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The Generation of a Biodiversity Hotspot: Biogeography and Phylogeography of the Western Indian Ocean Islands

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1. Introduction

The importance of islands in revealing evolutionary processes was highlighted already at the birth of evolutionary biology as a science (Darwin 1859; Darwin and Wallace 1858). Since the thrilling discoveries revealed by Darwin's work on the Galapagos (Darwin 1909) and Wallace's work in the Malay (Indonesian) archipelago (Wallace 1876), island biogeography has experienced an explosive growth. The discipline has provided many elegant examples of the evolutionary mechanisms involved in generating biodiversity, especially the interplay of geological processes and colonization and isolation (Emerson 2008; Gillespie, Claridge, and Goodacre 2008; Parent, Caccione, and Petren 2008; Ricklefs and Bermingham 2008). Islands have provided particularly strong insights into adaptive radiations (Camacho-Garcia and Gosliner 2008; Blackledge and Gillespie 2004; Cowie and Holland 2008; Gillespie and Roderick 2002; Losos and DeQueiroz 1997; Schluter 2000), the processes of colonization and extinction (Ricklefs and Bermingham 2008; Goldberg, Lancaster, and Ree 2011), the formation of species (Emerson 2008; Pickford et al. 2008; Gillespie and Roderick 2002; Schluter and Nagel 1995; Vences et al. 2009), and convergent evolution and formation of ecomorphs (Bossuyt and Milinkovitch 2000; Gillespie 2004, 2005; Losos 1988; Wildman et al. 2007; Burridge 2000; Rothe et al. 2011). Naturally, islands have also played a key role in revealing the causes and consequences of long distance dispersal, in particular, the ecological and evolutionary consequences of varying dispersal propensities of different lineages, and the evolutionary changes in dispersal propensity, such as the loss of dispersal ability following island colonization (Cowie and Holland 2006, 2008; Hedges and Heinicke 2007; Holland and Cowie 2006; Byrne et al. 2011; Bell et al. 2005; Darwin 1909; Clark 1994; Gillespie et al. 2012).

The field of phylogeography, in contrast, is much younger. Phylogeography—the study of phylogenetic data in a geographical context aimed to understand species distribution and diversity—is a rapidly expanding discipline that grew from a seminal paper by Avise and

colleagues in 1987 (Avise et al. 1987). With the advent of easy sequencing, Avise foresaw a conceptual revolution in evolutionary biology: the boundary between population genetics (genetic studies within species) and phylogenetics (studies of the history of divergences among species) was dissolving (Avise et al. 1987; Avise 2000; Knowles and Maddison 2002; Hickerson et al. 2010), as is now the distinction between ecological and historical biogeography (e.g. Avise 2004; Ricklefs and Jenkins 2011). The genealogical history of a single locus, the "gene tree", is a common currency for both those biologists looking within species to study evolutionary dynamics of populations, and those looking across species to reconstruct and interpret phylogeny (Hickerson et al. 2010; Maddison 1997; Maddison 1995). Phylogeography was originally portrayed as the mitochondrial DNA link between these disciplines (Avise et al. 1987). However, phylogeography has since broadened immensely (for a recent review, see Hickerson et al. (2010)), with a current focus on gathering multiple gene trees. In animals, these usually represent mitochondrial and nuclear markers (Hare and Avise 1998; Charruau et al. 2011; Peters et al. 2007; Bryson, Garcia-Vazquez, and Riddle 2011; Fijarczyk et al. 2011; Rocha, Harris, and Posada 2011; Smykal et al. 2011; Witt, Zemplak, and Taylor 2011; Zhan and Fu 2011), and in plants, plastid and nuclear data (Buerki et al. 2011; Cuenca, Asmussen-Lange, and Borchsenius 2008; Manns and Anderberg 2011; Pokorný, Olivan, and Shaw 2011; Thiv et al. 2006). Modern phylogeography also incorporates other tools and disciplines, such as spatial analyses using GIS, and ecological niche modelling (Chan, Brown, and Yoder 2011; Raxworthy et al. 2007) and the emerging statistical coalescence theory (Maddison 1997; Knowles and Maddison 2002). Current development in next generation sequencing technology promises to complete the union of population genetics and phylogenetics: 'phylogenomics' will offer a wealth of data to unravel with increased confidence the histories of individuals, populations, and lineages at any level.

Phylogeography and biogeography are both sciences lying at this disappearing interface between genetic studies within and among species (Avise 2004; Avise et al. 1987). Both study genetic structure of populations in a geographical context and to both the concepts of climatological history, geographical barriers, and dispersal, are fundamentally important. Phylogeography could be defined simply as the phylogenetic analysis of data in a geographical context. However, the actual reach of phylogeography is much broader than such a definition implies. It aims to reveal the interplay of geological and climatological phenomena, life history traits, dispersal, and species distributions, in the generation of biodiversity. The data are typically genetic, for one thing because many data are available, and for another because they allow estimates of divergence dates. Conceptually, however, nothing rules out using morphological, behavioral, acoustic, chemical, and other heritable data that vary among individuals and populations to infer on phylogeography. Comparative phylogeography then aims to analyze data from multiple codistributed taxa and thus gets at broad questions about how historical global events (changes in geology, climate and so on) have shaped, and are shaping, the distribution and diversity of organisms on earth (Avise 2000; Hickerson et al. 2010). Codistributed taxa, especially those that are of comparable ages, are likely to have experienced similar geological and climatological histories and thus can offer insights into broader patterns than studies confined to single species/lineages.

Isolated archipelagos such as Hawaii and the Galapagos provide examples where cycles of evolutionary radiation have produced replicated patterns of endemic, often bizarre, forms

(Cowie and Holland 2008; Dunbar-Co, Wieczorek, and Morden 2008; Parent, Caccone, and Petren 2008). Yet, the extreme isolation of these islands reduces the interplay between islands and continents—interchange is typically one-way (islands as sinks) and limited to rare chance dispersal events (Cowie and Holland 2008). Other archipelagos that are geologically closer to continental landmasses, such as the West Indies and the islands of the western Indian Ocean, can have very different geological and biological histories than highly isolated archipelagos (see, e.g. Leigh et al. 2007). The origin of such islands may be volcanic, or represent fragmentation from a continental landmass (such as Madagascar, and the Greater Antilles), and thus the origin and evolution of biota inhabiting these islands are expected to be more varied and dynamic (Ricklefs and Bermingham 2008). For example, colonization events are expected to be more frequent such that an island's diversity may not be dominated by adaptive radiations of a few lineages, but a mixture of many. Furthermore, especially when islands are close to continents, and/or very large, islands may function as a source of continent fauna, not just as sinks (Heaney 2007; Bellemain, Bermingham, and Ricklefs 2008; Bellemain and Ricklefs 2008). The biota of highly isolated oceanic islands is characterized by the near exclusive presence of excellent dispersers, some of which may have secondarily lost their dispersal ability, such as many spider lineages on Hawaii (e.g. Gillespie et al. 2012). In contrast, on archipelagos near continents, a complex mixture of good and poor dispersers is present, and the diversity and history of any given organismal lineage will strongly depend directly on its dispersal ability (Cowie and Holland 2006, Gillespie et al. 2012).

Our aim here is to review phylogeographic and biogeographic patterns of multiple, partially or fully codistributed taxa, to understand the broad strokes of the history of the terrestrial and freshwater biota of the land masses of the western Indian Ocean. First, we are interested in understanding the major shared biogeographical patterns in the region, and specifically how the dispersal abilities of different taxa affect those patterns. The basic prediction is that the better the dispersal abilities of a taxon, the less likely it is to share biogeographical patterns with many other taxa. Excellent dispersers, such as active day flying animals, can colonize islands stochastically practically from any direction, or source landmass (Gillespie et al. 2011). Poorer dispersers, on the other hand, are likely to show shared patterns that reflect geological history, climatological events, trade winds, direction of oceanic currents and other abiotic factors shaping species distributions. Second, we are interested in the impact of dispersal ability on patterns of species diversity to test a model presented in Agnarsson and Kuntner (in prep.). We predict that on near-continent archipelagos, poor dispersers will show patterns akin to organisms on isolated oceanic islands, that is: within island radiations on those islands where they occur as the result of speciation processes (e.g. Pearson and Raxworthy 2009, Gillespie et al. 2012). Radiations of poor dispersers will mostly occur on fragment islands, or larger islands (Leigh et al. 2007) relatively close to continents, but will not be present on most isolated volcanic islands. Excellent dispersers are expected to be found on most islands. However, radiations are not expected within islands, and may not occur among islands either if dispersal ability is sufficient to maintain among island gene flow (Kisel and Barraclough 2010, Gillespie et al. 2012). Thus, on near-continent archipelagos we predict the highest diversity of intermediate dispersers (Kuntner and Agnarsson 2011a-b; Agnarsson and Kuntner in prep.)—a diversity pattern that may be very general (Vilgalys and Sun 1994)—as those lineages have the opportunity to colonize even

isolated volcanic islands, but may do so rarely enough such that gene flow is disrupted and among island genetic divergence begins to form immediately following colonization (Garb and Gillespie 2009, Gillespie et al. 2011). Intermediate dispersers therefore should be found on many islands and show divergence among them. They may also show divergences across barriers within the largest islands. In this chapter, we review various biogeographical studies on the terrestrial and freshwater biota of Indian Ocean islands to summarize biogeographical patterns in the western Indian Ocean and we test if diversification patterns across lineages follow the 'intermediate dispersal model' (Agnarsson and Kuntner In Prep).

The major islands of the western Indian Ocean, such as Madagascar, Comoros (including Mayotte), Réunion, Mauritius, Rodrigues, the Seychelles (including Aldabra), and Socotra (Figure 1), combine species richness with high endemism resulting in high biodiversity. The region is one of Conservation International Biodiversity Hotspots (see <http://www.biodiversityhotspots.org/xp/hotspots/madagascar/Pages/default.aspx>). Yet, the diversity of many lineages, in particular invertebrate animals, for example spiders, has barely begun to be studied in the region, and in general, the origin of the Indian Ocean biota, and mechanisms that have generated this diversity, are poorly understood and much debated (reviewed in Yoder and Nowak (2006), and Vences et al. (2009), see also Gage et al. (2011), Warren et al. (2010), and Kuntner and Agnarsson (2011a-b)). The origin and diversification of Indian Ocean lineages are challenging research topics because of the interplay of the complex geographic and geologic history of the islands, the varying dispersal abilities of local biota, and the proximity to the African continent. For example, Gondwanan vicariance dating back over 100 million years explains the origin of a portion of the diversity known on Madagascar (Briggs 2003), but not that found on the smaller, younger islands. The origin of those lineages that naturally occur there needs to be explained by Cenozoic dispersal from Africa, Madagascar, Asia, or Australasia (Yoder and Nowak 2006; Kohler and Glaubrecht 2010). The mixture of origins and the proximity of the islands combined provide a dynamic interaction and interchange of biota between continents and islands, which is quite different to the more isolated archipelagos, such as Hawaii (Gillespie, Claridge, and Goodacre 2008). Such mechanism likely represents an important force in the generation of biodiversity of the archipelago. Furthermore, a paradigm shift is underway in island biogeography, where molecular phylo/biogeographic studies are revealing an increasing importance of 'reverse colonization,' from islands to continents (e.g. Heaney 2007), in addition to the more commonly invoked model of colonization from continents onto islands. Some primary examples supporting this new paradigm come from the Indian Ocean, such as the diversification of chameleons on Madagascar followed by 'reverse colonization' of Africa, likely via rafting over the Mozambique Channel (Raxworthy, Forstner, and Nussbaum 2002). The islands of the Indian Ocean are thus not just a "museum of biodiversity" but also a cradle that has provided an important evolutionary source of diversity for the African continent. Indian Ocean taxa have provided a means to understand general evolutionary principles, including multiple textbook examples of adaptive radiation, ranging from dung beetles (Orsini, Koivulehto, and Hanski 2007), to day geckos (Harmon et al. 2008), to chameleons (Raxworthy, Forstner, and Nussbaum 2002), and to lemurs (e.g. Martin 2000), to name but a few (see also Yoder and Nowak 2006; Kuntner and Agnarsson 2011a-b).



Fig. 1. The western Indian Ocean and the islands this review focuses on (white), and those briefly mentioned (yellow). Oceanic ridges and banks are indicated in green and their outlines can be seen in gray. Dotted white lines surround island archipelagos.

2. Paleogeology of the western Indian ocean

The geological history of the western Indian Ocean islands is complex, and not completely resolved. The western Indian Ocean contains both 'Wallacean' or 'fragment' islands such as Madagascar, Socotra, and the granite Seychelles that once formed a part of Gondwana, as well as 'Darwinian' or 'de novo' volcanic islands of varying ages, such as the Comoros, the coral Seychelles, and the Mascarenes. Sprinkled throughout the area are also many small to tiny coral islands and atolls that also are Darwinian, and some large continental Wallacean islands that have only recently been separated from Africa, such as Zanzibar. We here summarize the broad strokes in the geological history of the area. We focus on the patterns displayed by the larger offshore islands, while offering some remarks on other islands in the region. Very few comparative data are available on the biota of the many tiny islands scattered through the western Indian Ocean, such as Europa, Bassas da India, Juan de Nova, Glorioso, Agalega, Cargados Carajos, and Tromelin islands, labelled yellow in Fig. 1. Several studies have looked at bird and turtle populations on some of these, but little is otherwise known about their biota and their origins. However, they represent fascinating opportunities for biogeographical studies. The relatively large islands lying very close to Africa in the Zanzibar archipelago (25-60 km away from the mainland) were connected with Africa during the last ice age and are thus very recently separated from the mainland, except Pemba, which has been isolated for probably several million years. Socotra is an old and isolated Gondwanan fragment of the African continent, but very distant from the remaining islands and thus, at least in part, has a different biogeographical history.

2.1 Wallacean islands

'Wallacean islands', or 'fragment islands' are islands that once formed a part of a larger landmass, but that through tectonic plate activities and fragmentation of continental crust became secondarily isolated. In principle, such islands were 'born' with continental biota and ought to be species rich upon birth, with ecological space initially filled. Species richness then changes after fragmentation as a function of extinction, colonization, and in situ speciation (Gillespie and Roderick 2002). However, many geological Wallacean islands, including the granite Seychelles are biologically better characterized as Darwinian as they have been submerged subsequent to their isolation, and thus most of the current biota will have arrived there via dispersal overwater after the emergence of the islands.

2.1.1 Madagascar

Madagascar is a large Wallacean island (~587,000 km²) separated from Africa by the Mozambique Channel, some 420 km at the narrowest point. Yoder and Nowak, and Masters and colleagues (Yoder and Nowak 2006; Masters, de Wit, and Asher 2006) offer detailed, but rather different, reviews of the complex geological history of Madagascar and its interaction with the rest of Gondwana (see also Leigh et al. 2007). Yoder and Nowak highlight recent phylogenetic evidence of numerous taxa and how results generally are at odds with predictions based on Gondwanan vicariance, rather pointing towards transoceanic dispersal during the Cenozoic as the primary biogeographical force. Masters and colleagues, however, highlight Gondwanan elements of the Malagasy fauna, and the possibility of land bridges allowing colonization after continental breakup over land rather than water. We will here

build on these reviews by succinctly summarizing them, and point readers to Yoder and Nowak's and Masters et al. papers for specific details and references. However, we also highlight more recent findings, largely in support of the view of Yoder and Nowak, that offer new evidence for transoceanic dispersal mechanisms in the Cenozoic (Ali and Huber 2010).

Madagascar formed a part of eastern Gondwana, which also contained India, Antarctica, and Australia, while western Gondwana included Africa and South America (Briggs 2003). During 165 to 155 Ma the parts that would form eastern Gondwana drifted southward along the eastern African continent, and by 140 Ma a body of ocean already separated Madagascar from Africa at which point biotic exchange would have been dramatically reduced (see Yoder and Nowak (2006) and references therein). By 118 Ma, and possibly as early as 130 Ma, Madagascar reached its current position relative to Africa, already separated by the deep and wide Mozambique Channel. However, Madagascar remained connected to India for much longer. The timing of separation is debated, but sometime between 100 Ma and 87 Ma India plus the Seychelles block was separating from Madagascar, moving northeast. Thus the separation occurred gradually over millions of years, with the final separation of Madagascar and India frequently being cited as 88 Ma (Storey et al. 1995), but see (Rage 2003). The history of India and the connection between IndoMadagascar and the remainder of eastern Gondwana is complex, and seems far from settled. Some argue that India was already isolated by 130-125 Ma, while others suggest, based on recent fossil findings, that connections existed between IndoMadagascar and Antarctica and from the latter to S. America until as late as 80 Ma (see Yoder and Nowak 2006 and references therein). Such land bridges might explain the presence of elephant birds in Madagascar, as well as abelisaurid dinosaurs, and mammals with close affinities to S. America. Furthermore, there are several groups, especially non-volant mammals, whose history does not fit well the Gondwanan breakup as currently understood, but whose presence in Madagascar also cannot be readily explained by long distance dispersal (Masters, de Wit, and Asher 2006). Instead, Masters and colleagues suggest that several plateaus, banks, and fracture zones may have emerged periodically from the ocean and facilitated biotic interchange between Africa, India, and Madagascar (Masters, de Wit, and Asher 2006). For example, the distribution of certain taxa such as lemuriform primates, boine snakes, hyperoliid tree frogs, iguanid lizards, and certain plant groups, has been suggested to imply a more recent connection between India and Madagascar. This prompted the "Lemurian Stepping-stones" hypothesis (Schatz 1996; Steenis 1962). The hypothesis proposes that dispersal to Madagascar from India and further from Asia was facilitated by existing islands in the Eocene (56-34 Ma), close to the time India assumed its current position. At that time, a global drop in sea levels may have exposed the Seychelles bank and the Mascarene and Chagos/Laccadive plateaus and these, in turn, may have served as 'stepping stones' facilitating the exchange of biota between India and Madagascar (Rage 2003). Similarly, the Davie fracture zone lying between Africa and Madagascar is hypothesized by some to have partially emerged from the ocean during episodes some 45-26 million years ago (Masters, de Wit, and Asher 2006). However, there are fundamental problems with such land bridge arguments. First, most of these ridges would have, at best, partially emerged, creating island chains which still would require, albeit shorter distance, transoceanic dispersal. Second, the existence of a solid land-bridge, for example between Africa and Madagascar makes specific predictions, among which are that many different groups of taxa should have arrived, while only a few did, and the taxa that did arrive should have done so more or less simultaneously, which is also not the case (Table 1, Ali and Huber (2010); Yoder and Nowak (2006)).

Kingdom	Taxon	Pattern summary	Estimated dispersal events	Estimated regional diversity	Reference
animals	<i>Hemicordulia</i> dragonflies	Likely two colonization events of W Indian Ocean islands and Africa from Asia assisted by westward storms, but precise routes unknown in the absence of phylogeny	2	5	Dijkstra (2007)
animals	Scops owls (<i>Otus</i>)	Multiple colonizations from Indo-Malaya (order undetected but estimated at 3.6 ma), and one back colonization of Asia; Indian Ocean radiation at 2.5 ma; Pemba colonization separate from Africa at 1.7	3	7	Fuchs et al. (2008)
animals	Parrots	Likely colonization from India via stepping stones	1	9	Hume (2007)
animals	Parrots	Dispersals twice from Australasia to Madagascar, once from Madagascar to Africa and once from Australasia to Africa	4	7	Schweizer et al. (2010)
animals	Hawksmoth genus <i>Hyles</i>	Dispersal from South America to Australia and Madagascar	1	2	Hundsdoerfer et al. (2009)
animals	Oscine passerine birds	Dispersal from Australia to Africa via Indian Ocean islands, then from Africa to other continents	1	n/a	Jonsson and Fjeldsa (2006)
animals	Golden orb spider (<i>Nephila inaurata</i>)	Africa to Madagsacar to Mascarenes	10+	1	Kuntner and Agnarsson (2011)
animals	<i>Colotis</i> butterflies	Multiple dispersals from Africa to Madagascar	6	7	Nazari et al. (2011)
animals	<i>Pteropus</i> fruit bats	Independent colonizations: Asia to Comoros/Pemba, Asia to Rodrigues and Asia to all other W Indian Ocean islands	8	8	O'Brien et al. (2009)

Kingdom	Taxon	Pattern summary	Estimated dispersal events	Estimated regional diversity	Reference
animals	<i>Dromogos</i> (Dicruridae)	Asia to Africa, from there to Indian Ocean islands and back to Asia; Madagascar to Mayotte, Madagascar to Aldabra, Madagascar to Comoros	6	4	Pasquet et al. (2007)
animals	Carpenter bees (Ceratinini)	Two or three dispersals from Africa to Madagascar between 25 and 9 ma	2	?	Rehan et al. (2010)
animals	Allodapine bees	Dispersal events from Africa via Indian Ocean to Australia, and from Africa to Madagascar	2	35	Schwarz et al. (2006)
animals	magpie robins (<i>Copsychus</i>)	Asia to Madagascar	1	2	Sheldon et al. (2009)
animals	Canthonini and Dichotomiini	Dispersal events from Africa to Eurasia and on to America and Africa to India, SE Asia and to Australia	n/a	n/a	Sole and Scholtz (2010)
animals	(Scarabaeinae) Scarabaeini beetles	Africa to Madagascar	1	3	Sole et al. (2011)
animals	White-eye songbirds (<i>Zosterops</i>)	Complex history with an early dispersal to W Indian Ocean and to Africa from Asia and a later one from Africa to Comoros, then to other W Indian Ocean	8	15	Warren et al. (2006)
animals	Parrots	Australasian origin, speciation though vicariance, then dispersal to e.g. Madagascar from Australia	1	n/a	Wright et al. (2008)
animals	Starlings and mynas (<i>Sturnus</i> , <i>Acridotheres</i>)	Asia to Reunion (for <i>Fregilupus varius</i>), a split about 4 ma	1	6	Zuccon et al. (2008)
animals	<i>Rattus rattus</i>	Introduced, likely each island separately	n/a	1	Tollenaere et al. (2010)
animals	<i>Bactrocera cucurbitae</i> (Diptera: Tephritidae)	Introduced	0	1	Virgilio et al. (2010)
animals	<i>Anelosimus</i> spiders	Two independent colonizations of Madagascar/Comoros from Americas and Americas or Africa, both less than 10 ma	4	12	Agnarsson et al. (2010)

Kingdom	Taxon	Pattern summary	Estimated dispersal events	Estimated regional diversity	Reference
animals	<i>Mormopterus</i> bats	Inconclusive	?	2	Goodman et al. (2008)
animals	<i>Rousettus</i> bats	Inconclusive; rare dispersal over 300 km leading to diversification	2	2	Goodman et al. (2010)
animals	<i>Chaerephon</i> bats	Bats maintain gene flow within Comoros, but not further	1	2	Goodman et al. (2010)
animals	Hermit spiders (<i>Nephilengys</i>)	Inconclusive, either Africa to W Indian Ocean islands or vice versa	0	1	Kuntner (2007)
animals	Hermit spiders (<i>Nephilengys</i>)	Africa to Madagascar, then to Mascarenes and Madagascar to Mayotte	3	4	Kuntner and Agnarsson (2011)
animals	<i>Drosophila mauritiana</i>	Gene flow from Mauritius to Rodrigues, but not vice versa	1	1	Legrand et al. (2011)
animals	<i>Triaenops</i> bats	At least two dispersals from Africa to Madagascar	2	4	Russell et al. (2008)
animals	<i>Scotophilus</i> bats	Two independent colonizations of Madagascar from Africa	2	4	Trujillo et al. (2009)
animals	<i>Miniopterus</i> bats	Madagascar to Comoros at least twice with limited or no subsequent gene flow	below	below	Weyeneth et al. (2008)
animals	<i>Miniopterus</i> bats	Madagascar to Comoros 180000 ya	2	2	Weyeneth et al. (2011)
animals	<i>Zaprionus</i> (Diptera)	Asia to Africa via Indian Ocean islands	2	7	Yassin et al. (2008)
animals	Geckos, skinks	Independent colonizations from Mauritius	2	3	Arnold and Bour (2008)
animals	<i>Leiopisina</i> skinks	Single dispersal event to Mauritius from Australia, then to Reunion	2	3	Austin and Arnold (2006)
animals	Slit-eared skinks	Madagascar (or Africa) to Mauritius, to Reunion	2	3	Austin et al. (2009)
animals	Haemadipisdae leeches	Not vicariant	3	8	Borda and Siddall (2010)
animals	Ranid frogs	Vicariant - apparently, but dispersal to Mayotte	1	130	Bossuyt et al. (2006)
animals	Freshwater crabs	Multiple colonizations from Africa and Eurasia (Socotra)	below	below	Cumberlidge (2008)

Kingdom	Taxon	Pattern summary	Estimated dispersal events	Estimated regional diversity	Reference
animals	<i>Seychellum alnuaudi</i> freshwater crab	Africa to Seychelles	below	below	Daniels (2011)
animals	Freshwater crabs	Dispersal to Madagascar and Seychelles	3	15	Daniels et al. (2006)
animals	<i>Homopholis</i> and <i>Blaesodactylus</i> gekkos	Africa to Madagascar	2	4	Greenbaum et al. (2007)
animals	Day geckos (<i>Phelsuma</i>)	Independent colonizations from Madagascar to Seychelles, Comoros, Mascarenes	10	49	Harmon et al. (2008)
animals	Day geckos (<i>Phelsuma</i>)	Colonizations of Mascarenes and Pemba from Madagascar	above	above	Raxworthy et al. (2007)
animals	<i>Pristionchius pacificus</i> nematode	Multiple independent invasions	?	1	Herrmann et al. (2010)
animals	Gecarcinucoidea freshwater crabs	African origin, stepping stone dispersal via W Indian Ocean islands towards Asia	5	19	Klaus et al. (2006)
animals	River snails Pachychilidae	Cenozoic dispersal	1	5	Kohler and Glaubrecht (2010)
animals	<i>Oplurin</i> iguanas	No differentiation between Comoro and Madagascar	1	7	Munchenberg et al. (2008)
animals	<i>Stenophis</i> and <i>Lycodryas</i> snakes		8	82	Nagy et al. (2010)
animals	podocnemid turtles	Vicariant	0	1	Noonan and Chippindale (2006)
animals	iguanid lizards	Vicariant	0	7	Noonan and Chippindale (2006)
animals	Boid snakes	Vicariant	0	3	Noonan and Chippindale (2006)
animals	Agamid and chamaeleonidae	Vicariant Madagascar-Indian	0		Okajima and Kumazawa (2010)
animals	Plated lizards (Gerrhosauridae)	Likely from Africa to Madagascar, followed by radiation	1	19	Raselimanana et al. (2009)
animals	Cetartiodactyla	Single dispersal from Africa	1	3	Yoder and Nowak (2006)

Kingdom	Taxon	Pattern summary	Estimated dispersal events	Estimated regional diversity	Reference
animals	Eulipotyphla	Single dispersal from Africa	1	1	Yoder and Nowak (2006)
animals	Rodents	Single dispersal from Africa	1	27	Yoder and Nowak (2006)
animals	Carnivora	Single dispersal from Africa	1	9	Yoder and Nowak (2006)
animals	Afrotheria	Single dispersal from Africa	1	30	Yoder and Nowak (2006)
animals	Perissodactyla	Present in Africa, no dispersal to the islands	0	0	IUCN
animals	Pholidota	Present in Africa, no dispersal to the islands	0	0	IUCN
animals	Onychopriion	Dispersal among islands frequent enough to maintain gene flow	frequent	1	IUCN
animals	Pantala	Dispersal among islands frequent enough to maintain gene flow	frequent	1	IUCN
animals	Primates	Suggests vicariant origin of primates	below	below	Heads (2010)
animals	Primates	Single dispersal from Africa	1	94	Yoder and Nowak (2006)
animals	Coastal lizards (Cryptoblepharus)	Colonization by transoceanic dispersal (from Australia or Indonesia) to Madagascar, from there to Africa, Comoros islands (twice), and Mauritius	5	Unresolved	Rocha et al. (2006)
animals	Mabuya lizards (Scincidae)	West to East across Comoros	4	14	Rocha et al. (2010)
animals	Streptaxid land snails	Africa to Madagascar, Africa to Seychelles, Africa to Mascarenes	12	240	Rowson et al. (2011)
animals	Crayfishes (Parastacidae)	Vicariant (Gondwana)	0	6	Toon et al. (2010)
animals	Archaius (Calumma) chameleons	Africa to Seychelles	1	1	Townsend et al. (2011)
animals	Polystomatid flatworms (amphibian parasites)	Two independent colonizations of Madagascar via amphibian hosts, maybe one from Asia the other from Africa	2	13	Verneau et al. (2009)
animals	Blindsnakes (Typhlopidae)	Vicariant (Gondwana)	1	14	Vidal et al. (2010)
animals	Giant pill-millipedes (Sphaerotheriida)	Vicariant (Madagascar)	0		Wesene and VandenSpiegel (2009)

Kingdom	Taxon	Pattern summary	Estimated dispersal events	Estimated regional diversity	Reference
animals	Giant pill-millipedes (Arthropsophaeridae)	Vicariant (Gondwana)	0	60	Wesener et al. (2010)
animals	Caecilian amphibians	Vicariant (Seychelles)	0	6	Zhang and Wake (2009)
animals	Hemidactylus geckos	Overocean dispersal to Socotra from northern Africa, and from Arabia	2	11	Carranza and Arnold (2006)
animals	<i>Chamaeleo monachus</i>	Vicariant	0	1	Macey et al. (2008)
plants	<i>Coffea</i> (Rubiaceae)	Africa to Grand Comore	below	below	Anthony et al. (2010)
plants	<i>Coffea</i> (Rubiaceae)	See Wikstrom et al. (2010)	below	below	Maurin et al. (2007)
plants	Coffee family (Rubiaceae)	Africa to Madagascar, Asia to Madagascar, Madagascar to Comoros, Madagascar to Seychelles, Madagascar to Mascarenes	30	803	Wikstrom et al. (2010)
plants	Chrysophylloideae (Sapotaceae)	Africa to Madagascar THREE times	4	40	Bartish et al. (2011)
plants	<i>Lilaeopsis</i> (Apiaceae subfamily Apioideae)	Likely a recent introduction	0	1	Bone et al. (2011)
plants	<i>Vanilla</i>	Overocean dispersal to Reunion	3	10	Bouetard et al. (2010)
plants	Sapindaceae (<i>Molinaea</i> , <i>Neotina</i> , <i>Tina</i> , <i>Tinopsis</i>)		4	100	Buerki et al. (2011)
plants	Palm tribe Chamaedoreae	Long distance dispersal (absent from Madagascar and Africa)	3	5	Cuenca et al. (2008)
plants	Scaly tree ferns	3 independent colonizations followed by speciation	8	56	Janssen et al. (2008)
plants	Hibisceae (Malvaceae)	Multiple colonizations of Madagascar	5	86	Koopman and Baum (2008)
plants	Fern genus <i>Platyserium</i>	Vicariant	4	6	Kreier and Schneider (2006)
plants	Euphorbs	Colonization of Madagascar/ Africa from Asia	1	11	Kulju et al. (2007)
plants	Dombeyoideae (Malvaceae)	At least 5 colonizations from Madagascar	15	273	Le Pechon et al. (2009)
plants	Dombeyoideae (Malvaceae)	Multiple Madagascar to Mascarenes	above	above	Le Pechon et al. (2010)

Kingdom	Taxon	Pattern summary	Estimated dispersal events	Estimated regional diversity
plants	tropical Anagallis (Myrsinaceae)	Africa to Madagascar twice	2	10
plants	Hernandiaceae	Dispersal to Madagascar from Asia, and to Reunion from Pacific	2	4
plants	Angraecoid orchids	Multiple from Madagascar	20	321
plants	Calypstrochaeta moss	Africa to islands?	3	1
plants	Monimiaceae	Australasia to Indian Ocean islands	6	63
plants	<i>Lomariopsis</i> ferns	Madagascar clade includes nested African species	3	7
plants	Cucurbitaceae	13 independent colonizations fo Madagascar from Africa	14	90
plants	Ferns (Lindsaeaceae)	Unclear	n/a	31
plants	<i>Warneckea</i> (Melastomataceae)	Madagascar from Africa, possibly Mauritius from Madagascar, the authors are not interested in biogeography	1	20
plants	<i>Aerva</i> (Amaranthaceae)	Eritreo-Arabian colonization of Socotra	5	8
plants	Baobab <i>Adansonia digitata</i>	Natural and human dispersal ot Madagascar from Africa	1	1
plants	<i>Diospyros</i> (Ebenaceae)	Colonization of Mauritius, followed by Reunion and Rodrigues	2	14
plants	<i>Euphorbia</i>	Africa to Madagascar several times	5	110
plants	<i>Echidnopsis</i> (Apocynaceae)	Dispersal from E. Africa to Socotra	1	5
plants	<i>Thamnosma</i> (Rutaceae)	Africa to Socotra	1	2

Table 1. A summary of recent literature on the phylogeography and biogeography of the western Indian Ocean. The dispersal events represent our own interpretation of the data presented in the reference paper. Estimated regional diversity represents our own attempts to estimate the number of species of each clade in the region, this number comes from the referenced paper, but from various external sources. Estimates in many cases are approximate, based on current knowledge and scattered information. Exemplar studies of Indian Ocean taxa that provide phylogeographic information are listed in the “Review of studies and patterns” for details on filtering the literature search results.

Any dispersal model needs to consider not only the geological separation of landmasses, but also the direction of dispersal agents, such as trade winds and oceanic currents, through history. After the separation of Madagascar with Africa and India, oceanic currents are thought to have been favourable to dispersal on rafts from Africa to Madagascar, however, in the present day, currents go in the opposite direction, and are more favourable for colonization from Madagascar to Africa. How long the present day currents have persisted is debated, and some have suggested they may have prevailed for as much as 50 Ma (Masters, de Wit, and Asher 2006 and references therein), thus drastically reducing opportunities for colonization of Madagascar from Africa. However, an exciting new paleo-oceanographic modelling study concluded that strong oceanic currents did flow from eastern Africa to Madagascar during the Palaeogene, with occasional currents strong enough to cross the Mozambique channel in less than a month (Ali and Huber 2010). Starting soon after the great faunal turnover at 65 Ma (see below) and lasting until about 20 Ma (Ali and Huber 2010), these favourable currents coincide in time with the arrival of non-volant mammals as reconstructed by dated phylogenies: lemuriform primates (60-50 Ma), tenrecs (42-25 Ma), carnivorans (26-19 Ma), and rodents (24-20 Ma) (Poux et al. 2005; Yoder and Nowak 2006). Under this model, the timing of currents shifting towards their present day flow, from Madagascar to Africa, also fits observation as this time more or less marked the end of non-volant mammal arrival. Furthermore, this scenario does not predict the simultaneous arrival of groups of organisms, but requires only the very rare occurrence of successful overwater dispersal (once per several million years) under relatively favourable conditions.

Though the geological history of Madagascar and related landmasses and oceanic plateaus is complex, Madagascar is clearly Wallacean in its geological origin. However, catastrophic geological events may have wiped out a portion of the Gondwanan fauna and flora on Madagascar about 65 Ma, through meteor impact in India and the subsequent Deccan volcanism (see below).

2.1.2 The granite Seychelles

The Seychelles is an archipelago of 155 islands, islets, and rocks, lying about 1.100 km northeast of Madagascar and 1.500 km east of Africa, with a total land area of only 220 km². About 42 of these are granite islands that are thought to be continental fragments that were once part of the Indo-Madagascan block that broke away from India during its passage northeast to Asia (Rabinovitz, Coffin, and Falvey 1983). These islands may have been isolated for upwards of 65 Ma (Plummer and Belle 1995), however they have all been mostly or completely submerged at various times with changes in sea level presumably wiping out most of the terrestrial biota. Thus from a biogeographical standpoint the granite Seychelles have many characteristics of Darwinian islands (Rabinovitz, Coffin, and Falvey 1983) with most of the biota having arrived via dispersal. Even some 'classic' examples of vicariant taxa, such as freshwater crabs, are now thought to have arrived via transoceanic dispersal (Cumberlidge 2008; Daniels 2011; Daniels et al. 2006). The notable exceptions are burrowing animals: caecilians (Zhang and Wake 2009) and sooglossid frogs (Biju and Bossuyt 2003), and possibly some ferns (Lehtonen et al. 2010), that appear to have persisted on the islands even during the periods of high sea levels. Some taxa, such as the sooglossid frogs, show genetic divergence among the granite Seychelles e.g. (Van der Meijden et al. 2007), highlighting the need for thorough sampling and biogeographical analyses of these islands.

2.1.3 Socotra archipelago

The Socotra archipelago (Yemen) consists of four islands, Abdel Kuri, Samha, Darsa, and by far the largest island – Socotra – measuring 3,625 km². The archipelago is isolated (240 km from nearest point in Africa, 380 km from Arabia) having separated from the Arabian peninsula probably over 30 Ma, in the Oligocene (Thompson 2000). The Arabian peninsula itself started to separate from northern Africa about 60 Ma (Thompson 2000) eventually crashing into the Eurasian plate about 15 Ma. While the islands are separated by shallow seas and may have come in contact with each other during episodes of low sea levels, they are separated from the continents by a deep trench (Busais 2011). Thus the biota of Socotra is characterized by high endemism. Of the large flora of Socotra, counting over 800 species, some 37% are endemic (Miller and Miranda 2004). Socotra is home to over 30 lizard species, 80% of which are endemic (Rösler and Wranik 2004), and also hosts a range of other endemic animals including geckos (Busais 2011), chameleons, colubrid snakes, and freshwater crabs (Cumberlidge 2008). The smaller islands also have endemics, such as the Abdel-Kuri Sparrow, and the day gecko *Hemidactylus forbesii* (Carranza and Arnold 2006). Some of Socotra's biota is thought to be vicariant, including the Socotran chameleon (Macey et al. 2008), and possibly some geckos (Arnold 2009; Gamble et al. 2008), while other elements are thought to have arrived via transoceanic dispersal from Eurasia such as freshwater crabs (Cumberlidge 2008; Daniels et al. 2006; but see Shih, Yeo, and Ng (2009)), colubrid snakes, and various plants (Thiv et al. 2006). Yet others have arrived from Africa (Thiv and Meve 2007), and day geckos apparently arrived once from Arabia and once from Africa (Carranza and Arnold 2006).

2.1.4 Zanzibar archipelago

The Tanzanian Zanzibar archipelago consists of over 40 islands and islets, of which three are by the far largest: Unguja – collectively referred to as Zanzibar – (2,461 km²), Pemba (980 km²), and Mafia island (394 km²). All are parts of continental Africa, and Unguja and Mafia are separated from the continent only by 25-30 km stretch of shallow ocean. These islands have therefore periodically been connected to continental Africa during low sea levels, with the last connection as recent as 10,000 Ya (Kingdon 1989). Thus their biota is mostly shared with the continent, with notable exceptions as noted below. Pemba differs in being a little further away (about 55 km) and is separated from the continent by a very deep trench, such that it has been isolated at least for some million years (Kingdon 1989). Thus Pemba has several well-known endemics such as the Pemba flying fox (Robinson et al. 2010), a *Mops* bat (Stanley 2008), Pemba scops-owl (Fuchs et al. 2008), Pemba white-eye (Vaughan 1929), and four other bird species, or subspecies (Vaughan 1929; Catry et al. 2000), a day gecko (*Phelsuma parkeri*) (Rodder, Hawlitschek, and Glaw 2010), a damselfly (Dijkstra, Clausnitzer, and Martens 2007), and several others. Coastal lizards have unique haplotypes on Pemba, differing from those found on the other islands, and those shared between, Unguja and the Tanzanian coast, which is consistent with relatively long island isolation (Rocha et al. 2006). Freshwater snails may have an endemic species on the archipelago, and also show genetic divergence among Pemba and Mafia islands (Stothard, Loxton, and Rollinson 2002). Land molluscs have several endemic species on the archipelago but apparently no more on Pemba than Unguja (Rowson 2007; Rowson, Warren, and Ngereza 2010), though DNA evidence is still lacking. Unguja has other endemics, the most striking perhaps the now presumed extinct Zanzibar leopard (a subspecies of *Panthera pardus*) and the Zanzibar red colobus

(Nowak and Lee 2011), but others include a species of frog (Msuya, Howell, and Channing 2006), crustaceans (Kensley and Schotte 2000; Olesen 1999) and other taxa. Nevertheless, the proximity with Africa means that most of the Zanzibar archipelago biota, including Pemba, is shared with Africa (e.g. (Clausnitzer 2003; Kock and Stanley 2009)), even among relatively poor dispersers such as freshwater crabs, species are shared with Africa (Cumberlidge 2008).

2.2 Darwinian islands

Darwinian islands provide a clean slate to colonists where species richness increases initially through immigration and later through formation of neo-endemics. For highly isolated islands, and for large islands, adaptive radiation may fill empty niches (Gillespie and Roderick 2002; Gillespie 2004). As noted above, some islands that are Wallacean in their geographical origin, have subsequently become mostly biologically Darwinian, for example due to periodic submergence with changing sea levels. The larger and older Darwinian islands are generally volcanic in origin, and island chains such as the Comoros and the Mascarenes have formed as tectonic plates move over a hot spot (Duncan and Storey 1994; Emerick and Duncan 1982), a common pattern of island chain formation.

2.2.1 The Comoros archipelago

The Comoros are a group of volcanic islands a little over 300 km NW of Madagascar and with a total land area of about 2200 km². The oldest island, Mayotte, is in the east, closest to Madagascar, with successively younger islands to the west, Grand Comore being the youngest and closest to Africa. Grande Comore is thought to be the result of very recent volcanic activity, some 0.01–0.5 Ma. Mayotte consists of two volcanoes that emerged from the ocean, probably a little less than 10 Ma (Audru et al. 2006, 2010). Estimates of the exact dates of the islands vary. In the geological atlas of Africa (Schlüter 2006), the island ages are given as 0.01 Ma (Gran Comore), 3.9 Ma (Anjouan), 5.0 Ma (Moheli), and 7.7 Ma (Mayotte). Nougier et al. (1986) estimate that the Comoros started forming around 10–15 Ma, such that land area may have been available for colonization for over 10 Ma. The terrestrial biota arrived mostly via overwater dispersal from Madagascar and from mainland Africa. Due to the relatively old age of the islands and their isolation, they are home to numerous endemic species of animals and plants, including 16 species of birds, two chiropterans, several *Phelsuma* day geckos, two *Furcifer* chameleons, other reptiles and amphibians and many invertebrates (Harris and Rocha 2009).

2.2.2 The Mascarene Islands

The Mascarene Islands, the principal of which are Réunion, Mauritius, and Rodrigues, lie about 700, 900, and 1500 km east of Madagascar, respectively, and have a total land area of 4500 km² including a few small offshore islands. All are of volcanic origin and have never been connected to any other landmasses (McDougall and Chamalaun, 1969), their biota thus necessarily has arrived via transoceanic dispersal. The age of the islands has long been debated, especially that of Rodrigues, which traditionally has been thought to be the youngest island at 1.5 Ma (McDougall and Chamalaun, 1969), but recent evidence favours the contrary conclusion, that it is the oldest island (Thébaud et al. 2009). Thus, most authors now seem to agree that Réunion is the youngest island of the Mascarenes. Age estimates are often given at some 2–3 Ma (Deniel, Kieffer, and Lecointre 1992), but it may be as old as 5 Ma

(Gillot, Lefèvre, and Nativel 1994). Mauritius is estimated to have emerged some 8-10 Ma (McDougall and Chamalaun, 1969), with the major components of the island being formed about 6 Ma. Rodrigues is then thought to be at least as old as Mauritius, or 8–15 My (Anon. 1998; Cheke and Hume 2008, Thébaud et al. 2009). Geologically, the Mascarene Plateau is as old as 40 Ma (Morgan 1981), so the possibility exists that a portion of the archipelago's land area was above ocean surface even earlier than 10 Ma. Islands now submerged are thought to have played an important role in the biogeographical history of some organisms in the region, such as the dodo, day geckos, and Laurales and palms, where colonization of the archipelago may have occurred before the current islands arose from the sea (Austin, Arnold, and Jones 2004; Cuenca, Asmussen-Lange, and Borchsenius 2008; Shapiro et al. 2002; Renner et al. 2010).

2.2.3 The coral Seychelles and Aldabra atoll

As outlined above, the Seychelles consist of 155 islands and islets, 42 of which are ancient Wallacean fragments of Gondwana—the granite islands—and the remainder are coral islands and atolls. These coral islands vary greatly in age and size, with Aldabra Atoll being one of the oldest with proto Aldabra dating to the late Pleistocene (i.e. less than 2.5 Ma), the largest (155 km² land area, 224 km² lagoon), most isolated (425 km NW of Madagascar, the nearest major landmass), and mostly undisturbed by humans. All the coral islands have in common that they have been submerged periodically through changes in sea level. For example, the most recent emergence of Aldabra Atoll from the ocean occurred about 125,000 years ago (Warren et al., 2005). Yet, Aldabra has some endemic biota, including the Aldabra drongo and the now presumed extinct Aldabra warbler (IUCN 2011), and several endemic plants. For the other smaller coral islands the frequency of submergence and the timing of the most recent emergence relate to island size and, especially, altitude. Regardless, all coral islands in the region can be considered as recent Darwinian islands from the perspectives of terrestrial biogeographical and phylogeographical studies.

2.2.4 The 'minor' islands of the western Indian Ocean

This review focuses on the larger islands of the Indian Ocean, mainly because their biota is in general much better known. There are, however, scattered throughout the western Indian Ocean a number of highly isolated small islands, most of which are home to breeding colonies of oceanic birds, and turtles. Notable among these are, in the Mozambique Channel, Europa island, Bassas da India, and Juan de Nova island (Fig. 1). North of Madagascar are Glorioso island, and some of the furthest outlying coral Seychelles, such as Assumption (close to Aldabra), and Farquhar atoll (Fig. 1). In between the granite Seychelles and the three main Mascarene islands are further highly isolated islands: Coetivy island, one of the outlying Seychelles, Agalega and Cargados Carajos, two outlying Mascarene islands, and then Tromelin island sitting between Madagascar, and the Mascarenes and Mascarene bank (Fig. 1). Though all of these are interesting from a biogeographical standpoint, and indeed some are known to harbour endemic forms, few molecular studies have included taxa from these islands such that their biogeographical history is in general poorly known; for information on many of these see Stoddart (1970), Stuart and Adams (1990), Caceres (2003). **Europa** island (28 km²), about 300 km from Madagascar and 500 km from the African coast is an important breeding ground for sea turtles and oceanic birds. An endemic 'race' of the white tailed tropicbird occupies the island, and Europa populations of some other bird

species appear to have little or no gene flow with other populations (WWF, 2008). The island also is host to subspecies such as Europa white eye and a snake-eyed skink. A few invertebrate species may be endemic, including the little known termite *Neotermes europae*, cockroach *Elliptorhina lefeuvri*, and leafcutter bee *Megachile pauliani* (see <http://Intresures.com/fsal.html>). Interestingly, breeding populations of green turtles are rather unique in Europa compared to the rest of the Indian ocean, and differ, for example from populations on Juan de Nova island (Bourjea et al. 2007). **Bassas da India** is a small atoll (~ 80 km² including lagoon) about 100 km north of Europa, that is mostly underwater during high tide and thus supports no vegetation, nor terrestrial fauna. **Juan de Nova island** is a tiny island (4 km²), home to a large colony of sooty terns (Jaquemet, Le Corre, and Quartly 2007) and has a unique genetic stock of green turtle (Bourjea et al. 2007). Of notable terrestrial fauna is a possibly endemic species of skink, *Cryptoblepharus caudatus*, and ant species shared with Madagascar *Camponotus hova*. **Glorioso islands**, consisting of five islands totalling about 5 km² in size, is home to several species of oceanic birds and a possibly endemic cone shell (*Conus veillardii*). **Assumption** is a small island (11 km²) close to the Aldabra atoll that is home to the endemic subspecies Assumption Island day gecko (*Phelsuma abbotti sumptio*), and a number of widespread oceanic birds. **Farquhar atoll** consists of a group of small islands that, although encircling a large lagoon, have a very small total land area (7.5 km²). The atoll is one of the few breeding places of Roseate terns, but both flora and fauna consist mostly of widespread species lacking endemics, though both are poorly known (Stoddart 1970; Stuart and RJ 1990). **Coetivy island** is a small sand cay (9.3 km²), apparently lacking endemics (Stuart and RJ 1990). **Agalega** consists of two islands with a total land area of 24 km² and is home to an endemic subspecies of the Réunion day gecko, (*Phelsuma borbonica agalegae*) (Cheke 2010; Rocha et al. 2009), **Cargados Carajos** is a group of tiny islets with a total land area of 1.3 km² and no terrestrial endemism. **Tromelin** is a tiny rock (0.8 km²), but is a host to some apparently endemic insects, such as the homopteran *Pulvinaria tromelini* (Stoddart 1970), and is the stronghold breeding place of a western Indian Ocean endemic subspecies of terns (*Sula dactylatra melanops*).

3. Review of biogeographical and phylogeographical studies and patterns

We present a review of studies on various terrestrial and freshwater taxa occupying the larger western Indian Ocean islands. The review does not aim to be exhaustive, but is explicitly exemplary in its approach, focusing on recent literature. For our review of patterns we focus on the islands that have been best studied, while highlighting the many fascinating isolated tiny islands that deserve research attention (Fig. 1). We survey in particular detail the literature published since the review of Madagascar biogeography (Yoder and Nowak 2006). In Web of Science we used the following literature search criteria: (Biogeography AND Madagascar OR Comoros OR Reunion OR Mauritius OR Rodrigues OR Socotra OR Seychelles OR Zanzibar) AND Year Published=(2006-2011); the hits were then refined by Web of Science categories: (Zoology OR Ecology OR Plant sciences OR Evolutionary biology) and by document type (Article OR Review), then further filtered by hand to retain only relevant works. The resulting Table 1 lists all those works that treat non-marine Western Indian Ocean taxa explicitly and contain information on the phylogenetic relationships of those taxa. For these taxa, we extracted a biogeographically useful summary of the pattern of colonization—those we tally up across all taxa and summarize in Fig. 2—and diversification in the archipelago. We also collected information on genetic divergence among landmasses, and estimated timing of colonization events, however such data were

available in far too few studies for any comparative analyses, thus these results are not included in Table 1. Additionally, we discuss selected studies taken from older literature, and from the reviews of Yoder and Nowak (2006) and Masters, de Wit, and Asher (2006). We note that the sampled histories have a strong bias towards Madagascar, as many more studies are published that include taxa from Madagascar than any other island in the western Indian Ocean. Hence, when tallying independent dispersal histories, a comparison of absolute numbers is not very informative. Instead we interpret the main patterns of colonization of each archipelago and summarize observed histories in Fig. 2. We also attempt to estimate the relative role of vicariance, by counting putative vicariant histories and divide them by the total number of observed histories (total number of colonization events or vicariance events across independent lineages). However, this is necessarily a crude estimate, both because we look only across recent studies, and because many of the putative vicariant histories yet lack testing through molecular dating. We start this review with summarizing examples from various relatively well studied groups of animals and plants, and then move to studies on spiders, mostly from our own work. We summarize general patterns observed for each taxon, and then attempt to draw broad and general conclusions about Indian Ocean biogeography across taxa, the common colonization routes, and the general role of dispersal abilities in shaping both distributional and diversification patterns.

3.1 Biogeographical patterns in the western Indian Ocean

3.1.1 Vicariance versus dispersal

Oceanic dispersal played a central role in the early biogeography of Darwin and Wallace (Darwin 1859; Wallace 1876; Clark 1994; Hommersand, Fredericq, and Freshwater 1994), and for many decades afterwards. However, after continental drift and plate tectonics (Wegener 1912, 1966) became generally accepted, the field of biogeography shifted towards favouring vicariance explanations of biogeographic patterns, sometimes with dispersal serving as the 'poor cousin' explanation to be used only as a last resort when patterns were inconsistent with vicariance (de Queiroz 2005; Waters 2008; Nelson and Platnick 1981). Nelson (1979) famously characterized dispersalism as 'a science of the improbable, the rare, the mysterious, and the miraculous' because, at the time and before the molecular revolution in phylogenetics, inferring dispersal histories of organisms was too speculative. Thus many terrestrial and freshwater lineages occurring on Madagascar and some other islands in the Indian Ocean were long thought to have been present already before Madagascar separated from India and Africa during plate tectonic history (Yoder and Nowak 2006; Ali and Aitchison 2008). Support for vicariance hypotheses came both from morphology-based phylogenetic patterns that were consistent with the origin of Malagasy organisms from Africa or India, the two continents it was in connection with most recently, and from intuitive arguments based on the perceived limited dispersal ability of many of the highlighted lineages. For example chameleons, other lizards, frogs, lemurs, tenrecs, carnivores, and freshwater fish in Madagascar all were at one point or another thought to be examples of a common vicariance pattern (Yoder and Nowak 2006). However, a crucial component of vicariance hypotheses is the concurrent timing of geographic breakup of landmasses, and speciation events. Even when vicariance explanations are plausible based on phylogenetic relationships among species, and presumed dispersal abilities of the taxa in question, they must be rejected if the timing of speciation events is inconsistent with the geological history (Grande 1985; Lundberg 1993; Hunn and Upchurch 2001; Yoder and Nowak 2006). Molecular data offered a revolution in biogeography, as in phylogenetics in

general, as they allow simultaneous estimation of relationships among species, and timing of speciation events (Drummond et al. 2006; Sanderson 2002). As massive DNA evidence is accumulating, dispersal biogeography is currently enjoying a renaissance, with these new data pointing towards relatively recent origins of lineages and thus more frequently than not rejecting vicariance in favour of dispersal hypotheses for a wide range of taxa and landmasses (de Queiroz 2005; Yoder and Nowak 2006). Presumably, a common pattern is the occurrence of long distance dispersal events frequently enough to allow island colonization, but sufficiently rarely such that colonization events restrict gene flow and eventually lead to speciation (Gillespie et al. 2012).

The terrestrial and freshwater biota of the western Indian Ocean is no different – a review of recent literature (Table 1, see also Yoder and Nowak (2006)) provides compelling evidence for the origin of the majority of the Indian Ocean island's biota at a much more recent geological time than the major tectonic events of the ancient Gondwana; the origin of these groups, then, has to be explained via Cenozoic dispersal rather than via Gondwanan vicariance (Vences et al. 2001; Yoder and Nowak 2006; Kuntner and Agnarsson 2011a-b; Agnarsson and Kuntner In Prep). The ancestor of most lizards, frogs, lemurs, tenrecs, and at least some freshwater fish, are now all thought to have arrived via relatively recent long distance dispersal during the time the landmasses were in, or close to today's position (Vences et al. 2004; Raxworthy, Forstner, and Nussbaum 2002; Austin, Arnold, and Jones 2004; Rocha, Carretero, and Harris 2005; Rocha et al. 2006, 2007). In fact, our review (Table 1) demonstrates that the majority, some 230 independent biogeographic histories (clades), must be explained by ancestral dispersal followed by diversification, while only 16 clades reviewed are potentially old enough to be explained by diversification through Gondwanan vicariance. One should bear in mind 1) that dated molecular phylogenies are far from infallible. Calibration points are crucial, and fossils and geological events that are used for calibration are often not fully understood, and in any case usually only offer minimal ages. Further advances in molecular dating may yet favour vicariance for some of the clades recently suggested to be examples of dispersal biogeography. Further, 2) the possibility exists that oceanic ridges, which may have facilitated dispersal, may have emerged above the surface periodically (Masters, de Wit, and Asher 2006). Thus, for example, not all Africa-Madagascar sister clades that are younger than the split between these landmasses must have dispersed over ocean. However, recent paleo-oceanographic models predict ocean currents favourable for colonization of Madagascar from Africa occurring exactly during the episode when many taxa with presumably poor dispersal abilities, such as non-volant mammals, arrived (Ali and Huber 2010). The agreement between dated phylogenetic trees for multiple groups and paleogeographic modelling, and limited evidence for and lack of fit of data to land-bridge theories argue for transoceanic dispersal having been the major biogeographical force in the region (Ali and Aitchison 2009; Ali and Krause 2011).

The sources of colonizers of western Indian Ocean islands are diverse, but Africa is dominant, especially for poorer dispersers, while elements from Asia– most notably India and Australasia also occur (Warren et al. 2010) among the better dispersers such as flying insects (dipterans and dragonflies), fruit bats, and several groups of birds such as parrots and passerines (Table 1). Madagascar, in turn, is the most common source of colonizers of the Mascarenes and Comoros, while the Seychelles have received dispersers from Madagascar, but also directly from Africa (Table 1). The complex tectonic history of the region (Ali and Aitchison, 2008) and many potential source landmasses mean that identifying the primary

biogeographical forces contributing to the biota is challenging, and patterns are often taxon specific (Table 1). The modes of dispersal must be either aerial (wind or bird-assisted; Gillespie et al. 2012), ocean rafting over the more than 400 km wide Mozambique Channel between Africa and Madagascar, or from even further afar, or a mix of both (Table 1), although as mentioned above, potential ridges above the ocean may have facilitated island hopping in the past. In some cases, recent colonisations have been assisted by human transport (Vences et al. 2004). Whatever the route and means of dispersal, the available data clearly imply the importance of dispersalism. Thus, long distance dispersal may well be the study of the improbable and the rare but hardly the mysterious nor the miraculous (see Nathan 2006). As it turns out, rare and individually improbable events are extremely important historically, and indeed such 'waif biota' (Carlquist 1966) is responsible for much of the distribution and diversification of organisms on islands.

Nevertheless, vicariance remains an important biogeographical force in the region and molecular data has corroborated vicariance hypotheses for a number of extant groups (see below, Table 1, and Yoder and Nowak (2006). Many extinct Malagasy groups are also thought to represent vicariant elements. Indeed the relative scarcity of extant vicariant groups may relate to faunal turnover following meteorite impact and associated volcanic activity 65 Ma (see below). It is also worth noting that detecting vicariance may be challenging due to sampling errors, extinction, and species expansion following disappearance of historical geological barriers (Upchurch 2008). Current methods may thus to some extent be underestimating the importance of vicariance. Calibrating species phylogenies using island ages, commonly done when fossil data are not available, including in our own recent studies (Kuntner and Agnarsson 2011a-b), may also be misleading (Heads 2011). Clades endemic on islands may be older than the islands, having e.g. persisted on older nearby islands that are now submerged, and thus using island age to calibrate phylogenies will tend to bias studies towards accepting dispersal hypotheses over vicariance. Future studies, through improved knowledge of the fossil records and better understanding of 'molecular clocks', will no doubt lead to reinterpretation of some dispersal hypotheses. Nevertheless, overwhelming evidence suggests that rather than treating dispersalism as explanation of the last resort, transoceanic dispersal has strongly influenced the distribution of organisms globally (Carlquist 1966; Crisp et al. 2009; Gillespie et al. 2012). In sum, ancestors of most of the biota of Madagascar, and indeed other Wallacean islands in the western Indian Ocean, arrived there in the last 65 Ma, after it was isolated from other landmasses, and the current evidence does not favour tentative Cenozoic land-bridges as influential in the colonization of Madagascar or other islands (Ali and Aitchison 2009; Ali and Krause 2011).

3.1.2 Cenozoic dispersal from Africa to Madagascar, and from Madagascar to the Comoros, Seychelles, and Mascarenes – The dominant patterns

The Cenozoic dispersal from Africa model (i.e. younger than 65.5 Ma) seems to apply to the majority of the Malagasy fauna and flora (Yoder and Nowak 2006), although Warren et al. (2010) conclude that Asian elements are nearly as important as African ones in Madagascar, especially among vertebrates. The colonization of Madagascar is often followed by subsequent colonization of the Seychelles, Comoros and Aldabra to the north, and the chain of volcanic Mascarene islands (Réunion, Mauritius and Rodrigues) to the south and east (Fuller, Schwarz, and Tierney 2005; Yoder and Nowak 2006; Raxworthy et al. 2007; Le Pechon et al. 2010). Examples of Cenozoic dispersal from Africa to Madagascar include

various elements of herpetofauna such as geckos, tortoises, scincid lizards, and colubrid snakes (Raxworthy, Forstner, and Nussbaum 2002; Vences et al. 2001; Hume 2007; Nagy et al. 2003; Austin, Arnold, and Jones 2004; Caccone et al. 1999; Mausfeld et al. 2000), mammals (Tattersall 2006; Masters, de Wit, and Asher 2006; Masters, Lovegrove, and de Wit 2007; Russell, Goodman, and Cox 2008; Goodman, Buccas, et al. 2010), fig wasps (Kerdelhue, Le Clainche, and Rasplus 1999), allodapine bees (Fuller, Schwarz, and Tierney 2005), Scarabaeinae dung beetles (Sole and Scholtz 2010), carpenter bees (Rehan et al. 2010), pierid butterflies (Nazari et al. 2011), fig wasps (Kerdelhue, Le Clainche, and Rasplus 1999), spiders (Agnarsson and Kuntner 2005; Agnarsson et al. 2010; Kuntner and Agnarsson 2011a-b), ants (Fisher 2007), freshwater crabs (Daniels et al. 2006; Klaus, Schubart, and Brandis 2006), snails (Kohler and Glaubrecht 2010), parasitic flatworms (Verneau, Du Preez, and Badets 2009; Verneau et al. 2009) and many groups of plants (Renner 2004; Weeks, Daly, and Simpson 2005; Dick, Abdul-Salim, and Bermingham 2003; Kita and Kato 2004; Bartish et al. 2011; Schaefer, Heibl, and Renner 2009; Manns and Anderberg 2011; Pokorny, Oliván, and Shaw 2011; Renner 2004), although many plants seem to have a more complicated biogeographical history (Renner 2004). This pattern of colonization is also seen intraspecifically, for example the bryophyte *Calypstrochaeta asplenoides* colonized Madagascar from E. Africa about 6 Ma, then subsequently the Mascarenes about 3 Ma from Madagascar, also likely reaching the Comoros from Madagascar (Pokorny, Oliván, and Shaw 2011). Many groups of birds have also arrived in Madagascar via Cenozoic dispersal from Africa (Yamagishi et al. 2001; Marks and Willard 2005; Warren et al. 2003, 2005; Groombridge et al. 2002), but being generally excellent dispersers, many have also arrived from other continents further away (see below). In several of these groups, such as various groups of bats (Weyeneth et al. 2008, 2011; Goodman, Chan, et al. 2010), skinks (Austin, Arnold, and Jones 2009), day geckos (Harmon et al. 2008; Raxworthy et al. 2007), nephilid spiders (Kuntner and Agnarsson 2011a-b), fig wasps (Kerdelhue, Le Clainche, and Rasplus 1999), and in plants (Le Pechon et al. 2009, 2010; Wikstrom et al. 2010; Pokorny, Oliván, and Shaw 2011), colonization of Madagascar was likely followed by dispersal from Madagascar to other islands, including the Comoros and/or the Mascarenes. In at least some groups the data are consistent with stepwise colonization to Mauritius and Réunion, and on to Rodrigues (Venkatasamy et al. 2006; Kuntner and Agnarsson 2011b). In fact, Mauritius emerges as an important source of colonizers to Réunion (Fig. 2), consistent with its older age. In coastal lizards Madagascar was colonized from Australasia, followed by colonization of Comoros and Mauritius from Madagascar (Rocha et al. 2006). There are, however, also cases of direct colonization of Mascarenes or Comoros from Africa, for example in birds (Warren et al. 2006), land snails (Rowson, Tattersfield, and Symondson 2011), and plants (Anthony et al. 2010). Similarly, East Africa is an important source of colonizers of the Seychelles, as seen in *Archaius* chameleons (Townsend et al. 2011), freshwater crabs (Daniels 2011) and land snails (Rowson, Tattersfield, and Symondson 2011).

3.1.3 Diverse origin and biogeographic patterns of excellent dispersers

Stretches of ocean present the least effective barriers to strong flyers such as birds, bats, bees, and dragonflies, and to plants that disperse with birds or with readily airborne seeds - and these groups have the most diverse regions of origin in the Indian Ocean. Indeed, many of the 'secondary' colonization routes for Madagascar depicted with grey arrows in Fig. 2 have predominantly been taken by excellent dispersers, while intermediate-poor dispersers tend to follow similar colonization patterns, based on trade winds, currents, and other abiotic

For example, colonization of Comoros is probably more complex than shown here, the importance of Africa may be more as several bird species not included here have colonized Comoros from Africa. The historical importance of Asia as source of colonizers for Africa may also be greater than implied here (see Warren et al. 2010). Also, certain rare routes are omitted for simplicity - there is at least one possible colonization of Comoros from India, by scops owls (Fuchs et al. 2008).

factors. For example, oscine passerines arrived via overwater dispersal from Australia to Asia, moving over the Indian Ocean and eventually to Africa, where they radiated (Jonsson and Fjeldsa 2006), parrots probably colonized the Mascarenes from India (Hume 2007), scops owls colonized Asia from the Indian Ocean (Fuchs et al. 2008), and magpie robins colonized Madagascar from Asia (Sheldon et al. 2009). Among flying mammals, *Pteropus* bats repeatedly colonized the islands from Asia (O'Brien et al. 2009), and *Triaenops* bats colonized Madagascar repeatedly from Africa resulting in several Malagasy radiations (Russell, Goodman, and Cox 2008). For *Rousettus* bats current phylogenies are inconclusive, but they may have arrived from Asia, or the Middle East (Goodman, Chan, et al. 2010). Flying insects have also arrived from all directions, e.g. *Zaprionus* dipterans colonized the Indian Ocean islands enroute from Asia to Africa (Yassin et al. 2008). Similarly, dragonflies also dispersed over ocean to colonize the western Indian Ocean islands from India, Africa, and Asia (Dijkstra 2007). One species dispersed from Asia to Mauritius (Clausnitzer 2003), while a damselfly colonized Pemba island most likely from Madagascar (Dijkstra, Clausnitzer, and Martens 2007). Some dragonfly species are widespread, for example throughout the Seychelles, Africa and Asia, and are known to migrate long distances over water (Clausnitzer 2003). Allodapine bees colonized Madagascar several times from Africa in the Miocene, and then moved on to Asia and Australia (Fuller, Schwarz, and Tierney 2005). Several plant groups also show a pattern of Australasian origin of Indian Ocean islands colonizers (Kulju et al. 2007; Renner et al. 2010), with others arriving from S. America to Madagascar (Bone et al. 2011) or directly to the Mascarenes (Cuenca, Asmussen-Lange, and Borchsenius 2008). Among non-flyers, the pattern is more difficult to explain in reptiles, where e.g. coastal lizards as potentially poor dispersers nevertheless achieved transoceanic dispersal from Australia or Indonesia to Madagascar and from there to Africa, Comoros and the Mascarenes (Rocha et al. 2006). However, many factors indicate that these lizards are exceptionally successful at over ocean dispersal, such as their presence on very numerous islands and islets throughout the Pacific and western Indian Ocean, and the low genetic divergences found between species in the western Indian Ocean and the Pacific ocean, and among western Indian Ocean islands. Finally, *Pristionchus pacificus* nematodes that are cosmopolitan parasites of scarabid beetles have arrived to Réunion island from many different directions (Herrmann et al. 2010), demonstrating the ability of this nematode to travel with various different species and thus collectively be an excellent disperser.

3.1.4 The impact of 'reverse colonization' in the Indian Ocean

The traditional thinking in biogeography has long been to view islands as sinks and continents as sources of colonizers. However, results from many recent studies highlight over ocean 'reverse colonization' events, from islands to continents as an important biogeographical force (Sturge et al. 2009; Heaney 2007; Bellemain and Ricklefs 2008) especially from large islands close to continents (Gillespie et al. 2012). Reverse colonization

has played an important role in the Indian Ocean, including islands as sources for other islands as outlined above, a pattern often seen in organisms that use birds as dispersal vectors (Gillespie et al. 2012) (Fig. 2). Chameleons, as an example, originated and radiated in Madagascar after the Gondwana breakup, then subsequently colonized Africa via rafting from Madagascar (Raxworthy, Forstner, and Nussbaum 2002). They also reached the Comoros, Seychelles and Réunion, resulting in minor radiations. *Phelsuma* geckos are also thought to have originated in Madagascar, though their ancestor may have arrived there via dispersal from Africa, where its sister lineage occurs (Austin, Arnold, and Jones 2004). *Phelsuma* subsequently dispersed overwater multiple times colonizing the Mascarenes, Aldabra, Comoros, Seychelles, Andamans and Pemba. Coastal lizards (*Cryptoblepharus*) colonized Madagascar from Australia or Indonesia, then diversified in Madagascar, and subsequently 'reverse colonized' the East African coast, the Comoros islands and Mauritius (Rocha et al. 2006). In fact, the colonization of mainland Africa may have been a result of multiple island hopping events; African haplotypes nest within a Zanzibar clade (Rocha et al. 2006) consistent with the colonization of Zanzibar and the subsequent colonization of Africa from these offshore islands. A platycnemis damselfly is thought to have colonized Pemba from Madagascar, but not moved to the mainland due to unsuitable habitat (Dijkstra, Clausnitzer, and Martens 2007). Scops owls reverse colonized Asia from western Indian Ocean islands (Fuchs et al. 2008). *Zaprionus* dipterans reached Africa from Asia where the Indian Ocean islands served as stepping stones (Yassin et al. 2008). Similarly, though in the opposite direction, Gecarcinucoidea freshwater crabs reached Asia from Africa via the Indian Ocean islands (Klaus, Schubart, and Brandis 2006), and allodapine bees dispersed from Africa to Australia, also via the islands (Schwarz et al. 2006). One of the most spectacular examples of Madagascar as a source of colonizers comes from the coffee family, Rubiaceae (Wikstrom et al. 2010). Plants of this family have dispersed 'out of Madagascar' at least 13 times, colonizing Africa at least three times, Asia at least twice, Seychelles twice or more, Comoros multiple times, and the Mascarenes at least twice (Wikstrom et al. 2010; Maurin et al. 2007).

3.1.5 Vicariant elements in the Indian Ocean and the great faunal turnover

Despite the renaissance of dispersalism, vicariance remains crucially important in biogeography, and for the western Indian Ocean, vicariance explanations are supported by molecular data for several lineages. Lineages that seem to represent ancient Gondwanan Malagasy radiations include: typhlopoid blindsnakes (Vidal et al. 2010), boid snakes, podocnemid turtles, and iguanid lizards (Noonan and Chippindale 2006), ranid frogs (Bossuyt et al. 2006; Bossuyt and Milinkovitch 2000), the extinct elephant birds (Cooper et al. 2001), and possibly some cichlid and rainbow fishes (Chakrabarty 2004; Sparks 2004; Sparks and Schelly 2011; but, see Ali and Aitchison (2008)). Many extinct vertebrate lineages with a fossil record in Madagascar from ca. 88-65 Ma, are also thought to be vicariant (Masters, de Wit, and Asher 2006). These include several dinosaurs, 'proto-birds' seemingly related to *Archaeopteryx*, and gondwanatherian mammals (see Masters, de Wit, and Asher (2006) for summary and references). On the granite Seychelles, vicariance seems the best explanation for the existence of ancient caecilian amphibians (Zhang and Wake 2009) whose closest relatives are from India (Gower et al. 2011) and sooglossid frogs (Biju and Bossuyt 2003),

both lineages of burrowing organisms. On Socotra, vicariance may be more important than on the other Wallacean islands. Putative examples include the Socotran chameleon (Macey et al. 2008), geckos (Arnold 2009; Gamble et al. 2008), and possibly some freshwater crabs (Shih, Yeo, and Ng 2009). One reason to expect greater importance of vicariance in Socotra is that it separated from the continental landmasses long after the catastrophic meteor impact and Deccan volcanism, unlike Madagascar (see below), and it did not become mostly submerged in the sea during high ocean levels, unlike the Seychelles. Thus our prediction is that a greater portion of as yet studied lineages will show vicariance patterns on Socotra compared to Madagascar or Seychelles.

Some invertebrates may also be of vicariant origin on the islands of the western Indian Ocean, such as crayfish (Toon et al. 2010), giant pill-millipedes (Wesener, Raupach, and Sierwald 2010; Wesener and VandenSpiegel 2009), migid and archaeid spiders (Griswold and Ledford 2001; Wood, 2008; Wood, Griswold, and Spicer 2007) and Troidini butterflies (Braby, Trueman, and Eastwood 2005). Several groups of plants are also thought to be vicariant 'relicts', evidenced not necessarily by available molecular dates but by shapes of phylogenetic trees (Heads 2009): the Malagasy genus *Humbertia*, for example, is sister to the presumably old family Concolculaceae, and the genus *Takhtajania* is sister to Winteraceae (Schatz 1996, cited in Yoder and Nowak (2006). Ferns (Lindsaeaceae) from Seychelles are most closely related to the ones from Sri Lanka and India, and long branches indicate an ancient split of these groups (Lehtonen et al. 2010). Similarly, *Didymeles* containing two species distributed in Madagascar and the Comoros, is sister to the order Buxales. For this last split an approximate molecular date estimate is available and, at 99 Ma for the crown group Buxales, is consistent with vicariance (Anderson, Bremer, and Friis 2005). However, several of these vicariance hypotheses still require testing through dated phylogenies. Recent examples, including from our own work, show that speculations based on phylogenetic patterns, presumed poor dispersal abilities, and suspected old age of a group, such as clitaetrine spiders (Kuntner 2006), still fail to find support for vicariance in dated molecular phylogenies (Agnarsson and Kuntner in prep.). Upcoming dated phylogenies will also test the hypothesized Gondwanan origin on Madagascar of migid and archaeid spiders (Griswold and Ledford 2001; Wood, 2008; Wood, Griswold, and Spicer 2007), and other groups.

The relative scarcity of unequivocal vicariance examples may reflect the apparent massive faunal turnover of vertebrates, and likely also other groups, that is hypothesized to have resulted from a meteor impact some 65 Ma in western India (Krause (2003) cited in Yoder and Nowak (2006)). The meteor possibly triggered the massive Deccan volcanism in the Western Ghats that may have spanned 30,000 years and resulted in the release of huge amounts of volcanic gases, with direct effects on biodiversity and indirect effects through a drop in global temperature (Schulte et al. 2010; Bryan et al. 2010; Negi et al. 1993). While the evidence for faunal turnover stems mostly from vertebrates, in part due to their better fossil record, this is probably a more general pattern. It seems plausible that a mass extinction event, not restricted to vertebrates, occurred around 65 Ma, rendering the post-impact Madagascar, effectively, a 'Darwinian' or *de novo* island for many lineages. This hypothesis would explain the dominant support for the Cenozoic dispersal scenario among a very diverse set of organisms in Madagascar, and the relative scarcity of vicariant elements. In turn, the partial submergence of the Seychelles during high ocean levels may have

dramatically reduced vicariant elements, while for Socotra, vicariant elements should not have been wiped out by such catastrophic events.

A curious vicariance example is the presence of caecilians in Seychelles, and equally curious is their absence from Madagascar. If a vicariance hypothesis is true, it would not be surprising to discover hitherto not found caecilian fossils in Madagascar. Such a find would verify vicariance and the faunal turnover hypotheses.

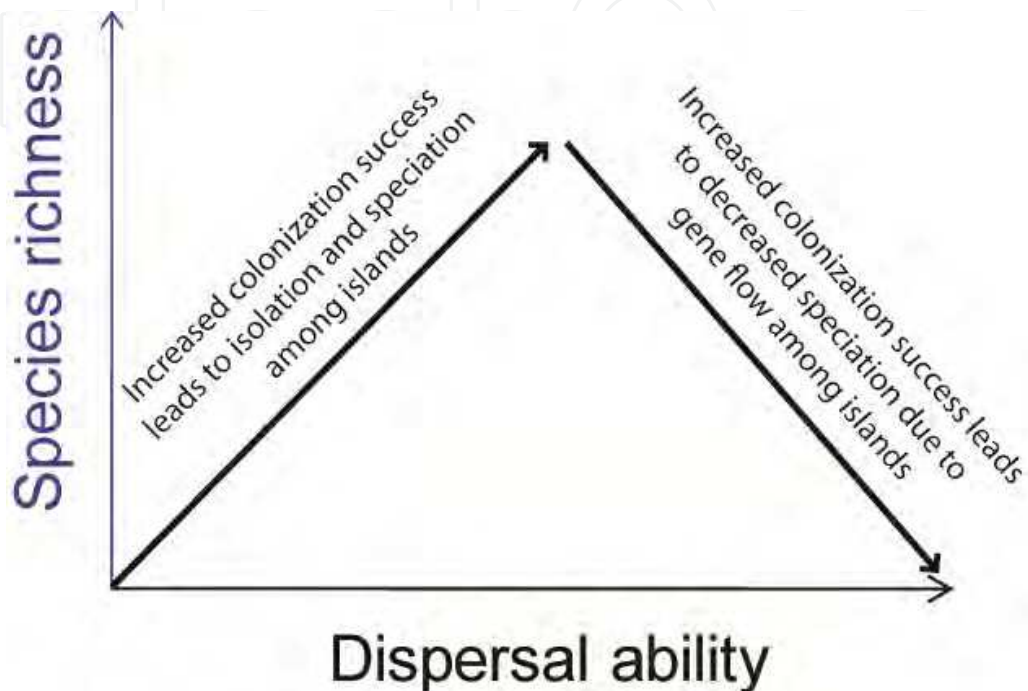


Fig. 3. A conceptual model of dispersal biogeography (adapted from Agnarsson and Kuntner In Prep). Dispersal ability positively relates to probability of island colonization. Initially increased dispersal ability leads to colonization followed by isolation and speciation among islands. As dispersal ability increases further, more islands are colonized but dispersal begins to retain gene flow among islands and thus restricting speciation. The highest species richness is thus expected in intermediate dispersers.

3.2 Biogeography and phylogeography of spiders in the Indian Ocean

The spider fauna of Madagascar and other Indian Ocean islands has been studied for a long time, but very few biogeographical studies exist. A few groups of spiders have been recently revised, or revisited, in some cases offering preliminary biogeographical speculations (Coyle 1995; Platnick 1995; Griswold 1997; Corronca 2003; Huber 2003; Agnarsson and Kuntner 2005; Agnarsson 2006; Knoflach and Van Harten 2006; Kuntner 2006, 2007; Huber and El-Hennawy 2007; Wood, Griswold, and Spicer 2007; Wood 2008; Logunov 2009; Lyle and Haddad 2010; Ubick and Griswold 2011). Though the evidence is not strong, these studies generally indicate the closest living relatives of the Indian Ocean island fauna being from Africa, consistent with the Cenozoic dispersal model outlined above, the likely exception being the seemingly Gondwanan migids and arhaeids (Griswold and Ledford 2001; Wood, 2008; Wood, Griswold, and Spicer 2007). Testing broad biogeographical hypotheses in a molecular phylogenetic framework has just begun, with our own studies on three nephilid

(*Clitaetra*, *Nephila*, *Nephilengys*) and four theridiid lineages (*Anelosimus*, *Argyrodes*, *Faiditus*, *Neospintharus*) (Agnarsson and Kuntner 2005; Agnarsson et al. 2010; Kuntner and Agnarsson 2011a-b; Agnarsson and Kuntner In Prep).

The social theridiid spiders of the genus *Anelosimus* were once thought to only occupy the neotropics (with solitary congeners found in Europe), however, we have recently discovered a radiation of subsocial *Anelosimus* in the mountains of eastern and northern Madagascar (Agnarsson and Kuntner 2005). Though existing phylogenies are ambiguous as to what the closest relatives of this Malagasy radiation are, the most recent study suggests the sister lineage is African, and the group as a whole much too recent to have a vicariant history in the region (Agnarsson et al. 2010). Thus, dispersal from Africa seems the most likely source of social Malagasy *Anelosimus*. Curiously, the solitary *A. decaryi*, found on the beachfront in Madagascar, Comoros and Aldabra atoll, represents a different evolutionary lineage, having independently colonized the western Indian Ocean (Agnarsson et al. 2010), and this colonization must be very recent given the age of Aldabra and Comoros. Apparently gene flow is retained among the coastal *A. decaryi* between Madagascar and Mayotte, however within Mayotte the lineage has diverged into two species including the non-coastal *A. amelie*. It is remarkable that the 'solitary' beachfront habitat was colonized from overseas, rather than by the *Anelosimus* lineage that lives in the nearby mountains, suggesting that these spiders more readily disperse between landmasses than switch habitats. The closest relatives of *A. decaryi*, and its sister species *A. amelie* from Mayotte, are unknown; they nest within an American clade, also containing European species, in the study of Agnarsson et al. (2010), but *Anelosimus* spiders are so poorly documented in Africa that biogeographical interpretations are inconclusive at this stage.

Within the spider family Nephilidae, three genera are distributed with one to several species in the islands of the western Indian Ocean (Fig. 4). The best known is *Nephila*, which was thought to have two species in the region, the widely spread *N. inaurata* found in Africa, Madagascar, and numerous of the smaller islands in the region, and *N. ardentipes* thought to be endemic to Rodrigues (Kuntner, Coddington, and Hormiga 2008). Being that *Nephila* occupies many landmasses globally and that most species show extremely wide ranges that sometimes spread over several continents (Kuntner and Agnarsson 2011b), *Nephila* is thought to be an excellent aerial disperser. Its excellent dispersal ability begged the question if the Rodrigues *A. ardentipes* might not simply represent a population of the widespread *N. inaurata*. We set out to test that hypothesis and our phylogeographic analysis based on the sampling of *Nephila* over the island area from Mayotte through Madagascar, Réunion, Mauritius and Rodrigues revealed that *Nephila* likely maintains, or recently maintained, gene flow over the islands, preventing speciation such that all these populations indeed belong to the widespread *N. inaurata* (Kuntner and Agnarsson 2011b). The phylogeny and haplotype network analyses both suggested an ancestral dispersal from Africa to Madagascar and Comoros (likely, also to the Seychelles, though we did not have specimens to test it), and from Madagascar to the Mascarenes, possibly stepwise to Mauritius and Réunion, and then on to Rodrigues, all these taking place relatively recently, less than 4 Ma (Kuntner and Agnarsson 2011b). Yet, our results were consistent with a recent cessation of gene flow, with each of the Mascarene islands and Madagascar having accumulated some island-unique haplotypes, a scenario we referred to as a possible 'speciation in process'.

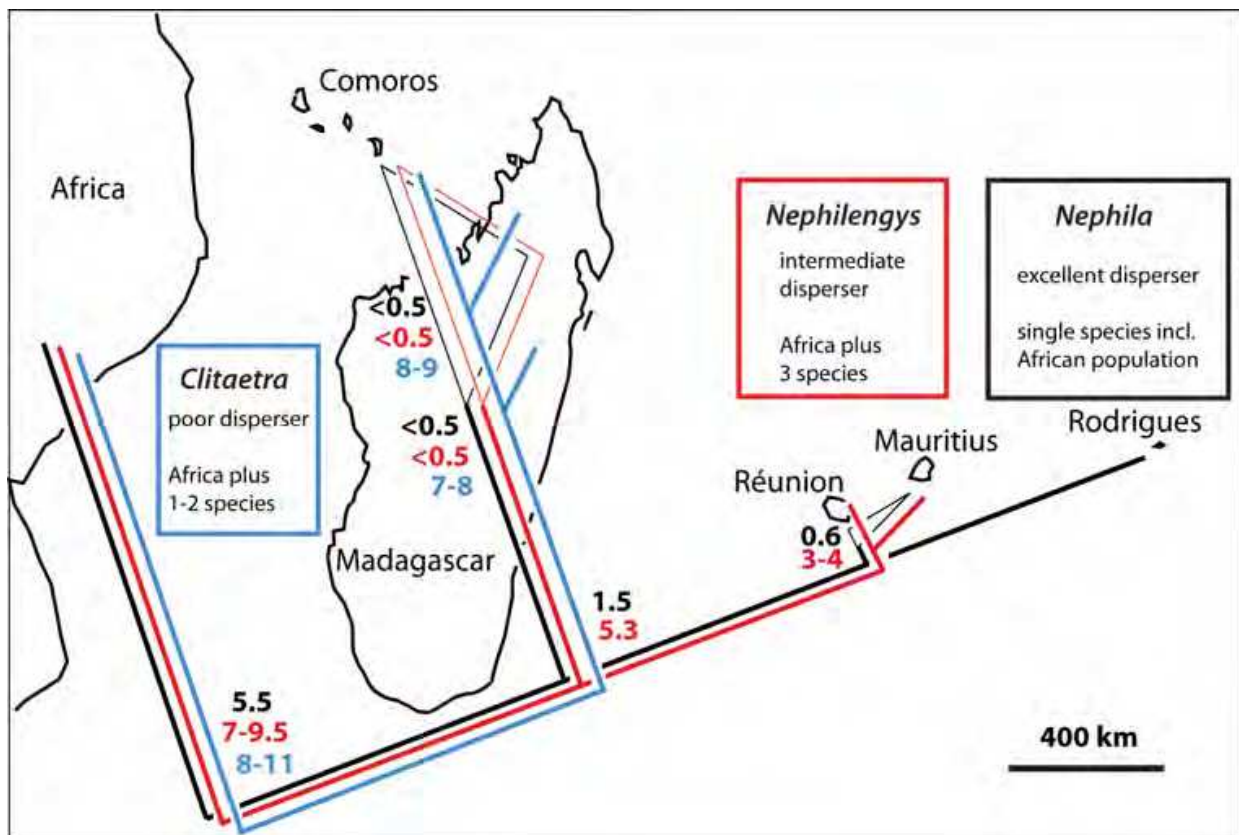


Fig. 4. Distribution, colonization patterns, and mtDNA genetic structure and divergence among three codistributed and closely related lineages of Nephilidae spiders, differing in dispersal ability. The best disperser, *Nephila*, is most widely distributed, but shows the shallowest divergences among islands, with a single species in the area. The poorest disperser, *Clitaetra*, is the most narrowly distributed, and with the deepest genetic divergences in shared clades, and additional genetic structure lacking in the other species (within Madagascar, between Madagascar and Mayotte). It is represented by 1-2 species in the region. The intermediate disperser, *Nephilengys*, has colonized most islands, but appears to do so sufficiently rarely such that island colonization is followed by speciation. Thus, there is an endemic species each on Madagascar, Réunion, and Mauritius, plus African species. Data from Kuntner and Agnarsson (2011a-b); Agnarsson and Kuntner (in prep). See text for details.

The second nephilid genus, *Nephilengys*, had been thought to be only represented in the region by a single widespread species *N. borbonica*, which is distinct from the related African mainland *N. cruentata* (Kuntner 2007). However, given that *Nephilengys* is much more narrowly distributed than *Nephila*, and is thought to be a poorer disperser, this scenario also seemed suspect. We set out to study the phylogeography of this species across the same islands as above, and found that indeed, each of the colonized Mascarene islands, Mauritius and Réunion had a genetically distinct population. We thus delimited all island populations into three species: *N. livida* inhabiting Madagascar and Mayotte (and possibly, other Comoros and Seychelles, though that remains to be tested), *N. borbonica* endemic to Réunion, and *N. dodo* endemic to Mauritius (Kuntner and Agnarsson 2011a). Consistent with its lesser dispersal ability, no *Nephilengys* was found in Rodrigues. However, the colonization pattern in *Nephilengys* was otherwise identical to *Nephila*, with relatively recent colonization of Madagascar and Comoros, and subsequent colonization of the Mascarenes.

In contrast, the third nephilid genus, *Clitaetra*, has not colonized the Mascarenes nor Seychelles, but is confined to Africa, Madagascar, and the Comoros, with an additional species in Sri Lanka (Kuntner 2006). The very narrow distribution of the genus, and its specialized arboricolous habits with seemingly limited local reach (Kuntner and Agnarsson 2009) hinted at poor dispersal abilities of *Clitaetra* spiders in comparison to its close relatives *Nephila* and *Nephilengys*. We should emphasize here that dispersal abilities of nephilid spiders were assessed a priori and not from the resulting genetic divergencies, thus avoiding circularity (Agnarsson and Kuntner in prep.). Our phylogeographic analyses of the Indian Ocean *Clitaetra* populations, including representatives of all but one African species of the genus, confirmed the prediction that the poor disperser will exhibit the most limited distribution and at the same time the greatest genetic structure among islands.

Preliminary data on Argyrodoinae spiders also hint at recent African origin of the species found in Madagascar, Comoros, Mauritius and Réunion, but remarkably suggest that the native Rodrigues *Argyrodes*, the only species we encountered on the island, belongs to a different genetic lineage than those on other islands, although the affinities of the Rodrigues species are as yet unknown (Agnarsson et al. unpublished)

In sum, spiders in general, and certainly the lineages we have examined so far are mostly consistent with the Cenozoic dispersal model, with the colonization of Madagascar from Africa, and the subsequent colonization of Comoros, and the Mascarenes from Madagascar (Fig. 2). As noted above, the likely exceptions are the Gondwanan elements on Madagascar of the families Migidae and Archaeidae. Dated phylogenetic studies indicate colonization of Madagascar from Africa 2-8 Ma, and subsequent colonization of Comoros and the Mascarenes, most likely from Madagascar no more than 4 Ma. The patterns observed are clearly dependent on dispersal abilities of the taxa. In all cases we found a distinct and well supported western Indian Ocean clade with a relatively deep divergence between it and the sister African clade. However, the better the disperser, the less genetic divergence it shows between Africa and the outer Indian Ocean islands. All taxa we examined have reached the Comoros, but only the poorest disperser (*Clitaetra*) shows divergences between Madagascar and the Comoros. Only the better dispersers among the lineages examined have reached the Mascarenes, and only the best dispersers (*Nephila*, *Argyrodes*) reached the isolated island of Rodrigues, and only the intermediate disperser *Nephilengys* has speciated within the Mascarenes.

3.3 The role of dispersal ability in distribution and diversification

Our work on the Indian Ocean nephilids was inspired by the conceptual model presented in Agnarsson and Kuntner (In prep, see Fig. 3). The model predicts an approximately linear relationship between a taxon's dispersal ability and the number of islands it occupies, but that due to the interplay of colonization and gene flow, intermediate dispersers, rather than good or poor dispersers, should be most diverse on archipelagos. One should note that this relationship can be complicated if there is a change in dispersal abilities upon colonization and radiation. Many island taxa have secondarily lost dispersal ability after colonizing isolated islands, including many groups of spiders (Gillespie et al. 2012). Nephilids offered an ideal opportunity for initial test of this model, with three closely related lineages occurring in the region, differing in dispersal abilities. Taken together, our studies on these

related and codistributed spider lineages, outlined above, are consistent with the model: *Nephila* as the best disperser is the most widespread, *Clitaetra* as the poorest disperser the most narrowly distributed and most genetically structured, and *Nephilengys* as the intermediate disperser the most diverse (Fig. 4).

Is this pattern repeated in the bigger picture examination of the range of taxa examined here? In other words, how does dispersal ability in general relate to diversity across archipelagos? Table 1, and table 1 from Yoder and Nowak (2006), include a large range of organisms differing from poor to excellent dispersers. Of the taxa examined the least diverse in the region are the very poor, and the extremely good, transoceanic dispersers. Active and strong day-fliers are arguably the best dispersers, including birds, fruit bats, and dragonflies. Many plants are also excellent dispersers via their airborne seeds, as are some spiders that get readily airborne using silk strands. Oceanic birds, probably the best dispersers of all, have colonized practically all vegetated islands in the western Indian Ocean, but have not radiated extensively (Yoder and Nowak 2006; Hume 2007). Among these, for example, the sooty tern (*Onychoprion fuscatus*) occurs on a large number of islands, pantropically in all major oceans, with clear evidence of gene flow among islands and even oceans that has prevented diversification, though several 'clinal' subspecies are recognized. In fact, the genus *Onychoprion* though extremely widespread and abundant, contains only four species in total. *Triaenops* fruit bats, also good dispersers, have repeatedly colonized Madagascar and adjacent islands in the relatively recent past, but remain species poor (Russell, Goodman, and Cox 2008), presumably due to continuous gene flow across their Malagasy range. Some of the strongest flying insects such as dragonflies have colonized all the islands but only diversified very moderately and many species are widespread and known to disperse long distances overwater (Dijkstra 2007). Several species that stick to strong flying organisms, such as many plant seeds and invertebrates that stick to birds, can also be excellent dispersers, and certain rafters such as coconuts are also excellent dispersers (e.g. Gillespie et al. 2012). Night flying organisms, such as most bats and moths are in general less capable of dispersal over ocean. Yet these are found on practically all the major islands and some bats have endemic species on many of the larger and older Darwinian islands. Poorer dispersers still are many of those that do not fly and rely on rafting to disperse. Even these have reached a large number of islands, and typically show patterns of single-island endemism. Exceptionally diverse among these are chameleons on Madagascar, *Phelsuma* geckos, and coastal lizards, conforming to the model prediction that diversity on large Wallacean islands will be skewed towards relatively poor dispersers (Fig. 3). Non-volant mammals and amphibians, are even poorer dispersers, mammals being relatively large and thus requiring much larger 'rafts' than most reptiles and amphibians or insects, and amphibians are probably particularly unlikely to survive a trip on an oceanic raft due to their general sensitivity to dessication. These groups are absent on nearly all the islands, except Madagascar where they have radiated extensively (Yoder and Nowak 2006), typically as a result of a single successful colonization event. This highlights the extreme rarity of such events and thus how poor dispersal ability can severely restrict diversification among islands, but may promote it within the few islands they by chance manage to colonize (Fig 3). Indeed, the western Indian Ocean has been colonized only by a small subset of the lineages 'available' on nearby continents, and the lineages lacking are mostly poor dispersers such as wingless insects, burrowing animals, and several orders of non-volant mammals.

The excellent dispersers are relatively species poor due to maintenance of gene flow. Many oceanic birds have populations on numerous islands, among whom gene flow is maintained. Similarly, several dragonfly species are widespread in the region, with among island speciation prevented by gene flow. The exceptions from this pattern are poor dispersers that are present on Wallacean islands, some of which are very diverse. These include vicariant lineages that thus did not disperse over ocean to reach the island, and taxa that have reached the Wallacean islands via dispersal, such as carnivores, tenrecs and rodents. In both cases, their relatively poor dispersal ability means that isolation among populations is created even by minor barriers such as rivers, mountain ridges, different vegetation types etc, which thus may lead to diversification. Here, again, dispersal ability relates to diversification patterns. However, these poor dispersers have only reached Madagascar, which invites the question of why it is that poor dispersers are found only on Wallacean islands, even when they had to disperse to get there. The general answer is likely simple probability, Wallacean islands have, in general, been around much longer than volcanic Darwinian islands, thus there has been a much longer time for that rare dispersal event to occur. Wallacean islands also started their lives close to continents, gradually moving away. Finally, in the case of Madagascar, not only has it been around for a long time, it is also a very large island and is thus a huge target making colonization there, by any disperser, much more likely than on smaller islands.

4. Conclusions

We summarized recent data on the biogeography of the terrestrial and freshwater fauna and flora of the western Indian Ocean, with some emphasis on our own work on spiders. As convincingly demonstrated by Yoder and Nowak (2006) for Madagascar, the dominant biogeographical pattern for the western Indian Ocean is ancestral Cenozoic dispersal from Africa to Madagascar. We show here that dispersal from Madagascar, in turn, to the smaller islands to the north and east of Madagascar is the main mode of colonization of most major islands in the western Indian Ocean. Two other notable elements are, first, the diverse origin of the best dispersers, having arrived from Africa, Asia, Australia, and the Americas, clearly indicating the importance of considering different dispersal abilities of lineages when studying broad biogeographical patterns. And second, the presence of a limited number of extant vicariant (Gondwanan) lineages. We believe that the scarcity of vicariant lineages, and the dominant pattern of colonization of Madagascar from the physically most proximate current-day continent are best explained with a mass extinction event occurring approximately 65 Ma having wiped out much of the Malagasy biota. Hence despite being geographically a Wallacean island that once formed a part of Gondwana, from a biogeographical perspective, Madagascar by and large shows patterns expected from a large Darwinian island. We also conclude that dispersal ability of taxa not only affects their distribution but also patterns of genetic divergences and speciation, such that species richness peaks at intermediate dispersal abilities.

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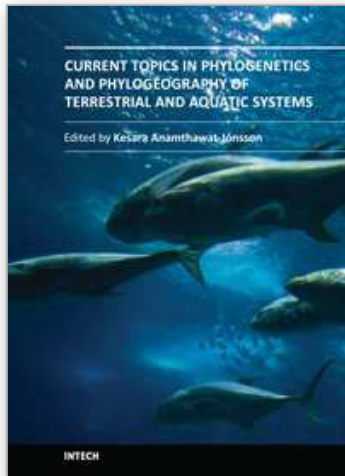
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Mapping phylogenetics on geographical scales is one of the most important scientific aspects of bioscience research. Changes in the environment have evidently shaped the geographical distribution of organisms on land and in the oceans seen today. Overexploitation of key species has caused not only changes in the distribution and diversity of organisms and composition of the ecosystems, but is also leading to species extinction at accelerating rates. It is our duty as scientists to find ways of protecting the species endangered with extinction and preventing other species from entering the endangered stage. To manage this effectively, we need to map species distribution, understand life-history traits, define genetic variation within species and populations, identify lineages - especially at the molecular level - and correlate the historical, phylogenetic components with the spatial distributions of gene lineages. In this book, phylogenetics and phylogeography of a diverse range of organisms are reviewed: from microorganisms causing gastroenteritis in humans, fishes in the Southwest Atlantic Ocean and spiders of the western Indian Ocean, to mountain tapirs in South America and birch tree species of the Arctic tundra.

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