowe *et al.*, 2008; Gelfo *et al.*, 2009; Rougier *et al.*, 2011).

At the very end of the Cretaceous and the beginning of the Palaeocene, approximately 65 Ma, a wave of mammals invaded (Gelfo *et al.*, 2009), although there is no geological evidence for a land bridge between the Americas at that time (Ezcurra & Agnolín, 2012). They quickly replaced nearly all their Gondwanan predecessors (Gelfo *et al.*, 2009), far more completely than the North American mammals invading South America during the last few million years have yet done, although one dryolestoid, *Necrolestes*, survived until 16 Ma (Rougier *et al.*, 2012). Among these invaders were marsupials of North American ancestry (Case, Goin & Woodburne, 2005), which arrived in time to cross via Antarctica to Madagascar in the late Cretaceous (Krause *et al.*, 2006) and to Australia near the beginning of the Cenozoic (Nilsson *et al.*, 2010). These marsupials were accompanied by a variety of hoofed mammals, 'condylarths' which reached Tiupampa, Bolivia, by the very beginning of the Palaeocene. Like their marsupial associates, Tiupampa's 'condylarths' and its one pantodont had identifiable relatives in the late Cretaceous or early Palaeocene of North America, often of the same family (Gelfo *et al.*, 2009). None of North America's creodonts, however, crossed to South America. Surviving invaders quickly adapted to their new home: the marsupials and condylarths of the mid-Palaeocene in Patagonia, presumably descended from these immigrants, all belong to endemic families (Gelfo *et al.*, 2009).

Ezcurra & Agnolín (2012) suggested that at least some South American ungulates crossed from Africa in the late Cretaceous. The fossil deposit containing the two or three marsupial and the two ungulate species on which they based their conclusion was reassigned to the late Palaeocene by Sigé *et al.* (2004), a paper not cited by Ezcurra & Agnolín (2012). The marsupial teeth in this deposit were tentatively assigned to North American families Peradectidae and Didelphidae (Sigé *et al.*, 2004, p. 780). There is no clear evidence that any mammals reached South America from Africa between the time these continents separated and the Eocene.

Xenarthra—sloths, anteaters and armadillos—are also considered part of Australia's early Cenozoic heritage (Simpson, 1980). The earliest known armadillo lived in South America in the late Palaeocene, over 55 Ma (Pascual & Ortiz-Jaureguizar, 2007, p. 120), whereas the earliest known tamanduas lived in Germany 49 Ma (Storch & Richter, 1992), and non-armadillo Xenarthra appear to have lived in South China more than 55 Ma (Storch & Richter, 1992) and in the Antarctic Peninsula approximately 40 Ma (Reguero *et al.*, 2002). Perhaps Xenarthra also reached South from North America, but this is less certain. Well into the Eocene, marsupials, condylarth-derived ungulates and xenarthrans were the three principal non-volant mammal stocks in South America (Simpson, 1980). Finally, flightless carnivorous birds, Phorusrhacidae, appeared in Brazil around 55 Ma (Feduccia, 1999, p. 237). It would appear that, near the end of the Palaeocene, the terrestrial mammals of the two Americas were equally competitive, a circumstance that changed radically in the next 50 Ma.

Descendants of these immigrants radiated extensively. The immigrant marsupials gave rise to mouse-like animals (Flynn, Wyss & Charrier, 2007), small insectivores which also ate fruit and sometimes pollen, convergent on the small lemurs of Madagascar and other basal primates (Rasmussen, 1990; Leigh *et al.*, 2007), and carnivores of various sizes (Patterson & Pascual, 1968, 1972). The physiology of marsupials limits their metabolic rate, which in turn limits their activity level, making them much less effective predators than their placental counterparts (McNab, 2005), thereby providing an opening for predatory phorusrhacid 'terror birds'. The immigrant condylarths soon gave rise to four endemic orders of ungulates, including litopterns and notoungulates. The last survivors of these orders were eradicated by human hunters only 11000 years ago: whereas pyrotheres died out in the late Oligocene, and astrapotheres in the late Miocene (Simpson, 1965, 1980; Patterson & Pascual, 1968; MacFadden, 2006; Gelfo, 2007). Armadillos were diversifying by the end of the Eocene (Pascual & Ortiz-Jaureziguar, 2007, p. 125).

This mammal fauna evolved in splendid isolation (Simpson, 1980) until caviomorph rodents crossed the sea from Africa in the late Eocene, 41 Ma (Antoine *et al.*, 2012) and monkeys crossed from Africa by the late Oligocene (MacFadden, 2006a; Flynn *et al.*, 2007), presumably using as stepping stones the large islands that then existed between the continents (Ezcurra & Agnolín, 2012). In the early Miocene, about 18 Ma, Panama was a peninsula of North America (Kirby, Jones & MacFadden, 2008), well populated with camels, horses, rhinoceroses, peccaries, beardogs and

geomyoid rodents (MacFadden, 2006b; MacFadden et al., 2010; B. J. MacFadden, personal communication; Rincon et al., 2013; Whitmore & Stewart, 1965). A boa dispersed from South America to Panama at least 19 Ma (Head et al., 2012), but no more walking mammals crossed between the continents until about 10 Ma (Campbell et al., 2010), when the land bridge was briefly nearly complete. During the Neogene, South American sloths evolved into a diversity of slow-moving herbivores, terrestrial and arboreal, with ecological analogues among Madagascar's giant lemurs which, like most of Madagascar's mammals, presumably had lower metabolism, longer lives and fewer young than ecological counterparts in more competitive continental settings such as Pleistocene North America (Leigh et al., 2007). An early Miocene litoptern, Thoatherium, had teeth like a browsing horse and one-toed legs convergent on those of the most modern grazing horses (Simpson, 1980), which it may have used to outrun terror birds. Glyptodonts, larger, more heavily armoured, grass-eating relatives of armadillos (Simpson, 1980), and 700 kg grazing dinomyid rodents (Sánchez-Villagra, Aguilera & Horovitz, 2003) also diversified, and the first marsupial (thylacosmilid) sabertooth appeared (Forasiepi & Carlini, 2010), in the Miocene. In the Pliocene, caviomorph rodents gave rise to 1-ton browsing dinomyids (Rinderknecht & Blanco, 2008) and tapir-sized capybaras (Patterson & Pascual, 1972, p. 279) with an elephant-like dentition capable of dealing with tall, coarse grasses (Maglio, 1972, p. 644), and the largest marsupial sabertooth, Thylacosmilodon, evolved (Patterson & Pascual, 1972, p. 261). In the Pliocene, South America's indigenous herbivores were apparently as well adapted to cope with their diets as any in the world. Before the land bridge closed, South America's largest herbivore was probably a 2–3 ton rhinoceros-sized megatheriid ground sloth, and its largest meat-eater was either an unknown phorusrhacid or Thylacosmilus atrox. These were smaller than their largest North American counterparts. With its slow herbivores and relatively ineffective marsupial carnivores, South America's non-volant mammal fauna had become quite vulnerable to invasion.

Other, equally isolated, South American groups were more competitive. Bats probably reached South America in the early Eocene, over 50 Ma, perhaps immigrating from Australia (Teeling et al., 2005). Descendants of an original invading phyllostomid bat include blood-lappers, fish-eaters, predators on small land vertebrates, insect-eaters, nectar-eaters and fruit-eaters (Teeling et al., 2005; Altringham, 2011). Bats, too, evolved in splendid isolation until insect-hawking emballonurid bats crossed the sea from Africa during the Oligocene, about 35 Ma (Teeling et al., 2005). In the late Miocene, molossids had reached Amazonia (Czaplewski, 1996). South American suboscine birds diverged from their old-world counterparts and started diversifying in South America 60 Ma or more (Barker et al., 2004). These suboscines now number 1100 species, ranging from ground-dwelling ovenbirds and ant-followers to fruit eaters and tyrant flycatchers of the canopy (Chesser, 2004). One of these 1100 species, Sapoyoa aenigma, descends from a bird that immigrated from the Old World less than 10 Ma: the others represent an indigenous radiation older and far more diverse than the radiation of phyllostomid bats. Hummingbirds appeared in the South American lowlands 30 Ma and diversified extensively in both lowland and montane habitats (Barker et al., 2004; McGuire et al., 2007). These are fast-moving, high-performance pollinators, competitive with any other pollinating bird. A nectar-eating stem-group hummingbird capable of hovering flight was fossilized in Germany 32 Ma, suggesting that the ancestors of swifts and hummingbirds had diverged in Laurasia (Mayr, 2004).

The contrast with North America was remarkable. North America was a larger continent, intermittently connected to Eurasia, itself intermittently connected to Africa (Webb, 1985). Its terrestrial mammal fauna included gomphotheres and mammoths of African origin, and many Eurasian lineages: horses, deer, camels, rhinoceros, bison and the like, which arrived in successive waves of invasion during times when Alaska was connected to Siberia. Euprimates also dispersed rapidly from Asia through Europe to North America, America's first artiodactyls crossed from Europe, and the first perissodactyls, such as the 'dawn horse' Hyracotherium, spread over Asia, Europe and North America during the Palaeocene-Eocene Thermal Maximum 55 Ma (Gingerich, 2006; T. Smith, Rose & Gingerich, 2006a). One would expect North American terrestrial mammals to be far more competitive than their South American counterparts, because in North America, new mammal species were tested by encounters with a far wider variety of competitors and predators, each of which had survived numerous similar encounters (Darwin, 1859).

Two factors made South American plants, birds, bats and forest mammals much more competitive than many of its open-country non-volant mammals. First, other things being equal, competition is most intense, and pest pressure highest, in the tropics, where productivity is highest and climates most equable (Dobzhansky, 1950; Janzen, 1970; Leigh et al., 2004). This is especially true in large blocks of tropical forest (Leigh et al., 2007). South America has always had large tracts of tropical forest, especially near the coasts facing North America. North America had vast expanses of tropical forest in the Eocene, the 'boreotropical forest' best known from England's London Clay. North America's climate became cooler and drier after the end of the Eocene, however, and this trend continued except for a warm wet period in the middle Miocene. The boreotropical forest's range accordingly shrank drastically (Wolfe, 1975, 1985; Retallack, Bestland & Fremd, 2000). When the Panama land bridge was completed, North America's lowland tropical forest extended no further north than Mexico's Caribbean coast, and North America's tropical forest no longer harboured primates (Wolfe, 1975; T. Smith et al. 2006a). Most of North America suffered from freezing winters or a dry climate, as it does now.

Second, in contrast to mammals, and even birds, new genera of plants have invaded South America from overseas ever since it separated from Africa 100 Ma (Pennington & Dick, 2004). South America's plants have survived many

invasions by boreotropical plants, including *Protium* (Burseraceae), descendants of Burseraceae that evolved in Mexico 60 Ma (Weeks, Daly & Simpson, 2005), Cinchonoideae (Rubiaceae) that crossed from Africa via Europe and North America to South America 50 Ma, when Greenland had a subtropical climate, giving rise to 130 modern species (Antonelli *et al.*, 2009), and Meliaceae (Muellner *et al.*, 2006), including *Cedrela*, which reached the boreotropics from Africa 48 Ma and invaded South America 23 Ma (Muellner *et al.*, 2010). Even after North America's boreotropical forest had begun to shrink, *Ocotea* (Lauraceae) of dry forest ancestry invaded 23 Ma. A descendant passed from thence to South America 20 Ma (Chanderbali, van der Werff & Renner, 2001): its descendants number 200+ species, lowland and montane (Erkens *et al.*, 2007). The genus *Guatteria* (Annonaceae) originated in Africa over 50 Ma, crossed via Greenland to North America's boreotropical forest, and reached South from Central America some time during the Miocene (Erkens, Maas & Couvreur, 2009). The descendants of the *Guatteria* that invaded South America now number 200+ species (Erkens *et al.*, 2007).

Trees and shrubs have also invaded across the water from Africa, among them Chrysophylloideae (Sapotaceae), which crossed to South America 70 Ma (Bartish *et al.*, 2011), *Carapa* (Meliaceae), *Saccoglottis* (Humiriaceae), and *Psychotria* (Rubiaceae) (Nepokroeff, Bremer & Sytsma, 1999; Renner, 2004), and *Symphonia globulifera* (Guttiferae), which crossed to South America 20 Ma (Dick, Abdul-Salim & Bermingham, 2003). These and many other invaders, who survived confrontation with many efficient competitors and herbivores at their place of origin, must have enhanced the South American vegetation's competitiveness and resistance to herbivory. To be sure, during the Eocene the boreotropical forest of North America must have been more competitive than its counterpart in South America, for it was extensive, and received immigrants from Asia, Europe and South America (Wolfe, 1975; Davis *et al.*, 2002). After the climate cooled, however, tropical North America received no further immigrants from Asia, and far fewer from Europe. Yet Mesoamerica was invaded 20 Ma by *Symphonia globulifera* (a different lineage from that reaching South America) and less than 5 Ma by understorey herbs of the genus *Costus*, both from Africa (Dick *et al.*, 2003; Kay *et al.*, 2005). Nonetheless, botanically speaking, when the land bridge formed, tropical North America was a satellite of tropical South America, in the same sense that Madagascar is a satellite of Africa.

Some plant families originated in South America and subsequently dispersed through the boreotropics of North America and Europe to Africa and Asia, including Malpighiaceae (Davis *et al.*, 2002) and Bignoniaceae (Grose & Olmstead, 2007; Olmstead *et al.*, 2009). Compositae, the most diverse plant family on earth, may have originated in subtropical Patagonia about 50 Ma (Barreda *et al.*, 2010).

Two phenomena suggest that South America's plants have experienced, and coped with, herbivore pressure as severe as anywhere in the world. First, continents where large herbivores knocked over trees, as elephants do in Africa and recently did in southeast Asia, have fast-growing trees that rapidly occupy the gaps opened by such megaherbivores. The same was true of South America, where huge ground sloths could knock down trees. Two of the world's major blocks of tropical forest harbour fast-growing pioneer trees that house aggressively protective ants: *Macaranga* in southeast Asia (Heil *et al.*, 1997; Davies *et al.*, 2001), and *Cecropia* in South America (Schupp, 1986); in Africa, the pioneer *Musanga* resembles *Cecropia* but lacks protective ants (Mabberley, 2008). By contrast, islands as large as Madagascar lack such aggressive secondary vegetation (Koechlin, 1972; Phillipson, 1994). As a result, secondary forest of isolated islands, even those as large as New Guinea, is far more vulnerable to introduced invaders, including *Cecropia*, than is their mature forest (Lugo, 2004; Novotny *et al.*, 2004; Rakotonirina, Jeannoda & Leigh, 2007).

Second, like other continents and unlike isolated islands, even Madagascar, whose ecosystems are less competitive (Leigh, Vermeij & Wikelski, 2009), South America evolved both grasslands—a response to vertebrate herbivory—and grazers, which both exploited grasslands and protected them from colonizing forest trees (Retallack, 2001*b*, p. 316; Leigh *et al.*, 2007; Leigh, 2010). To understand this phenomenon, recall that the driest forests are the most susceptible to vertebrate herbivores. Woodlands receiving 200–400 mm of rain per year were the first to be replaced by short-sod grassland (Retallack, 2001*a*). This grassland was adapted to sustain enough vertebrate herbivores to keep trees out, rather than to minimize their consumption (McNaughton, 1985; Retallack, 2001*a*, 2007). Such grassland was maintained by grazers with high-crowned hypsodont teeth, designed primarily to withstand wear from grit consumed while grazing close to the ground (Damuth & Janis, 2011). Short-sod grassland evolved 19 Ma in Nebraska and 17 Ma in Kenya (Retallack, 2001*a*).

A fauna dominated by hypsodont notoungulates appeared in Tinguiririca, Chile 32 Ma (Flynn *et al.*, 2007, 2003), over 10 myr before hypsodont grazers and short-sod grassland coevolved elsewhere (Retallack, 2001*a*, 2007). Although South American mammals first evolved hypsodonty in Patagonia 38 Ma, grassland did not evolve there before 18.5 Ma (Strömberg *et al.*, 2013): indeed, there is no evidence of grassland anywhere in South America before the middle Miocene (Jacobs, Kingston & Jacobs, 1999). Although hypsodont notoungulates with broad muzzles characteristic of grazers evolved in the Oligocene (Jacobs *et al.*, 1999), and the hypsodont Tinguiririca notoungulates looked like grazers to their discoverers (Flynn *et al.*, 2003), this hypsodonty did not evolve for grazing. Late Cretaceous gondwanatheres evolved hypsodonty to cope with grit consumed while burrowing (von Koenigswald, Goin & Pascual, 1999), and South American ungulates first evolved hypsodonty to cope with grit ingested while browsing low vegetation (Billet, Blondel & De Muizon, 2009; Damuth & Janis, 2011), or volcanic ash that dusted the forest leaves they ate (Strömberg *et al.*, 2013).

Fire played little role in the evolution of short-sod grasslands in Oregon and Nebraska (Retallack, 2004,

p. 231). This was probably true in South America as well: fire-resistant savanna shrubs and trees only evolved there 5–10 Ma, when tall, flammable C4 grasslands were spreading in South America and in other continents (Retallack, 2001a; Simon et al., 2009).

(b) Invasions associated with the new land bridge

To make sense of what follows, we show that successful invaders exploit niche opportunities: they succeed because they can exploit some habitat or set of resources, or resist would-be consumers, better than any native. Consider *Symphonia globulifera*, a tree species that invaded South America from Africa 20 Ma (Dick *et al.*, 2003). Its descendants have spread throughout tropical lowland moist and wet forest in South America on both good soils and poor. Before human settlement, it averaged more than one tree at least 10 cm diameter at breast height (dbh) per hectare in South America's half-billion hectares of lowland moist and wet tropical forest. Presumably it had at least 10 million reproductives, 1 per 50 ha. If a neutral lineage, whose trees' prospects of death and reproduction are identical to those of the forest's average tree, is lucky enough to survive n generations, the probability that it has nk reproductives at generation n is $\exp - k$ (Fisher, 1930; Leigh, 2007). For a tree generation time of 50 years, so that *Symphonia globulifera* in South America had 400000 generations, the probability of its spreading so far by chance alone is e^{-25}, less than 10^{-10} (Leigh, 2007); therefore it must have spread due to some advantage over its competitors. If climate never reduced South America's lowland forest area by more than two-thirds over more than a million years, then climate change does not impugn this conclusion.

A second conclusion follows from this invader's spread. Although its descendants could spread over tropical South America, there are few hectares where these descendants comprise more than 2% of the trees. Other trees differed enough from *Symphonia globulifera* to avoid competitive replacement by this invader. In other words, the many tree species of South America differ in ways that allow them to coexist (Leigh *et al.*, 2004).

Similar conclusions emerge from the manner in which South American freshwater fish invaded Central America after the land bridge was complete. Different genera invaded at different times: one genus did not prevent the invasion of another. Indeed, each genus spread rapidly once it invaded, separating into adjacent, allopatric species. Only once did a species invade a part, and that only a small one, of a congener's range. Here too, successful invasion depends on niche opportunity (Reeves & Bermingham, 2006).

Bear-sized ground sloths of the family Megalonychidae had reached North America, perhaps 10 Ma when a nearly complete land bridge was briefly available (Coates *et al.*, 2004, p. 1342), whereas coati-like animals of the family Procyonidae, gomphotheres, tapirs and peccaries reached South America at least 7 Ma (Simpson, 1965; Webb, 1997; Campbell *et al.*, 2010). After the land bridge was completed approximately 3 Ma, but before humans arrived, 19 families

of non-volant land mammals had moved north, and 17 south, across it (Webb, 2006). Far fewer genera moved north than south, however, and the northward-moving genera diversified far less than their southward-moving counterparts. Thirty-five percent of North America's pre-human tally of mammal families, but only 20% of its genera, derived from South America. By contrast, 40% of South America's mammal families, and 50% of its genera, derive from North America (Marshall *et al.*, 1982).

When the land bridge was completed approximately 3 Ma, a corridor of savanna and grassland allowed grazers and other open-country animals to move between North and South America (Webb, 1991, 1997). Thus, in the first phase of the interchange, grazing ground sloths of three families, rhinoceros-like ungulates (*Toxodon*), capybaras [huge grazing rodents with an elephant-like dentition: their modern relatives are the only native mammals that eat *Saccharum spontaneum*, a tall coarse grass introduced to Panama from south Asia, where elephant and rhinoceros, but no smaller mammals, graze upon tall stands of this grass (Karki, Jhala & Khanna, 2000)] and glyptodonts with powerful plant-grinding jaws, often pictured with maces at the end of their tails, crossed from South into Central America. Other open-country animals, such as armadillos, termite-eating giant anteaters (*Myrmecophaga*), marsupial opossums and the carnivorous open-country 'terror bird' *Titanis*, crossed with them. Of these, only opossums, megalonychid ground sloths and porcupines reached 50° N. Armadillos, glyptodonts and mylodontid ground sloths reached 35°N, capybaras, 30°N. Few of the other invaders from South America left the tropics (Webb, 1991). None of these invaders diversified sufficiently in North America to produce new genera (Webb, 2006), although both megatheriid ground sloths such as the 6-m tall *Eremotherium* (Simpson, 1980, p. 91; Webb, 1997, p. 110) and phorusrhacid terror birds attained maximum size after they invaded North America.

Fates of first-phase mammal invaders from North America were quite different. North American grazers such as horses and Camelidae, and open-country deer and gomphotheres, moved south to the Argentine pampas and Patagonia. Descendants of these invading ungulates steadily replaced their South American counterparts, perhaps because they coped better with placental carnivores, with which they evolved: cursorial ungulates of South American origin suffered most (Webb, 1991). When humans arrived, the notoungulates *Toxodon* and *Mixotoxodon*, and the litopterns *Macrauchenia* and *Windhausenia*, were among the few surviving ungulates of South American stock (Martin, 1984). Other animals of open country and thorn scrub, such as field mice, which diversified spectacularly in South America, and scrubland peccaries, came with these invading grazers. Finally, five families of carnivores, including cats of all sizes and the placental counterpart of *Thylacosmilus*, *Smilodon*, moved south. Although the late Miocene invasion of omnivorous procyonids did not depress the abundance or diversity of South America's marsupial carnivores, no fossil stratum contains both marsupial and placental meat-eaters.

Indeed, 2 million years separate the last record of marsupial carnivores (and the last certain records of South American phorusrhacids) from the first appearance there of placental carnivores (Prevosti, Forasiepi & Zimicz, 2013), but it would be odd for mammalian carnivores to be absent from a modern continent for 2 myr. The terror bird *Titanis walleri* of Florida's late Pleistocene warns us that marsupial carnivores might well have lived to encounter, and be ousted by, placental flesh-eaters, just as placental dingos ousted thylacines and Tasmanian devils from continental Australia (McNab, 2005).

In contrast to their South American counterparts, North American invaders diversified sufficiently to produce at least 110 new mammal genera in South America—46 or more among the Muridae alone (Webb, 2006). Moreover, North American invaders penetrated more deeply into South America than vice versa. Gomphotheres, horses, Camelidae and deer all penetrated to 50°S, as did field mice, shrews, wolves, mustelids and cats. As a group, mammals of the North American plains, tested by innumerable competitors and predators from Eurasia, should have proved superior to their South American counterparts, which evolved for so long in isolation, in a smaller expanse of open country, populated by far less effective carnivores (Webb, 1991).

Later, tropical forest took over the land bridge, especially its eastern end, preventing such late-arriving grazers as bison, antelopes and mammoths from reaching the grasslands and open woodlands of South America (Webb, 2006). The role of tropical forest in blocking open-country immigrants is revealed by the capybaras that reached the Panama Canal after 1970 (the capybaras that had invaded in the late Pliocene had died out since), because only then was enough land deforested between their native llanos of Venezuela and the Panama Canal for them to spread into Panama. Because South America had much the larger block of tropical forest, monkeys, marmosets, agoutis, pacas, spiny rats, armadillos, forest anteaters and tree sloths of two families, as well as bats, immigrated into Central America's moist and wet forests, coexisting with the squirrels, forest deer and peccaries, cats, mustelids, coatis and mice from North America. The forest presumably provided cover that made its mammals far less vulnerable than open-country counterparts to placental predators. Is it an accident that so many of the mammals of South American origin that now live in Central American forests descend from the monkeys and caviomorph rodents that crossed over from Africa during the Palaeogene?

The story is somewhat similar for passerine birds except that, in the absence of fossils, we must rely on molecular phylogenies, which do not reveal groups that crossed but died out afterwards. Birds of diverse families well represented in open habitats, such as the tyrant flycatchers and tanagers of South America or the wrens and thrushes of North America, colonized Caribbean islands and crossed between continents long before the land bridge formed. Most of these early crossers moved from North to South (Weir, Bermingham & Schluter, 2009). On the other hand, birds of families restricted to tropical forest, such as antbirds, woodcreepers and tapaculos never colonized Caribbean islands, and they moved from South to North America after the land bridge formed (Weir *et al.*, 2009).

Comparing families of plants, birds, and the few other terrestrial vertebrates whose phylogenies have been assembled, plants crossed between the Americas sooner than animals, even birds (Weir *et al.*, 2009), as one would expect considering their ability to invade from overseas. Most of the plants of Central American lowland forest immigrated from South America. This is true even for genera that immigrated to South from North America long before the land bridge formed, such as *Ocotea* and *Guatteria*. After all, South America had a much larger area of tropical forest. Most of Central America's canopy trees and large lianas, especially those of seasonal forest, immigrated from Amazonia, whereas most epiphytes and understorey herbs, shrubs and treelets (including trees as large as *Inga*; Richardson *et al.*, 2001) colonized from the foothills of the northern Andes (Gentry, 1982).

Central America, however, abounded in mountains, bordered on the west by the extensive highlands of Mesoamerica. Many Central American tree genera either originated in these highlands or immigrated through them from temperate-zone North America. Other mountain genera immigrated to Central America from the South American Andes: some of them reached the Mesoamerican highlands.

Quercus is the most conspicuous montane genus in Central America. Oaks dominate many Central American montane forests (Nixon, 2006). *Quercus* evolved in North America early in the Eocene, and spread since to Europe and southeast Asia. Nowadays *Quercus* is most diverse in southern Mexico. Costa Rica has 14 species of *Quercus*, some of which have spread into the dry Pacific lowlands; Panama has 12, all montane. One species reached the Colombian Andes 350000 years ago (Hooghiemstra, 2006), ousting the former dominant, *Podocarpus*, a conifer that originated in Gondwana. Nonetheless, *Podocarpus* itself spread across the new land bridge, and has reached Mexico (Ornelas, Ruiz-Sánchez & Sosa, 2010).

In Central America, oak forests shelter many other species of both North and South American ancestry (Kappelle, 2006). Genera from North America and Eurasia include *Magnolia*, *Alnus*, *Cornus*, *Prunus*, *Salix*, *Styrax* and *Viburnum*: South American genera include *Drimys*, *Weinmannia* and *Podocarpus*, all with impeccable Gondwanan credentials, and many others. In Panama, these genera have few species (*Magnolia*, 4; *Alnus*, 1; *Cornus*, 1; *Prunus*, 3; *Salix*, 1; *Styrax*, 4; *Viburnum*, 3; *Drimys*, 1; *Weinmannia*, 6; *Podocarpus*, 4). All these species are confined to the highlands except for *Podocarpus guatemalensis*, which extends from 1200 m to sea level (Smithsonian Tropical Research Institute and University of Panama Herbaria database: Correa, 2011). Many of the plants invading Neotropical mountains from eastern North America belong to the same genera that invaded the tropical mountains of Southeast Asia from eastern China.

Very high Andean habitats were colonized by long-distance dispersal after the isthmus formed. For example, *Lupinus* (Leguminosae) dispersed to the Andes from western North America less than 2 Ma. This invader has 81 living

species among its descendants, most of which grow in paramo and other montane grasslands above 3000 m altitude. The two species of *Lupinus* in Panama are part of a clade originating in Mexico that spread toward, but not into, South America (Hughes & Eastwood, 2006).

In sum, many North American invaders, especially placental carnivores and open-country herbivores, spread far, replaced all South American marsupial carnivores and many open-country herbivores, and transformed its ecosystems. A few South American invaders spread far, but otherwise, they experienced no such success. South America's isolation had left it with relatively ineffective marsupial carnivores. In open country, with no place to hide, many larger herbivores were vulnerable to invading placental carnivores, even though surviving South American herbivores (and, presumably, those that went extinct) are as adapted to consume and digest plant matter as any in the world. South America's tropical mammals, and its birds and bats, which evolved in equal isolation, but were less vulnerable to placental carnivores, and its plants, which were continually tested by invaders from other continents, survived the interchange more successfully. As on other continents, but never on even large islands, South American vegetation parried herbivores by evolving aggressive pioneers, and by the coevolution of sod grassland with grazers. When climate permitted, South American rainforest crossed the land bridge and spread as far as Mexico. This forest's birds, bats and non-volant mammals accompanied it, and some birds and bats spread beyond its limits.

(c) The human onslaught and its impact

Less than 20000 years ago, humans crossed from Siberia to Alaska. At least 11000 years ago, they had spread throughout the isthmus and all its habitats, eradicating its gomphotheres, horses and ground sloths (Cooke, 2005). Humans had spread throughout South America by 10000 years ago, killing all North and South American species of mammals weighing 400 kg or more, including all Proboscideans and all ground sloths (Table 1). Indeed, in both Americas they extinguished most mammal species weighing 44 kg or more (Table 2). They did the same in Australia over 40000 years ago, and in Madagascar about 1000 years ago (MacPhee & Marx, 1997; Prideaux *et al.*, 2007; McGlone, 2012; Rule *et al.*, 2012).

Human colonists began altering vegetation in the seasonally dry forests of the Pacific lowlands as soon as they reached the isthmus. When productive varieties of maize

Table 1. Weight (kg) of largest herbivore H and largest carnivore C on various land masses before and after human settlement (data from Burness *et al.*, 2001)

	H (before)	C (before)	H (after)	C (after)
N. America	6000	340	540	80
S. America	4200	390	250	100
Australia	1150	73	90	25
Madagascar	400	18	8	8

Table 2. Number of genera on various land masses with mammals weighing ≥ 44 kg before and after human colonization (data from Martin, 1984)

	Before human settlers	After human settlers
North America	45	12
South America	58	12
Australia	19	3

arrived in Panama from Mexico 7000 years ago, agricultural clearing began in these lowlands (Cooke, 2005). Later, when cool-tolerant varieties of maize appeared, agriculture spread to seasonal forests at altitudes over 1500 m, and later to the more seasonal forests of the Caribbean lowlands (Cooke, 2005). By the time European invaders appeared, Panama's Pacific side was so thoroughly cleared that people there were eating open-country animals such as white-tailed deer, *Odocoileus virginianus*, but no forest animals such as agoutis, *Dasyprocta punctata*, whereas on the Caribbean side agoutis were still eaten. European colonization brought epidemics and oppression, reducing indigenous populations by 90% or more and allowing widespread forest recovery. After 1950, a wave of deforestation began that is now disrupting the forest's continuity and threatening to restrict it to well-protected parks and reserves. This deforestation may well cause major extinctions among both plants and animals.

(2) Vegetation types in the Isthmus

(a) Introduction

Many more or less distinct types of vegetation occur within the isthmus of Panama. In natural forest, the species composition of lowland wet forest, which receives more than 300 mm of rain in the year's driest quarter, differs from that of the more seasonal lowland moist forest, with 100–300 mm in the year's driest quarter. In turn, lowland moist forest differs from lowland dry forest, which receives less than 1600 mm rain per year and less than 100 mm in its driest quarter. This range of forest types can be seen as one passes through forests near the Panama Canal from Panama's wet Caribbean side to its drier Pacific side (Pyke *et al.*, 2001; Condit *et al.*, 2005). The structure, dynamics and species composition of lowland forest varies with soil quality. Swamp forest, and seasonally flooded riparian forest have a distinctive species composition. Mangrove forest, flooded daily or less often by salt or brackish water, have a distinctive structure and species composition. Finally, lowland and montane forests also differ in species compositions.

(b) Trade-offs and divergence among vegetation types

What causes vegetation differences? Do they arise by chance, or do they reflect adaptation to different conditions? Simply by chance, two trees are more likely to belong to different species if they are further apart. After all, different species

arise in different places, and young are dispersed only a limited distance from their parents (Chave & Leigh, 2002; Condit *et al*., 2002). Gilbert & Lechowicz (2004) accordingly compared the impacts of distance and habitat difference on differences in species composition among $50\,\text{m}^2$ plots. All plots were within a hilly $10\,\text{km}^2$ reserve near Montréal, Canada. Plots were positioned so that difference between the habitats of two plots—as defined by slope, topographic position, soil acidity, fertility, moisture content, light availability etc.—was not correlated with the distance between them. Habitat differences had a large impact on differences in the plots' species composition, distance between them did not.

Therefore, we assume that differences in vegetation reflect environmental differences. Environmental conditions impose many trade-offs on plants. One trade-off is between growing rapidly where there is no dry season versus drought resistance. Common-garden experiments show that trees in the Malay-Thai peninsula that grow in both aseasonal and mildly seasonal rainfall regimes have denser wood, and stronger xylem vessels, more resistant to cavitation, than congeneric trees that grow only in ever-wet forests. Denser wood and stronger xylem vessels lower maximal stomatal conductance and therefore photosynthetic capacity, which makes trees growing in both seasonal and ever-wet forests grow more slowly than congeners that grow only in ever-wet forests (Baltzer *et al*., 2009). Indeed, the Kangar-Pattani line, near the Malay-Thai boundary, which separates ever-wet from seasonal forest, is a 'demarcation knot', a site of major turnover among plant genera.

In Panama, seasonal drought clearly restricts many plant species to regions with milder dry seasons. Engelbrecht & Kursar (2003) and Engelbrecht *et al*. (2007) measured the drought sensitivity of seedlings of 48 tree species in central Panama by the proportionate decrease in their survival when left dry for 22 weeks relative to the survival of well-watered counterparts. The more sensitive to drought a tree species, the lower the number of stems at least 1 cm dbh in a 4-ha dry forest plot near Panama's Pacific side per stem in a wetter 5-ha plot with a shorter dry season on Panama's Caribbean side ($r^2 = 0.44$, N = 23: Engelbrecht *et al*., 2007).

On the other hand, it is most unlikely that wet-forest specialists exclude dry-forest species from wetter Panamanian forests by outgrowing them: here, wet-forest specialists have lower photosynthetic capacity than their dry-forest counterparts (Santiago *et al*., 2004*b*). Disease and pests are much more likely to be responsible for the observed exclusion. In comparable climates, more diverse forests suffer less damage from insect pests (Jactel & Brockerhoff, 2007). Pest pressure appears to promote tree diversity by attacking plants of each species more severely where they are more common (Comita *et al*., 2010; Mangan *et al*., 2010). Closely related, coexisting tree species of the diverse genus *Inga* differ most conspicuously in their anti-pest defences (Kursar *et al*., 2009), as if character displacement in defence mechanisms allows them to coexist. And indeed, as in tropical forests elsewhere (Leigh *et al*., 2004), Isthmian trees are more diverse in tropical forests with wetter dry seasons (Table 3), where pressure from pests and pathogens is presumably more intense (Givnish, 1999). Rainfall during the dry season, rather than total annual rainfall, is the decisive influence on tree diversity, as is shown by data from 25-ha plots in lowland continental tropical forests from around the world (Table 4).

Another well-documented trade-off is that between growing fast on rich soil and surviving on poor soil. In the Allpahuayo Reserve of Amazonian Peru near Iquitos, clay soil interdigitates with infertile white sand. Many white-sand specialists have sister species on adjacent clay soils. Fine, Mesones & Coley (2004) grew seedlings of several pairs of sister species, with one member specialized to each soil, on both clay and white sand. Seedlings of clay-soil specialists outgrew their white-sand sisters on both soil types, but on white sand, clay-soil specialists quickly succumbed to pests or pathogens (Fine *et al*., 2004). This trade-off arises because, on poorer soils, trees must devote more energy to the growth of roots needed to obtain nutrients, diminishing the energy available for trunk growth, thereby enhancing survival at the expense of slower growth (Keyes & Grier, 1981; Leigh, 1999, 2008). Indeed, this trade-off affects many aspects of plant life. In western Amazonia, where soils are more fertile than further east, trees are built to grow faster. On the poorer soils of Central and Eastern Amazonia, trees are built to last, with denser wood and tougher, longer-lived leaves with greater mass per unit area; they grow more slowly, produce less wood, and live longer than their counterparts to the west (reviewed in Leigh, 2008).

The trade-off between fast growth on good soil versus survival on poor influences the species composition in sites throughout the world. The 52-ha rainforest plot at Lambir, Sarawak (Table 4), has several very different soil types. The least fertile soil favours trees that grow slowest and live longest. The soil is most fertile in the poorly lit hollows between ridges; Lambir's fastest-growing, shortest-lived trees grow on somewhat less fertile soils where light is more abundant (Russo *et al*., 2008). The trade-offs between fast growth in good light and survival in shade, and between fast growth on good soil and survival on poor, are to a large extent facets of a single trade-off between growing fast in favourable conditions and surviving where some essential resources are in short supply (Baltzer & Thomas, 2010). This fundamental trade-off underlies the world-wide 'leaf economics spectrum' (Wright *et al*., 2004) which predicts that plants of favourable habitats have shorter-lived, lighter-weight leaves with higher concentrations of nitrogen and phosphorus, higher photosynthetic capacity and higher respiration rates. It appears, however, that, at least at Lambir, the phosphorus content of leaves primarily reflects soil quality (Baltzer & Thomas, 2010). As the trees on a particular soil type age, these trade-offs' consequences have more time to take effect, and species associated with a particular soil type become progressively more dominant there (Russo *et al*., 2005): these trade-offs appear to associate tree species with particular habitats.

Table 3. Dry-season severity and tree diversity in selected lowland tropical 1-ha neotropical forest plots

Site	P (mm)	P2 (mm)	N	S	Fisher's α
Santa Rosa, Costa Rica	1614	0	354	56	19
Barro Colorado Island, Panama	2600	60	429	91	35
Nusagandi, Kuna Yala, Panama	3324	123	559	191	102
Choco, Colombia	7000	400	664	252	148

Number of trees $\geq$ 10 cm in diameter at breast height (N), number of species (S) among them, and Fisher's α as calculated from the equation $S = \alpha \ln(1 + N/\alpha)$, for selected 1-ha plots with annual rainfall (P) and rainfall during the two driest consecutive months of the year (P2) Data for Santa Rosa are from Burnham (1997), data for Barro Colorado Island are from Leigh (1999), data for Nusagandi are from R. Paredes (unpublished) and data for Choco are from Faber-Langendoen & Gentry (1991).

Table 4. Dry-season severity and tree diversity in selected lowland tropical 25-ha forest plots

Site	P (mm)	P3 (mm)	N	S	Fisher's α
Huai Kha Khaeng, Thailand	1476	46	10938	185	32
Barro Colorado Island, Panama	2551	131	10278	206	36
Korup, Cameroon	5272	172	12296	261	47
Pasoh, Malaysis	1788	318	13276	604	130
Lambir, Sarawak, Malaysia	2664	498	15916	851	193

Number of trees $\geq$ 10 cm in diameter at breast height (N), number of species among them (S), and Fisher's α as calculated from the equation $S = \alpha \ln(1 + \mathcal{N}/\alpha)$, for selected 25-ha plots with annual rainfall (P) and rainfall during the three driest consecutive months of the year (P3). Climate data are from table 4.3 of Leigh (2004); tree data are from table 7.1 of Condit *et al.* (2004).

Along a gradient from strongly to weakly seasonal climates in central Panama, forests grade from fast-growing to slower-growing and more stress tolerant. Here, the trade-off between growing fast on good soil and surviving on poor overrides the trade-off between growing fast in less seasonal climates and surviving seasonal drought. In a series of four lowland forests with progressively shorter dry seasons, annual rainfall is 1800, 2300, 3100 and 3500 mm, respectively (Santiago *et al.*, 2004*b*). In the driest forest, canopy leaves have the shortest lives, the lowest mass per unit area, and the highest nitrogen content and photosynthetic capacity per unit leaf mass. Leaf lifetime, leaf mass per unit area, and leaf toughness are greater, and nitrogen content and photosynthetic capacity lower, in wetter forests, especially in the two wettest ones, in part because deciduous trees with shorter-lived leaves are less common in wetter forests (Santiago *et al.*, 2004*b*). In the canopy, longer-lived leaves are tougher and have higher lignin to nitrogen ratios. In fallen leaves, lignin to nitrogen ratios were higher in the two wetter forests. The higher this ratio, the lower the nitrogen mineralization rate (Santiago, Schuur & Silvera, 2005). Although there is more nitrogen in the soil in wetter forests, these soils are in effect less fertile. Moreover, leaf phosphorus content, and the soil's content of extractable phosphorus, are lower in wetter forests (Santiago *et al.*, 2005). As in Borneo (Baltzer & Thomas, 2010), lower leaf phosphorus content indicates poorer soil. Maximum hydraulic conductivity per unit leaf area and maximum stomatal conductance increased in proportion to photosynthetic capacity per unit leaf area, which was higher in drier forests; all three were lower in trees with denser wood, which were more common in wetter forests (Santiago *et al.*, 2004*a*).

Another trade-off with fundamental biogeographic impact is that between growing fast at low altitudes and surviving higher up. Temperature declines with altitude. As temperature declines, so does the rate at which nitrogen is recycled, photosynthetic capacity, and the weight of 'fine litter' falling per hectare per year (Marrs *et al.*, 1988; Heaney & Proctor, 1989; Pendry & Proctor, 1996). Does the change in species along an altitudinal gradient reflect the trade-off between exploiting abundant nutrients and photosynthate, and making do with a more restricted supply? Whether or not this is the driving trade-off, species composition changes with altitude before reaching the 'cloud line', suggesting that species have evolved a continuum of responses to some trade-off connected with altitude, as they do to the trade-off between growing fast in bright light and surviving in shade (Wright *et al.*, 2003). Altitudinal gradients in tree species composition have been documented for Costa Rica (Lieberman *et al.*, 1996). The tree species composition of montane forest also depends markedly on soil quality (Anderson, Turner & Dalling, 2010).

As a rule, cloud covers tropical mountains down to a certain altitude, which is lowest on isolated hills near the coast, and higher on larger mountain massifs, especially those further from the coast. Forest height drops sharply, and vegetation composition changes abruptly, at the cloud line (Sugden, 1982; Proctor *et al.*, 1988). Why this happens is unclear (Leigh, 1999). Where the clouds are present for many daytime hours, the soil becomes waterlogged, and transpiration falls disproportionately to the decrease in amount of sunlight received (Bruijnzeel *et al.*, 1993). But the vegetation changes similarly at a site where clouds come in only at night, and the soil dries out during the day (Cavelier & Mejia, 1990).

III. THE MARINE BIOTA

(1) Background: the marine biome before the isthmus began to form

The consequences of forming the Central American isthmus were as dramatic in the sea as they were on land, especially on the Caribbean side. Severe reductions in productivity and high rates of extinction and diversification transformed the western Atlantic, especially the Caribbean, from a region dominated by suspension-feeding animals to one with abundant reefs and clear water, where most of the primary production occurs on the sea floor. The Panama Paleontology Project, initiated by Jeremy Jackson and Anthony Coates at the Smithsonian Tropical Research Institute (Collins & Coates, 1999), has been instrumental in piecing together the events that have propelled this transformation. What were conditions like before the seaway began to shoal 13 to 11 Ma, and the isthmus began to close?

During the Oligocene and the first half of the Miocene, North and South America were separated by one or more wide, deep seaways connecting the Atlantic and Pacific Ocean (Droxler *et al.*, 1998), that had existed since the Jurassic (Smith, 1983). Central America was an island arc that became a North American peninsula (Coates *et al.*, 2003, 2005; Kirby *et al.*, 2008; Farris *et al.*, 2011). Biotas from Trinidad, or even easternmost Brazil, to Esmeraldas in Ecuador, the Greater Antilles (but not Florida or the northern Gulf coast) and Panama's island arc or peninsula were similar enough to prompt Woodring (1974) to name this region the Miocene Caribbean faunal province (Landau, Vermeij & da Silva, 2008). A relatively rich, peculiar fauna of molluscs, corals, benthic foraminifera, echinoids and bryozoans characterized this region (Woodring, 1974; Glynn, 1982; Jones & Hasson, 1985; Lessios, 2008). We prefer to emphasize that the marine tropical biotas of America and the eastern Atlantic (the Mediterranean and West Africa), together forming the Atlantic-Eastern Pacific realm (AEP), share a common Oligocene heritage. This realm was already taxonomically distinct from the Indo-West Pacific (IWP) realm by the Late Oligocene (Renema *et al.*, 2008). This happened well before the seaway connecting the Atlantic to the Indian Ocean in the Middle East was blocked by land, first in the Early Miocene (Burdigalian stage, 20 to 16 Ma) and then from the middle Miocene (Langhian stage, 16 to 14 Ma) onward (for review see Vermeij, 2012). Thereafter, the tropical American biota evolved and diversified nearly independently of that in the IWP, until the Pleistocene, when various species, including corals, the crown-of-thorns starfish, *Acanthaster planci*, and dozens of crustaceans and molluscs, invaded from the Indo-Pacific, enriching the Eastern Pacific biota without causing noticeable disruptions (Vermeij, 2005*a*). Biotas of the coasts and islands of the Atlantic and eastern Pacific have differentiated since the Oligocene as oceanic and land barriers have appeared and disappeared (see e.g. Woodring, 1974; Petuch, 2004; Vermeij, 2005*a*; Landau *et al.*, 2008). The degree of geographic differentiation varies among different groups of organisms according to their preferred habitats and their capacity for dispersal.

To understand the events surrounding the closing of the seaway, let us consider the marine biota when a wide, deep seaway still separated the Americas. During Late Oligocene time, the Caribbean region had large, diverse reefs; but these suffered a catastrophic decline near the end of the Oligocene (Johnson, Jackson & Budd, 2008; Johnson, Sanchez-Villagra & Aguilera, 2009), when plankton production increased greatly in the Caribbean (Edinger & Risk, 1994; Johnson *et al.*, 2008). Reefs in the Caribbean declined, and the Caribbean's plankton production increased, during the Early Miocene thanks to a general change in the direction of currents, corroborated by ocean simulations (von der Heydt & Dijkstra, 2005). A westward-flowing current through the Central American seaway during the Late Oligocene was replaced by an eastward-flowing current in the Early Miocene (Bartoli *et al.*, 2005; von der Heydt & Dijkstra, 2005, 2006; Schneider & Schmittner, 2006). Judging by the Pacific-type foraminifera and the cool waters prevailing in the latest Miocene Chagres Formation on Panama's Caribbean side, this eastward flow continued, at least intermittently, until the Early Pliocene (Collins *et al.*, 1996*a,b*).

The advent of this current coincided with the disappearance of large coral reefs from much of the Caribbean. This region's number of coral species continued to increase steadily from the early Miocene through the early Pliocene (Johnson *et al.*, 2008), but most of these corals were ahermatypic and lived in seagrass beds along with many species of arborescent bryozoans (Johnson, Budd & Stemann, 1995; Cheetham & Jackson, 1996; Klaus *et al.*, 2011). Originally, these widely occurring seagrass beds were thought to be over 20 m deep, which suggests clear water (D'Croz & Robertson, 1997), but in Indonesia such corals now live in seagrass beds in shallow productive water. Indeed, seasonal upwellings of nutrient-rich bottom water were enhancing productivity and reducing water clarity off the Caribbean coast of Panama for several million years before the growing isthmus snuffed them out (O'Dea *et al.*, 2007).

Evolutionary patterns emphasize the importance of this west-to-east current before the seaway closed. Many Caribbean species, such as the Pliocene *Chione pailasana* and *Cancellaria erosa*, the modern *Cancellaria cancellata*, *Conus ermineus*, *Macrocypraea zebra*, *Macrocypraea cervus* and sundry buccinids derive from Eastern Pacific ancestors (Roopnarine & Vermeij, 2000; Roopnarine, 2001; Meyer, 2003; Duda & Kohn, 2005; Vermeij, 2005*b*). The fossil record suggests that some of these groups, such as the buccinids *Northia* and *Nicema* (Woodring, 1964; Vermeij, 2005*b*), and the cancellariid *Hertleinia* (Jung & Petit, 1990) were restricted to the eastern Pacific after the Pliocene: Woodring (1966) called such species paciphiles. Similar fossil evidence points to a Pacific origin for six gastropod species that once occupied both sides of tropical America but have since become extinct in the Atlantic: *Persististrombus granulatus* (Jung & Heitz, 2001), *Scalina brunneopicta* (De Vries, 2007), *Stramonita biserialis* (Landau & da Silva, 2010), *Eupleura pectinata* (see

below), *Harpa crenata* (Landau & da Silva, 2010), and *Malea ringens* (Beu, 2010). Although Herbert (2005) suggested that *Eupleura pectinata* spread from the Atlantic to the Pacific, it appears to have evolved in the eastern Pacific, apparently from *E. thompsoni*, which is known from the Late Miocene of Baja California and the nearly contemporaneous Gatun Formation of Atlantic Panama (Herbert, 2005).

A current flowing east through the seaway would carry planktonic larvae of many species from the Pacific to the Atlantic. Landau, Da Silva & Vermeij (2009) showed that most, if not all, paciphile gastropods have planktonic larval stages. Did a rising isthmus cut off the supply of planktonic larvae from the Pacific, contributing, along with declining productivity, to the extinction of many Caribbean taxa (Landau *et al.*, 2009)? Within pairs of sister species on the Atlantic and Pacific sides of tropical America today, surviving Caribbean representatives often have nonplanktonic dispersal, whereas eastern Pacific representatives still disperse by planktonic larvae. This interoceanic difference is well documented for the *Strombina* group of columbellid gastropods (Jackson, Jung & Fortunato, 1996; Fortunato, Penchaszadeh & Miloslavich, 1998) and for arcid bivalves (Moran, 2004).

Many other Pacific taxa, however, have Atlantic origins, or at least appear earlier among Atlantic-side fossils. This pattern has been documented for the paciphile scallop *Leochlamys* (Waller, 2007), for the scallops *Euvola*, *Nodipecten*, and *Spathopecten* (Waller, 2007), the chionine clade of venerids and many of its subclades (Roopnarine, 2001), the strombid genus *Persististrombus* (Kronenberg & Lee, 2007), and paciphile gastropods such as the muricids *Eupleura*, *Pterorytis*, *Purpurellus*, *Neorapana* and the *Muricopsis zeteki* clade (Vokes, 1989; Gibson-Smith, Gibson-Smith & Vermeij, 1997; Vermeij & Vokes, 1997; Merle & Houart, 2003; Herbert, 2005), the pseudolivid *Macron* (Gibson-Smith *et al.*, 1997), and the pediculariid coral-feeding cowrie-like *Jenneria* (Groves, 1997). Other Caribbean-side examples include the Caribbean-restricted helmet-shell genus *Cassis* (Beu, 2010) and the tropical American clade *Hesperisternia* and its descendants (Vermeij, 2006). Most of these genera, together with many others (Vermeij, 2005*a*) were present in the western Atlantic during or before the Early Miocene. When they spread to the Pacific is not precisely known, but likely dates range from the middle Miocene to the Early Pliocene. It thus appears that the east to west expansion of taxa occurred throughout the Neogene, whereas cases of inferred west-to-east expansion are concentrated in the Late Neogene.

(2) Environmental changes caused by the growing isthmus

The growing land bridge tended to separate Pacific habitats (with productive, somewhat turbid, waters rich in plankton) from Caribbean settings which became progressively richer in carbonates (with clear, nutrient-poor water and an abundance of seagrass beds and large coral reefs). This separation was driven by contrasting patterns of selective extinction, multiplication and diversification, reflecting the trade-off between fast growth and effective defence (Coley,

Bryant & Chapin, 1985) which, by and large, favoured smaller, faster-growing, shorter-lived organisms in the Pacific and larger, slower-growing, longer-lived ones in the Caribbean. More specifically, this trade-off shaped a divergence in the organization of dominant communities. In the Pacific, upwellings are frequent, plankton in surface waters dominate primary production, and the sea bottom is populated by abundant, fast-growing suspension and detritus feeders. In the Caribbean, water is clear except near river mouths, and most primary production is in the benthos and is dominated by symbiotic algae housed and fertilized by long-lived corals and foraminifera, as well as seagrass beds and calcareous algae in relatively shallow water. By what stages did this separation occur?

Coates *et al.* (2003, 2004) postulated that the rise of the isthmus began when the Central American arc collided with South America over 12 Ma, causing a mid-Miocene shoaling of the seaway between the Americas. Renewed excavation of the Panama Canal's banks, however, shows that, between 25 and 23 Ma, the type of volcanic and tectonic activity in Panama shifted from mantle-wedge derived to localized extensional arc magmatism (Farris *et al.*, 2011). The resulting extension of the isthmus increased the frequency of extensional (normal) faults and depositional basins began to form on both sides of the growing isthmus. Farris *et al.* (2011) convincingly ascribe this tectonic shift to the fracturing of the Panama Block (essentially, the lower isthmus) after it collided with South America approximately 25 Ma, over 10 Ma earlier than postulated by Coates *et al.* (2004).

Coates *et al.* (2003, 2004) dated the completion of the land bridge to approximately 3 Ma. Montes *et al.* (2012*a*,*b*), however, reconstructed movements from the Campanian onwards of individual tectonic blocks in South America and the growing isthmus, and inferred that by 15 Ma these blocks must have been too closely packed to allow space for a seaway between the Americas. As Montes *et al.* (2012*a*,*b*) provide no evidence that these blocks were subaerial rather than submarine, their work cannot tell us when the isthmus joined the Americas and severed the seas (Coates & Stallard, 2013). Coates *et al.* (2003, 2004) based their date on many kinds of evidence: the depths of Neogene coastal marine sediments of various ages, the homogeneity of the marine faunas in Woodring's (1974) Miocene Caribbean Faunal Province, inferences of coastal and open-ocean sea surface temperature, salinity and productivity in the Caribbean and the Eastern Pacific, patterns in genetic divergence between geminate species divided by the growing isthmus (Lessios, 2008), and the fossil record of terrestrial vertebrates in North, Central and South America. Even narrow, shallow marine passages can permit massive inter-oceanic mixing with major effects on climate. If these passages last long enough, they can maintain major contrasts between terrestrial faunas on their two sides. Today, the Indonesian throughflow, which passes from the Western Pacific through several shallow passages to the Indian Ocean, is sufficient to prevent Indonesia from being as dry and cold as the coasts of Peru and Northern Chile (Wajsowicz & Schneider, 2001; Kuhnt *et al.*, 2004;

Qu *et al.*, 2005; Sprintall *et al.*, 2009). These passages are old; one of them, the Makassar Strait, has separated Borneo from Celebes for 25 myr (Kuhnt *et al.*, 2004). The striking contrasts between the terrestrial faunas on the two sides of the Indonesian throughflow are denoted by the biogeographic lines of Wallace, Weber and Lydekker (Wallace, 1860, 1880; Whitten, Mustafa & Henderson, 1987, pp. 6, 57–67; Whittaker & Fernández-Palacios, 2007, pp. 52–55).

In any event, the seaway between the Americas was narrowing and shallowing by the middle Miocene (Fig. 1), 13 to 12 Ma (Coates *et al.*, 2003, 2005). Isthmian sediments demonstrate shallowing from over 2000 m to less than 1000 m deep during this period (Coates, 1997). Extension of the Isthmus was splitting deeper-water marine populations long before the isthmus finally closed (Lessios, 2008): deeper-water populations of snapping shrimp, *Alpheus*, were split 7 Ma (Knowlton *et al.*, 1993). In Ecuador, benthic foraminifera, which were clearly part of what Woodring (1974) called the Miocene Caribbean faunal province of 10 Ma, were more like those of California than the Caribbean 4 Ma (Hasson & Fischer, 1986). In the southern Caribbean, the temperature and salinity of sea water and carbonate contents of sea-bottom sediments began to increase 7 Ma (Collins *et al.*, 1996*a,b*; Jackson & Budd, 1996). Shallow-water benthic foraminifera associated with carbonate sediments then began to diversify in earnest: 86% of the new species of benthic foraminifera that appeared after the Miocene ended 5.3 Ma were associated with carbonate sediments (Collins *et al.*, 1996*b*). Caribbean corals, which had been diversifying since the early Miocene, continued to diversify from the late Miocene into the early Pliocene (Johnson *et al.*, 2008), although most of these new species formed small colonies that lived in seagrass beds (Johnson *et al.*, 1995; O'Dea *et al.*, 2007). The rich variety of herbivorous marine mammals, dugongs and manatees, in the Caribbean during the Neogene (Velez-Juarbe, Domning & Pyenson, 2012) implies widespread and abundant seagrass beds, some subtidal (Cheetham & Jackson, 1996; Domning, 2001). The isthmus finally closed for the first time during the Late Pliocene, about 2.7 Ma, as the consequence of falling sea levels brought about by growing northern glaciers (Molnar, 2008). The isthmus closed permanently only during the early Pleistocene, 2.5 to 1.8 Ma (Cronin & Dowsett, 1996; Beu, 2010).

The most radical effects of the closing of the isthmus only began to appear slightly over 4 Ma, when the Caribbean's primary productivity began to decline due to the disappearance of upwelling. Arborescent bryozoa died out from the Caribbean after the isthmus closed, while crustose bryozoan colonies continued to diversify (Cheetham & Jackson, 1996; Jackson & Budd, 1996).

Other free-living bryozoans hold the secret to what drove most of these changes. Autozooids in cupuladriid bryozoan colonies which live on sandy bottoms grow larger in cooler waters. The strength of upwelling, which is reflected by the mean annual range in seawater temperature, can be gauged by the coefficient of variation of autozooid size
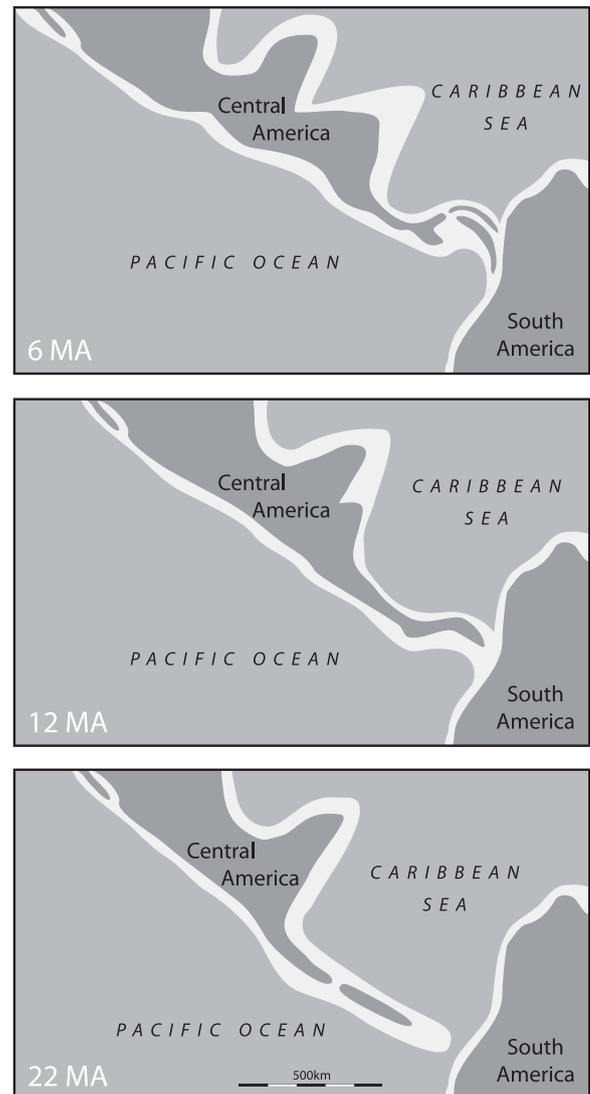

Fig. 1. Closure of the Isthmus of Panama. Palaeogeographic interpretations of land (dark grey), shallow seas (light grey) and deep seas (medium grey) in Central America at 22, 12 and 6 Ma. The position and form of the Central American volcanic arc is derived from Coates *et al.* (2003, 2004), Farris *et al.* (2011) and Montes *et al.* (2012*a*) and emergent land interpreted from evidence presented in Coates *et al.* (2003, 2004), Kirby *et al.* (2008) and O'Dea *et al.* (2012).

within a cupuladriid colony (O'Dea & Jackson, 2002). In cupuladriid colonies off the Caribbean shore of Costa Rica and Panama this coefficient of variation dropped to modern levels between 4.3 and 3 Ma, as the closing isthmus snuffed out upwelling in the Caribbean. In places far from river mouths spewing out muddy, nutrient-rich water into the sea, the proportion of sea-bottom sediment particles smaller than 2 mm made up of carbonate products rose from near 20% to near 60% during this period, and the ratio of masses of clam and snail to coral and calcareous algal fragments larger than 2 mm dropped from > 40 to between 1 and 2 between 4 and 2 Ma (O'Dea *et al.*, 2007), as the

progressive annihilation of upwelling diminished plankton productivity almost to vanishing point. In parallel with this increase, Leonard-Pingel, Jackson & O'Dea (2012) found that at such sites the proportion of reef-associated epifaunal bivalves and of seagrass-associated chemosymbiotic bivalves increased relative to infaunal suspension-feeders.

Cupuladriid bryozoans also provide other evidence of declining productivity in the Caribbean, at least near the isthmus. In productive waters cupuladriid bryozoans grow fast and reproduce clonally by fragmentation. On the other hand, slower-growing cupuladriids tend not to reproduce clonally. In the Caribbean, species whose reproduction was primarily clonal, and which could not switch to sexual reproduction, began to decline in abundance 4 Ma: all these species died out by 2 Ma. Those species that could adjust their level of clonality began to rely more on sexual reproduction about 4 Ma: these species still live in the Caribbean. Moreover, several new, exclusively sexual species of cupuladriid bryozoan appeared in the Caribbean about 4 Ma. The percent of clonal colonies in a sample was somewhat higher where upwelling, as measured by the mean annual range in seawater temperature, was stronger (O'Dea & Jackson, 2009).

There are other signs that productivity of plankton declined in the Caribbean as the isthmus closed. First, a large marine congener of the estuarine oyster *Crassostrea virginica*, well known from Chesapeake Bay but also still present in brackish, productive, Caribbean estuaries, died out before the Pliocene's end. In the Miocene and early Pliocene, oysters of this marine species grew 2.5 times faster in biomass, and five times faster in shell mass, than Panamanian *Crassostrea virginica*. After the isthmus closed, the open Caribbean could no longer support fast-growing oysters (Kirby & Jackson, 2004). Second, the proportion of predators among sampled snail shells declined from 63% in the Miocene to 36% when the Pleistocene began, suggesting that the supply of suitable prey, in the form of fast-growing suspension-feeding clams, was drying up. During the same period, the proportion of a formerly abundant genus of infaunal suspension-feeding snail, *Turritella*, among sampled snail shells dropped by nearly half. In the Caribbean, *Turritella* shell beds occur nowadays only in the few remaining upwelling areas, such as along the north coast of Venezuela. Large-bodied turritellids and chionine and corbulid bivalves all became extinct in the Caribbean, leaving behind only small-bodied survivors (Allmon, 1992; Roopnarine, 1996; Anderson, 2001). Finally, during this same period, the proportion of suspension-feeders among sampled clams decreased from 92 to 72% (Todd *et al.*, 2002) and the dominant type of scallop shifted from free-swimming to slower-growing byssally attached forms associated with reefs (Smith & Jackson, 2009). In all three cases, most of the drop occurred between the early and the latest Pliocene. It appears that closure of the isthmus seriously diminished the amount of food in the water suitable for suspension-feeders, without seriously compromising food supplies for deposit-feeders.

The decrease in planktonic productivity did not affect all parts of the western Atlantic. Fossil evidence indicates that the north coast of Venezuela has been a region of wind-driven upwelling for at least 19 myr (Landau *et al.*, 2008). This region, together with the mainland coast of tropical Brazil, has served as a geographic refuge for many taxa that at one time were more widespread in the Atlantic, such as the gastropods *Eburna*, *Turbinella*, and *Muracypraea* (Vermeij & Petuch, 1986; Vermeij, 1989*a*).

In the eastern Pacific, upwelling and productivity increased as the seaway to the Atlantic closed (Vermeij, 1997; Chaisson & Ravelo, 2000; Philander & Fedorov, 2003; Ravelo *et al.*, 2004; Fedorov *et al.*, 2006; Lawrence, Liu & Herbert, 2006; Dekens, Ravelo & McCarthy, 2007; Newkirk & Martin, 2009; O'Dea *et al.*, 2012). Thanks probably to this eutrophication, all reef-forming corals that lived in the eastern Pacific before the seaway closed became extinct when the isthmus formed. All reef corals living in the eastern Pacific today apparently came from the Indo-Pacific (Dana, 1975; Budd, 1989), as did most reef-associated eastern Pacific molluscs, fishes, and echinoderms (Lessios *et al.*, 1996; Lessios, Kessing & Robertson, 1998; Robertson, 2001; Vermeij, 2005*b*; Lessios & Robertson, 2006). Although a few sponge species now live on both sides of the isthmus, large, open-growing sponges have all disappeared from the eastern Pacific. Sponge diversity is much lower on the Pacific side of the isthmus, and the sponges there are all cryptic, living where sponge-eating fishes cannot reach them. For many other taxa, however, the eastern Pacific provided a post-Pliocene refuge. The list of paciphile molluscs continues to grow (Woodring, 1966; Landau *et al.*, 2009). There are currently at least 60 recognized paciphile subgenera of gastropods (Landau *et al.*, 2009) but only four caribphile subgenera (three shallow-water reef- or seagrass-associated taxa and one bathyal genus).

The western Atlantic witnessed dramatic extinction during and after formation of the isthmus, even among corals. More than 80% of Early Pliocene molluscan species have since become extinct, as compared to about 72% of Early Pliocene species in the Esmeraldas beds (Onzole Formation) of Ecuador on the Pacific side (see Vermeij, 2001). Although diversity of small bottom-dwelling mollusks continued to increase in the Caribbean, and the very largest molluscs (*Charonia*, *Fasciolaria gigantea*, *Cassis* spp.) survive only in the Caribbean, many species of larger clams and snails tended to survive only in the eastern Pacific, or as relicts in upwelling zones in the Caribbean, off the coast of Venezuela (Woodring, 1966). Every scallop genus present in the Caribbean over 5 million years ago is now extinct, whereas several old scallop genera persist in the tropical Eastern Pacific (Smith & Jackson, 2009). Some 64% of Early Pliocene coral species in the Caribbean have disappeared, as have most sirenians and seagrasses (Budd, Johnson & Stemann, 1996; Domning, 2001).

(3) The modern marine biota

Nowadays, ocean surface waters are much richer in nutrients and plankton and more productive in the Pacific—especially where upwellings occur—than in the Caribbean (D'Croz & Robertson, 1997; D'Croz & O'Dea, 2007; O'Dea

et al., 2007). The lower productivity of the Caribbean is reflected by the circumstance that offspring there are provisioned to a higher degree than in the Eastern Pacific. In echinoderm arcid bivalve species split by the isthmus, Caribbean populations have larger eggs and the proportion of strombinid gastropods with direct development is higher in the Caribbean (Lessios, 2008, p. 84). High productivity, which favours fast growth over defence, also favours intense herbivore and predator pressure in the plankton-rich eastern Pacific. Comparative studies on reefs show that the intensity of predation on corals and sponges is higher in the eastern Pacific than in the western Atlantic (Glynn, 1972; Glynn, Stewart & McCosker, 1972). Like eastern Pacific corals, the predators of these corals are mainly geologically recent imports from the Indo-West Pacific (IWP) realm, where selection in favour of defences and predatory pressure is intense. Notable examples of such predators include the puffers *Arothron* spp. and the crown-of-thorns starfish *Acanthaster planci*, neither of which has Caribbean counterparts. The paciphile cowrie-like gastropod *Jenneria pustulata*, however, is also a voracious predator of corals (Glynn *et al.*, 1972). There are predators specialized to eat sponges in the Caribbean—three angelfishes of the genus *Holacanthus*, and the starfish *Oreaster reticulatus* (Randall & Hartman, 1968; Wulff, 1995)—but not in the eastern Pacific; yet sponge-eating is more intense in the eastern Pacific, where exposed sponges are rare (see also Birkeland, 1977). The biomass of fleshy algae is generally lower in shallow waters of the eastern Pacific than in the Caribbean, but the intensity of grazing and the abundance of grazing fishes and gastropods are higher there (Hay & Gaines, 1984). In his experimental work on hermit crabs living in snail shells on the Caribbean and Pacific sides of Panama, Bertness (1982) showed that predation involving shell breakage is substantially more intense, and involves larger individuals, on Pacific shores. The higher incidence and greater expression of breakage-resistant shell architecture (narrow and obstructed aperture, short spire, thick shell, tuberculate sculpture) in eastern Pacific compared to Caribbean assemblages, and the tendency for breakage to account for a higher proportion of 'dead' shells on the Pacific side (Vermeij, 1978, 1989*b*, 1974), suggest that among intertidal organisms, predation pressure is also higher on the Pacific.

We urge caution in interpreting comparative studies of predation. Overfishing has eliminated top consumers worldwide, but this depredation by humans has been particularly devastating on Caribbean reefs (Jackson, 1997). The comparative expression of defence-related characteristics should be a better indicator of relative intensities of consumption (or at least of their evolutionary effects) than direct measurements of present-day consumption.

A comparison between sites on opposite sides of the Panama Canal emphasizes the impact of herbivore and predator pressure in the Bay of Panama, which is far more intense than in the nutrient-poor waters of Galeta Marine Station, 10 km east of the Caribbean mouth of the Panama Canal (Glynn *et al.*, 1972; Birkeland, 1987). In the Bay of Panama, corals survive and grow well on the side of Taboguilla Island exposed to upwelling (Birkeland, 1977). Indeed, healthy eastern Pacific reefs grow as fast as any in the world (Glynn, 1977). They face two problems, however. First, Panama's Pacific side, unlike the Caribbean, lacks sponges that glue fragments or coral rubble together, providing a stable substrate for new corals (Wulff, 1984). Thus eastern Pacific reefs may be far less likely to recover after destructive storms. Second, recruitment is a major problem. On settling plates suspended in these waters, coral recruits are quickly smothered by faster-growing filamentous algae and filter-feeders such as barnacles, tunicates, bryozoans and sponges, which cover the settling plate within 70 days. In the lagoon behind a reef flat at Punta Galeta, on Panama's Caribbean side, a hundred times as many corals recruit per settling plate, whereas colonization by other organisms is so slow that 70% of these plates' surface is still unoccupied after 70 days. Fish that feed on these plates' settlers avoid coral recruits exceeding 2.5 mm in diameter, while consuming their competitors (Birkeland, 1977). The Bay of Panama's intense consumer pressure keeps the benthos in a particularly productive state of arrested succession, similar to the effect of grazers in the Serengeti grassland (McNaughton, 1985).

Thanks to the contrast in productivity and consumer pressure, major marine ecosystems are very differently represented on the two coasts of tropical America. In the eastern Pacific coral reefs are small, restricted to shallow water (not more than about 10 m deep at low tide), and limited to relatively sheltered situations (Glynn, 1972, 1982; Glynn & Wellington, 1983). In the Caribbean, on the other hand, reefs are often extensive, reaching to depths of as much as 60 m, and resistant to intense wave action (Glynn, 1972, 1982). Some of this resistance to surge is due to ridges of crustose coralline red algae and to cementing by sponges, both of which are well developed in parts of the Caribbean but not in the eastern Pacific (Adey, 1978). Seagrass beds, composed of not more than two species, are small and of very limited extent in the eastern Pacific, where they never occur in the intertidal zone. In the Caribbean, seagrass beds with at least five species are extensive in shallow water (Glynn, 1972; Larkum & den Hartog, 1989; Domning, 2001). Because of the large tidal ranges in the tropical eastern Pacific (up to 6 m in the Bay of Panama), rocky shores and sandy beaches and tidal flats are very extensive and widespread (Glynn, 1972). Long stretches of sandy beach without rocky shores occur on the Pacific coasts of Mexico and parts of Central America (Reid, 2002). Sandy beaches and tidal flats are of much more limited extent in most of the western Atlantic except in Florida and the northern and eastern continental coasts of South America; but rocky shores are locally extensive, especially where limestone shores are exposed to strong surf as on the north coast of Jamaica and in the eastern Caribbean. Deep-water hard bottoms are widespread in the Caribbean but seem to be scarce in the eastern Pacific, probably because of more rapid deposition of organic material.

The emergence of the Central American isthmus has accordingly affected the taxonomic composition of its two

sides. First, the biotas of the two sides are almost entirely distinct at the species level. Among well-studied molluscan groups, only two bursid and six ranellid gastropods, all with nearly or entirely circumtropical distributions thanks to long-lived planktonic stages, are common to both coasts (Beu, 2010). Sister pairs or groups of species, in which one or more Atlantic species diverged from a single Pacific species, differentiated earlier among deep-water lineages than among many (but not all) shallow-water ones (Knowlton *et al.*, 1993). Molecular sequences of these sister pairs indicate that divergence often preceded final closure of the seaway by millions of years (Knowlton *et al.*, 1993; Marko & Jackson, 2001; Marko, 2002; Moran, 2004; Frey & Vermeij, 2008; Lessios, 2008).

Patterns of diversity also reflect the ecological contrasts between the two sides of the isthmus (Table 5). The reef biota is invariably much richer in the Caribbean than in the eastern Pacific. Reef corals are much more diverse in the Caribbean, as are reef fish, crinoids and ophiuroids, which live on reefs, and reef-associated molluscs such as helmets (Cassididae) and Ranellidae. Muricidae, associated with deep, hard bottoms, and scallops (Pectinidae) which tend to be found on reefs or on deep, hard bottoms, are also more diverse in the Caribbean. On the other hand, intertidal inhabitants such as Littorinidae, Rapaninae, Ocenebrinae (included under Muricidae in Table 5), Tegulinae and some Collumbellidae, and intertidal suspension-feeders such as Donacidae and Corbulidae, are more diverse in the eastern Pacific, with its greater intertidal range and expanse of intertidal habitat. Similarly, sand dwellers such as Nassariidae, photine buccinids, and many Collumbellidae, and deposit-feeders such as deposit-feeding tellinid and semelid bivalves, are more diverse in the eastern Pacific, where sandy habitats are more widespread and suitable food more widely available. Finally, the fauna on quantitatively sampled sandy beaches in Panama (crustaceans, polychaetes, and molluscs) is richer on the Pacific side than on the Caribbean side of Panama (52 versus 33 species, Dexter, 1974; see also Abele, 1974).

As we have seen, the ecological contrasts between the Caribbean and eastern Pacific are particularly striking in Panama, with its intense dry-season upwelling and huge tidal range in the Bay of Panama, whereas only 50 km away lies the perennially warm, almost tideless Atlantic side. Both the eastern Pacific and western Atlantic are, however, ecologically heterogeneous. The trade-off between fast growth in productive conditions, and effective defence in less-productive settings influences not only the contrast on the two sides of the isthmus but also the spatial patterns, local and regional, on each side. Pacific-like upwelling, driven by strong trade winds, occurs on the north coast of Venezuela in the Caribbean, and extensive run-off from large rivers makes for productive inshore conditions along much of South America's Caribbean and Atlantic coast.

In the eastern Pacific, the bottom fauna is different where upwellings are present. On Panama's Pacific coast, the species composition of the bottom fauna in the Gulf of Chiriquí, where upwellings do not occur, is nearly identical to that in the Bay of Panama with its frequent upwellings. Nevertheless, in the Gulf of Chiriquí, with its clearer water, herbivorous gastropods are much more common on the sea bottom, whereas in the plankton-rich waters of the Bay of Panama, filter-feeding bivalves and bryozoans predominate (O'Dea *et al.*, 2012). Indeed, O'Dea *et al.* (2012) used the abundances of bivalves and bryozoans vis-à-vis herbivorous gastropods in fossil deposits to infer the change in frequency of upwellings off western Panama's Pacific coast as the isthmus closed.

In the eastern Pacific, relatively widespread if species-poor coral reefs occur on the Pacific coast of Mexico, in the southern Gulf of California, and in the Gulf of Chiriquí, where there are no upwellings. The largest reefs are on small, distant, offshore islands such as Clipperton or Malpelo (Glynn & Wellington, 1983). The influence of upwellings on coral reef distribution is illustrated by the Galápagos Islands. Reef corals are scarce, and fleshy algae abundant, on those parts of the west coasts of Fernandina and Isabella most subject to upwelling, whereas coral reefs are best developed on the northeastern sides of the southernmost Galápagos Islands (San Cristóbal, Floreana, and Santa Fé), where upwelling is absent and the water is clearest, poorest in nutrients, and warmest at the coolest time of year (Glynn & Wellington, 1983; Graham *et al.*, 2007).

Local variation on the Caribbean shore is dominated by the interplay between coral reefs, which break the force of incoming waves, thereby protecting the seagrass beds in the lagoons behind, and mangroves fringing the shore. In turn, the mangroves protect the corals by trapping sediments which might smother them, and nutrients that might fuel the growth of competing algae, which are supplied by run-off from the land (Jackson, 1997). The nutrient content of sea water declines as one passes from mangroves to reefs, and the trade-off between fast growth and effective defence sorts species along this gradient. Sponges common on Caribbean coral reefs rarely occur on nearby mangrove roots and vice versa. Reefs are rich in sponge-eating predators and offer abundant hiding places for these predators, especially fishes, whereas mangrove roots tend to lack such predators, and the waters surrounding them are more nutrient rich and support more of the microorganisms that sponges eat. Sponges on reefs must accordingly invest heavily in defences, which slow their growth. These sponges, when transplanted to mangrove roots, are easily overgrown by faster-growing mangrove sponges which invest less in defence. Correspondingly, the mangrove-associated sponges are effectively barred from reefs because of their vulnerability to predation by fishes (Wulff, 2005). Although trade-offs like this are undoubtedly widespread for many groups, over many contrasting habitats, Wulff's (2005) study is one of the few to demonstrate them by reciprocal transplant experiments.

(4) The marine biota and the impacts of new human technologies

In the Isthmus of Panama, human beings were catching fish and sea turtles, gathering shellfish, and hunting manatees

Table 5. Number of species of different groups in the Caribbean and the Eastern Pacific

Phylum	Taxonomic group	Caribbean	Eastern Pacific
Cnidaria	Stony corals[1]	~60	~20
Cnidaria	Stony corals[2]	170	69
Echinodermata	Crinoids[3]	> 50	2
Echinodermata	Ophurioids[3]	> 50	10
Chordata	Reef fish[4]	~750	~650
Chordata	Actinopterygii[2]	1233	1088
Chordata	Elasmobranchii[2]	58	78
Mollusca	Ranellidae[5]	29	16
Mollusca	Cassididae[5]	11	6
Mollusca	Coralliophilinae[6]	10	6
Mollusca	Peristerniinae + Fasciolariinae[6]	37	16
Mollusca	Muricidae[6]	176	116
Mollusca	Photine buccinids[6]	11	16
Mollusca	Littorinidae[7]	16	22
Mollusca	Nassariidae[8]	13	25
Mollusca	Tegulinae[6]	6	19
Mollusca	Columbellidae[9]	50	126
Mollusca	Chitons[10]	4	6
Mollusca	Donacidae[11]	9	16
Mollusca	Corbulidae[12]	6	17
Mollusca	Tellinidae[6]	42	75
Mollusca	Semelidae[6]	6	27
Mollusca	Pectinidae[13]	22	11
Bryozoa	Cupuladriidae[14]	13	3

Sources of data: [1]Glynn (1972, 1982); [2]Ocean Biogeographic Information System (OBIS); [3]Chesher (1972); [4]Floeter *et al*. (2008); [5]Beu (2010); [6]New compilation; [7]Reid(1999, 2002, 2009); [8]New compilation, mostly from Cernohorsky (1984); [9]Jung (1989) and new compilation; [10]Bullock (1988); [11]Morrison (1971) and Coan (1983); [12]Mikkelsen & Bieler (2001), Coan (2002) and Anderson (2001); [13]Smith *et al*. (2006*b*); [14]O'Dea and Jackson (2009).

long before Columbus appeared (Borgogno & Linares, 1980). In Jamaica the average size of fish caught by pre-Columbian populations declined from 1.2 kg in 850 AD to 300 g in 1430, even though in 1430 people were ranging further from shore to catch fish, and the proportion of their diet comprised by fish was about half that in 850 (Hardt, 2009). Harvesting marine vertebrates, however, accelerated the transformation of Caribbean ecosystems during the last few centuries, after European colonists imported slaves needing to be fed and introduced new hunting techniques (Jackson, 1997, 2001, 2008). In the Cayman Islands the green turtle (*Chelonia mydas*), fishery was exhausted by 1800; overexploitation then began on the Nicaraguan coast (Jackson, 1997). The Caribbean had 90 million green turtles in 1750; only 300,000 are left today (Jackson, 2008). Manatees (*Trichechus manatus*), remained abundant far longer than green turtles, but now they, too, are rare. On Western Panama's Caribbean shore, manatee populations plummeted after the advent of the 0.22 rifle (Wing, 1980). Green turtles and manatees formerly cropped seagrass beds, keeping them nutritious, diverse and healthy. In the last few decades these seagrass beds have been plagued by disease (Jackson *et al*., 2001).

Overfishing has caused populations of top predators, such as large sharks and groupers, to crash (Myers & Worm, 2003). By 1972, Caribbean monk seals (*Monachus tropicalis*) of which there were over 200000 in 1750, had been eradicated. Many of these populations crashed within the last 100 years (Myers & Worm, 2003; Jackson, 2008). Nowadays, only reefs in uninhabited, unfished areas, such as the Northwest Hawaiian Islands or some of the Line Islands, have fish biotas of over 300 tons per square kilometer, top-heavy with predators, that used to be normal for most reefs (Sandin *et al*., 2008). Fish biotas of protected reefs such as Cuba and Cozumel, however, also have substantial biomass with many predators (Knowlton & Jackson, 2008). In the Caribbean, overfishing was so prevalent that sea urchins, *Diadema antillarum*, became the last remaining grazers of macroalgae. When a waterborne disease killed off over 90% of these urchins, macroalgae multiplied, smothering the corals.

Other threats face all reefs, not just Caribbean ones. Large-scale use of fossil fuels releases carbon dioxide, enough of which enters the atmosphere to cause global warming. Water temperatures 1°C above normal seasonal highs cause reef corals to 'bleach' by expelling their zooxanthellae. As the world warms, episodes of bleaching are becoming more frequent and severe (Hoegh-Guldberg *et al*., 2007; Jackson, 2008), rendering corals more vulnerable to other hazards such as disease or starvation. Zooxanthellae come in many strains, some more heat-tolerant than others (Rowan *et al*., 1997). Choosing more heat-tolerant zooxanthellae, however, will not enable reef corals to survive indefinite temperature increase. During past episodes of severe global warming in

the early Jurassic and the late Cretaceous, reef corals were replaced by reef-building bivalves (Fraser, Bottjer & Fischer, 2004); this time, the victors will probably be fleshy algae. About a quarter of the carbon dioxide released by burning fossil fuels is eventually absorbed by the ocean, where it forms carbonic acid. Surface water pH has fallen by 0.1 unit since pre-industrial times and may decrease by a further 0.3 units or more by 2100 (Caldeira & Wickett, 2005), which could diminish the calcification of shelly organisms by 11–40% (Reynaud *et al.*, 2003). Unfortunately, the combined effects of increased temperatures and more acidic waters may cause the greatest damage. Calcifying requires more energy in more acidic water, warmer water decreases oxygen availability, but the higher metabolic rates entailed by warmer water increase oxygen demand. If the symbiotic algae that could supply this oxygen are unhealthy or have been expelled, this oxygen demand will be hard to fulfil (Anlauf, D'Croz & O'Dea, 2011).

These worldwide events are making corals more vulnerable to other threats. Agricultural wastes—excess fertilizer, human and animal wastes, etc.—fertilize coastal seas, favouring the spread of coral-smothering algae, especially where there are too few fish and sea urchins to protect the corals by eating these algae. Wastes may also contain pathogens. Moreover, viable spores of fungal and bacterial pathogens are among the pollutants created by burning forest and scrub south of the Sahara and blown to Central America by prevailing winds. The soil fungus *Aspergillus*, viable spores of which are among these wind-transported pollutants, have caused coral die-offs around certain Caribbean islands (Stallard, 2001). The end result of all these misfortunes has been a Caribbean-wide decline in average cover of coral reefs by live corals from 55% in 1977 to 5% in 2001 (Gardner *et al.*, 2003). Moreover, disease is eliminating two conspicuous—even iconic—dominants, the elkhorn coral *Acropora palmata* and the staghorn coral *A. cervicornis*. Ecosystems associated with coral reefs have suffered far worse devastation that anything yet inflicted on tropical forests, but the full consequences have not yet played out. The eastern Pacific is much less well studied, but some coasts are clearly overfished, and widespread fish and shrimp farming threatens mangroves. Where these developments will lead is not yet known.

Unlike the elimination of the terrestrial megafauna, human impacts on tropical American marine ecosystems only recently became devastating, thanks to technologies imported from Europe or developed in the North Temperate Zone. Currently, humans, whose first representatives arrived only 15000 years ago, appear more devastating to marine than to terrestrial settings.

IV. CONCLUSIONS

(1) The isthmus which joined the Americas approximately 3 Ma provided a land bridge that allowed inhabitants of each America to invade the other. The resulting invasions transformed the terrestrial ecosystems of tropical America. As a sea barrier, the isthmus induced divergent environmental change that favoured contrasting marine ecosystems on its two sides.

(2) About 65 Ma, invading marsupials and ungulates of North American ancestry and xenarthrans of uncertain provenance replaced all native South American mammals. There is no geological evidence for a land bridge to North America at that stage. The Americas' mammal faunas must have been equally competitive 60 Ma. From 65 to 10 Ma, however, South American descendants of these invaders, supplemented only by caviomorph rodents, monkeys and emballonurid bats 42 to 30 Ma, evolved in isolation, like its birds. South America's isolation left it with ineffective marsupial carnivores, allowing many slow-moving herbivores to evolve, some resembling Madagascar's giant lemurs. Prolonged isolation thus left South America's non-volant mammals vulnerable to replacement by invaders.

(3) Unlike South America's land mammals, bats and birds, its plants were continually enriched, and their competitiveness and ability to cope with herbivores enhanced, by numerous invaders from overseas. Its plants evolved aggressive pioneers like those of Africa and Southeast Asia. Judging by surviving species, South America's non-volant mammals could accordingly handle plant defences effectively.

(4) The competitiveness of North America's mammals, especially those of open country, was maintained by waves of Eurasian invaders. As a rule, however competition, herbivory and predation are most intense in the tropics. Although the two Americas had similar expanses of tropical forest 55 Ma, by 3 Ma North America's tropical forest was confined to a far smaller area than South America's, making South America's tropical plants and animals less vulnerable to invasion.

(5) When the isthmus formed 3 Ma, it bore savanna. Open-country mammals crossed in both directions, and placental carnivores from the north quickly replaced their marsupial counterparts. Unlike invaders from South America, invading herbivores from North America diversified, and slowly replaced open-country southern counterparts. Were these counterparts especially vulnerable to efficient carnivores, thanks to lack of cover? When forest replaced savanna on the isthmus over 1 Ma, South American tropical forest spread, with its birds, bats and land mammals (protected from carnivores by the forest's cover?), as far as southeast Mexico. Some birds and bats spread beyond this forest. Invading humans wiped out larger animals, especially in South America, 12000 years ago. Since then they have altered habitats and destroyed forest on a grand scale.

(6) Trade-offs between being able to grow or compete in different settings or different climates play a major role in shaping contrasts in species composition of different vegetation zones. In Panama, the trade-off between surviving drought and coping with the diseases or nutrient scarcity characteristic of wetter settings shapes the relationship between rainfall regime and species composition in lowland forest. Altitudinal zonation reflects the trade-off between

exploiting lowland warmth and coping with the impact of cooler altitudes. Understanding how different plant species respond to such trade-offs is essential to an understanding of the eco-physiological basis of vegetation zonation.

(7) From the latest Oligocene until the seaway closed 3 Ma, a similar marine biota, with an array of characteristic molluscs, bryozoans, corals and benthic foraminifera, extended from east of Trinidad to Ecuador and Mexico's Pacific coast. In the earliest Miocene, the flow of water through the seaway reversed direction, henceforth flowing eastward. This plankton-rich flow wiped out the large Oligocene Caribbean reefs. From the Oligocene through the Pliocene, this biota evolved independently of the Indo-West Pacific biota.

(8) By the mid-Miocene, the seaway between the Americas was shoaling, shallowing from 2000 to 1000 m, 13 to 12 Ma. This shoaling began to split deeper-water populations 7 Ma. At this time, seawater temperature and salinity in the southern Caribbean, and the carbon content of its sediments, began increasing, and shallow-water benthic foraminifera of carbonate settings began diversifying rapidly there.

(9) By 4 Ma, the seaway's narrowing began to snuff out seasonal upwelling in the Caribbean, drastically lowering its plankton production. Diminished plankton supply eliminated arborescent bryozoa, fast-growing clonal cupuladriid bryozoans, and giant fast-growing oysters. As its water became clearer and poorer in plankton, the Caribbean's abundance of suspension-feeding molluscs and their predators plummeted, whereas bottom-dwelling corals and calcareous algae spread and multiplied, magnificent coral reefs appeared, and reef-associated organisms diversified. Many molluscan species living in the Caribbean before the seaway closed now survive only in the eastern Pacific, or in the upwelling zones that persist along Venezuela's coast. As the seaway closed, all the eastern Pacific's corals, and its large, open-growing sponges died out, perhaps because the seaway's closing increased upwelling and productivity in the eastern Pacific.

(10) Now, especially near upwellings, the eastern Pacific's surface waters are nutrient-rich, favouring fast growth: the Caribbean's surface waters are clear and nutrient-poor, favouring long life and effective defence. The contrast between the two marine ecosystems therefore illustrates the trade-off between fast growth and effective defence. The Pacific supports a plankton-based ecosystem with abundant pelagic fish and bottom-dwelling suspension and deposit feeders; the clear Caribbean waters support coral reefs, seagrass beds and bottom-dwelling calcareous algae. Consumer pressure on corals, sponges, molluscs and algae is far more intense in the productive eastern Pacific. The trade-off between fast growth and effective defence also affects variation among denizens of different habitats in each ecosystem.

(11) Humans have harvested tropical American marine animals for millennia. Human activities accelerated transformation of tropical American marine ecosystems when European colonists nearly eliminated sea turtles, and exterminated monk seals, during the last few centuries. Other populations crashed when European technologies allowed local peoples to overharvest manatees, and fish of ever-smaller sizes. Especially in the Caribbean, overfishing has exposed coral reefs and seagrass beds to devastating diseases, and allowed algae to overgrow, smother, and kill corals.

(12) Until recently, tropical American land ecosystems have been influenced primarily by invasions, and their marine counterparts primarily by environmental change. Now, its marine ecosystems are being devastated by a combination of invasions and ecosystem change.

V. ACKNOWLEDGEMENTS

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