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Review

Colonization and diversification of Galápagos terrestrial fauna: a phylogenetic and biogeographical synthesis

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Remote oceanic islands have long been recognized as natural models for the study of evolutionary processes involved in diversification. Their remoteness provides opportunities for isolation and divergence of populations, which make islands remarkable settings for the study of diversification. Groups of islands may share a relatively similar geological history and comparable climate, but their inhabitants experience subtly different environments and have distinct evolutionary histories, offering the potential for comparative studies. A range of organisms have colonized the Galápagos Islands, and various lineages have radiated throughout the archipelago to form unique assemblages. This review pays particular attention to molecular phylogenetic studies of Galápagos terrestrial fauna. We find that most of the Galápagos terrestrial fauna have diversified in parallel to the geological formation of the islands. Lineages have occasionally diversified within islands, and the clearest cases occur in taxa with very low vagility and on large islands with diverse habitats. Ecology and habitat specialization appear to be critical in speciation both within and between islands. Although the number of phylogenetic studies is continuously increasing, studies of natural history, ecology, evolution and behaviour are essential to completely reveal how diversification proceeded on these islands.

Keywords: adaptive radiation; diversification; evolution; phylogeny; phylogeography; speciation

The distribution of the tenants of this archipelago would not be nearly so wonderful, if, for instance, one island had a mocking-thrush, and a second island some other quite distinct genus [...]. But it is the circumstance, that several of the islands possess their own species of the tortoise, mocking-thrush, finches, and numerous plants, these species having the same general habits, occupying analogous situations, and obviously filling the same place in the natural economy of this archipelago, that strikes me with wonder.

(Darwin 1845)

1. INTRODUCTION

Islands have always attracted professional and amateur students of biology alike. By their very nature, islands are biologically simpler than continental regions and therefore provide ideal geographical and historical settings for the study of colonization and diversification of species. If the timing of their geological formation is known, such study can be conducted within a defined time frame. Moreover, if an island is part of an archipelago, then each island represents a replicate

natural experiment and therefore provides increased statistical power to test ideas related to patterns observed and processes inferred about diversification.

The Galápagos archipelago occupies a unique position in the history of evolutionary studies, mainly owing to its importance as a conceptual landmark (Darwin 1859) and because it continues to shape our understanding of evolutionary biology (Grant & Grant 2008). Notwithstanding its tropical climate, the Galápagos archipelago has been the stage of surprisingly few animal diversifications compared with other Pacific tropical island groups. With only one known exception, evolutionary radiations on Galápagos comprise fewer than 20 species, and include mainly lineages of land birds, reptiles and terrestrial invertebrates. Among vertebrates, the absence of amphibians and the virtual absence of mammals are particularly striking and nearly unique among terrestrial island ecosystems.

The goal of this review is threefold. It is (i) to review literature on Galápagos animal groups that have speciated on the island, (ii) to synthesize the available evidence in light of classic hypotheses related to colonization and diversification on islands, and (iii) to suggest future avenues in the study of Galápagos faunal diversification and how they can be used to aid in conservation efforts.

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One contribution of 15 to a Theme Issue 'Evolution on Pacific islands: Darwin's legacy'.

2. THE GALÁPAGOS ARCHIPELAGO

(a) *Geographical setting*

The Galápagos Islands are located in the Pacific Ocean, approximately 960 km west of the South American coast, straddling the equator at the 90th meridian west (figure 1a). The Galápagos archipelago is composed of 13 major islands larger than 10 km², 6 smaller islands, over 40 islets with official names and many smaller unnamed islets and rocks, for a total of approximately 8000 km² of land spread over 45 000 km² of water (Snell *et al.* 1996). Of these islands, Isabela is the largest (more than the total area of all the other islands combined) with an area of 4588 km² and the highest, with a maximum elevation of just over 1700 m. Isabela is formed by six volcanoes that are interconnected mostly by barren lava flows, which may represent a geographical barrier to dispersal analogous to open water for terrestrial animal species with low dispersal capacity such as flightless terrestrial invertebrates.

(b) *Geological history*

The Galápagos Islands are a young, oceanic and volcanic archipelago. Their geological history is relatively well understood (Nordlie 1973; Swanson *et al.* 1974; Bailey 1976; Cox 1983; Hall 1983; White *et al.* 1993; Geist 1996), with individual islands being formed as the Nazca plate moved over a hot spot. However, in contrast to the roughly linear arrangement by age of the Hawaiian Islands (Price & Clague 2002), the Galápagos Islands are clustered into groups of similar age (White *et al.* 1993). The age of the islands increases moving eastward along the plate, with the oldest islands located towards the southeast of the archipelago. K–Ar age determinations and marine fossils indicate a maximum age of the oldest land of the order of 3 Ma, whereas geological plate motion models set a maximum age of emergence around 4 Ma, depending on the velocity of the Nazca plate (Hickman & Lipps 1985; White *et al.* 1993; Geist 1996; D. Geist 2005–2008, unpublished data; figure 1a). The discovery of drowned seamounts east of San Cristobal extends the time the Galápagos have been available for colonization to at least 14 Ma (Werner *et al.* 1999). However, the history of island production over this hot spot could extend back 80–90 Ma, which is the estimated age of the birth of the Galápagos hot spot (Christie *et al.* 1992; Hoernle *et al.* 2002).

(c) *Biogeography and ecology*

The climate of the Galápagos Islands is unusually dry for the tropics and has marked seasonality. Since the archipelago is so isolated, ocean and wind currents mostly influence its climate. There are two main seasons: the warm season, typically January through May, and the cool season from June to December. The warm season is caused by warm ocean currents sweeping southward from the direction of Panama, which cause both sea and air temperatures around the islands to rise. During this time the skies are normally clear, with occasional heavy showers. During the cool season, the weather is influenced by the Humboldt Current, which brings cold water north from the Antarctic along the west coast of South America and then westward through the archipelago, which results

in cooler air temperatures. During the cool season, the skies are usually overcast, but with little precipitation in the lowlands. However, many parts of the highlands are constantly wet at this time owing to a mixture of light rain and mist. The higher islands have increasingly more rain at progressively higher elevations and a humid forest zone exists at 300–600 m on their windward (eastern) sides. Precipitation is variable in occurrence and quantity, even in the wet season. The direction of the wind and oceanic currents changes in response to a seasonal north–south shift in the Intertropical Convergence Zone (ICZ). On an irregular basis, but typically once every 3–6 years (Allan *et al.* 1996), this change in direction becomes more dramatic and warmer and wetter seasons occur with potentially 10 times more than the normal annual rainfall (referred to as El Niño events). In the cool season during these years, the ICZ moves greatly to the north of the islands, and the archipelago falls under the influence of the cool, dry wind and cool ocean currents (termed La Niña events). These cyclic changes in climate can have a pronounced effect on Galápagos vegetation (McMullen 1999) and fauna (Grant & Grant 1993; Grant *et al.* 2004; Steinfartz *et al.* 2007).

Vegetation on Galápagos can be separated into six (or seven) altitudinal zones (Wiggins & Porter 1971; van der Werff 1979) and the plant species composition of each zone is a reflection of the humidity level of the zone, with moisture level increasing with elevation (McMullen 1999). The Galápagos flora comprises 749 angiosperm species, of which 216 are endemic to the archipelago (just under 30%), and 7 of the 192 genera of flowering plants listed by McMullen (1999) are endemic to the islands.

(d) *Endemism and diversification*

Like that of many other isolated oceanic islands, the Galápagos fauna is impoverished and taxonomically unbalanced when compared with Neotropical source areas. Owing to their isolation and arid climate, the Galápagos Islands have been successfully colonized by only a subset of the diverse flora and fauna of the closest continent. Some lineages that have colonized the Galápagos archipelago have not differentiated from their continental ancestor (and thus are considered native) or have differentiated without radiating into multiple lineages. Both of these scenarios apply to all sea birds, more than one-third of land bird diversity, and the great majority of terrestrial invertebrates (Peck 2001, 2006).

Although relatively few lineages of Galápagos terrestrial fauna have diversified within the archipelago (associated with adaptation or not), the resulting species constitute a large proportion of the terrestrial vertebrate fauna of the islands (table 1). Bats (two species) and rats are the only terrestrial mammals that have naturally colonized the islands, and among them only the rice rats have diversified within the archipelago with 10 recognized species (three extant) representing three lineages (Clark 1984). Amphibians have not naturally colonized the islands. Seven reptile lineages have colonized the Galápagos and at least four diversified after their arrival, such that 34 of the 37 recognized reptile species are part of

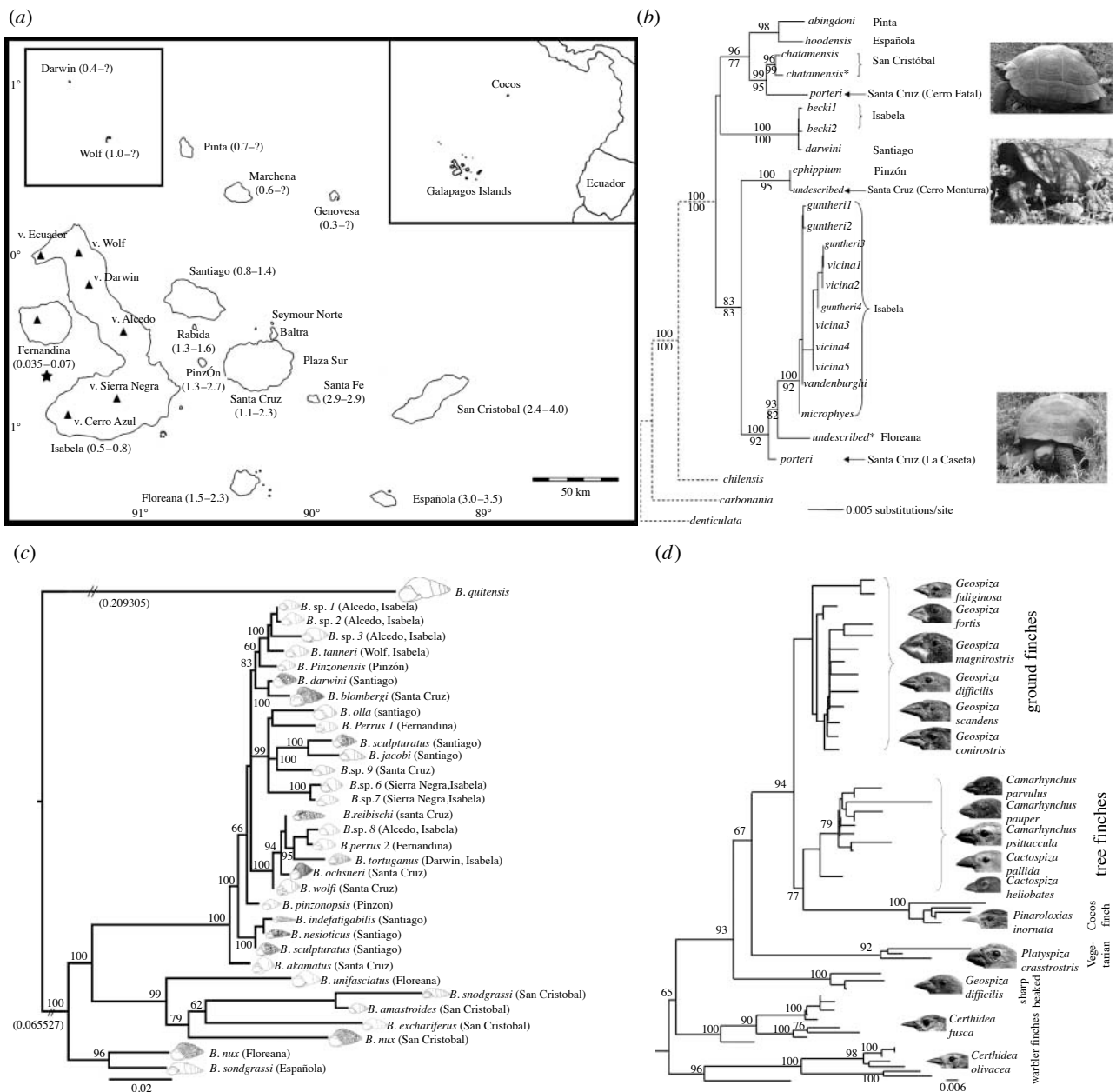


Figure 1. (a) Map of the Galápagos Islands and current hypotheses for the phylogenetic relationships of three Galápagos lineages as follows: (b) giant Galápagos tortoises, (c) terrestrial snails and (d) Darwin's finches. (a) Estimated minimum and maximum geological age for each island are in parentheses (D. Geist 2005–2008, unpublished data). Filled triangles indicate the summits of the six Isabela volcanoes. The star indicates the location of the hot spot, currently between Fernandina and volcano Cerro Azul of Isabela (Hooft *et al.* 2003). (b) Bayesian tree based on mtDNA control region sequences of extant and extinct Galápagos tortoises. Extinct taxa are asterisked. Placement of the three lineages on Santa Cruz is indicated with an arrow, and the pictures exemplify their different carapace morphologies. Redrawn from Russello *et al.* (2005). (c) Best maximum likelihood phylogenetic tree based on combined mtDNA COI and nDNA ITS1 sequence data. Two long branches were shortened and their actual lengths are reported in brackets below them. The snail outlines are roughly proportional to actual size. Species on older islands connect at deeper nodes, with a significant negative relationship between the depth of the clade encompassing an island's species and the island's age. For each tree, numbers above branches are Bayesian posterior probabilities. Maximum likelihood bootstrap proportions more than 50% are given below branches for *b*. (d) Phylogenetic tree of Darwin's finches estimated from cytochrome *b* sequences and neighbour joining (Petren *et al.* 2005). There is significant genetic structure and paraphyly among populations of sharp-beaked ground finches and warbler finches, but lack of resolution among the phenotypically distinct species of ground finches and tree finches. Photographs are proportional to actual size.

multispecies lineages. Of the 30 land bird species, 25 are endemic and 60% of the endemic species belong to two lineages that have speciated within the archipelago: Darwin's finches (14 species) and Galápagos mockingbirds (4 species). By contrast, the Galápagos Islands have approximately 1500 species of native insects of which only approximately 47% are

endemic. Very few terrestrial insect lineages have led to multiple species: only approximately 5% of the approximately 1000 insect genera that have successfully colonized the islands have diversified (Peck 2006) and those that have diversified have given rise to lineages of 20 species or fewer. With 71 described species, the radiation of Galápagos bulimulid land

Table 1. Species diversity of Galápagos terrestrial animals. (For each group, the numbers of native species in the following categories are given: undifferentiated from non-Galápagos relatives (indigenous); differentiated from a non-Galápagos relative but have not diversified within Galápagos (single-species endemic); diversified within Galápagos (multiple-species endemics with number of independent within-Galápagos lineages in parentheses); and total recognized native species. Numbers are not available for all terrestrial invertebrate groups; only data for beetles and land snails are reported.)

taxonomic group	indigenous	single-species endemic	multiple-species endemic (number of lineages)	total
mammals	1	1	10 (1)	12
land birds	5	7	18 (2)	30
reptiles	2	3	36 (5)	41
beetles	108	108	164 (42)	380
land snails	0	5	82 (5)	87

snails is the most spectacular in the fauna in terms of species number (Chambers 1991; Parent & Crespi 2006). None of the other nine land snail genera that have colonized the islands have diversified into more than four species (Smith 1966) and preliminary phylogenetic evidence suggests that the four species of the genus *Succinea* are descendants of at least two independent colonizations (B. S. Holland 2008, personal communication). Table 2 summarizes the within-archipelago diversification of Galápagos terrestrial fauna, and in the following sections we will describe the main diversification patterns.

3. ORIGINS AND AGE OF GALÁPAGOS FAUNA

(a) *Origin of the fauna*

The terrestrial Galápagos fauna that has diversified on the islands generally has close relatives on the South American continent. This is the case for Galápagos tortoises, which are closely related to the smaller bodied *Geochelone chilensis*, or Chaco tortoise, from South America (Caccone *et al.* 1999). The diversity of Galápagos lava lizards (*Microlophus* spp.) is the result of two independent colonizations, both from the west coast of South America (Wright 1983; Kizirian *et al.* 2004; Benavides *et al.* 2007). Likewise, Wright (1983) suggested that the leaf-toed gecko (*Phyllodactylus*) diversity stems from more than one colonization from South America; however, this suggestion has not been tested with phylogenetic analyses including possible mainland relatives.

The two land bird lineages that have diversified on Galápagos do not necessarily bear a strong relationship to relatives on the adjacent Ecuadorian mainland: Darwin's finches appear to be most closely related to grassquits (*Tiaris*) and their allies, a group with a wide distribution throughout Central and South America that has undergone a similar radiation in the Caribbean (Sato *et al.* 2001; Burns *et al.* 2002). The closest living relatives of Galápagos mockingbirds appear to be those currently found in North America, northern South America and the Caribbean, rather than the geographically nearest species in continental Ecuador (Arbogast *et al.* 2006). The endemic subspecies of the yellow warbler (*Dendroica petechia aureola*) probably migrated from Latin America, not North America, but it shows little evidence of divergence within Galápagos (Browne *et al.* submitted). Several other taxa in Galápagos (e.g. flamingos, isopods, snakes, moths) show biogeographical affinities

with populations in the Caribbean (Thornton 1971; Grehan 2001); but these proposed affinities have not been tested with molecular phylogenetic analyses.

The geographical origin of very few terrestrial invertebrate groups has been inferred with certainty. This gap in our knowledge is mostly because few detailed data exist on the continental distributions of possible sister species of Galápagos endemics. Schmitz *et al.* (2007) suggested that the source of the Galápagos microlepidopteran genus *Galagete* is probably coastal South America, but this remains to be tested. Likewise, based on morphological affinities, Galápagos bulimulid snails seem to be most closely related to continental South American bulimulids (Breure 1979). One must be cautious though, as the South American fauna is rather poorly known, especially the invertebrate fauna, and it is possible that sister clades of Galápagos lineages have recently become extinct, undergone range shifts or simply have yet to be identified. A striking example of this lack of knowledge is the genus of flightless beetles *Stomion*, whose non-Galápagos closest relative is unknown (Finston & Peck 2004).

(b) *Age of the fauna*

Colonization events have occurred over the last 3–4 Ma during the existence of the present islands, and might have happened earlier when now sunken islands were above sea level. The presence of several drowned seamounts on the Carnegie Ridge east of the Galápagos (Christie *et al.* 1992) suggests that earlier volcanic islands may have served as stepping stones for colonization by some of the terrestrial fauna. Because divergence times estimated directly from molecular data require independent calibration, all current dating methods require that specific assumptions be made before inferring any divergence time. These assumptions typically are related either to rates of molecular evolution (molecular clock hypothesis, local clocks models) or both rates and times (penalized likelihood, Bayesian methods). Among the few Galápagos taxa for which such estimations have been attempted, the divergence time between the mainland ancestor and island relatives seems in some cases to be older than the age of the existing emerged islands. The divergence between *G. chilensis* and the Galápagos tortoise lineage probably occurred 6–12 Ma, before the origin of the oldest extant Galápagos island (Caccone *et al.* 1999). However, the closest extant relative does not necessarily

Table 2. Summary of diversification of the terrestrial fauna of Galápagos, with the number of species per lineage that evolved on the archipelago, number of colonizing species from which they evolved, their probable geographical origin, as well as molecular estimates (millions of years) of the initial divergence within the lineage and the temporal window of divergence from their ancestor, whether a lineage follows the progression rule pattern (see text), whether multiple species are found within an island or volcano or whether there is evidence that the lineage is an adaptive radiation. (For invertebrates, only lineages with 10 species or more are listed.)

class	taxa	number of species or subspecies	phylogeny available?	number of colonization events	geographical origin	time of initial divergence within Galápagos (Ma)	divergence time with closest extant lineage (Ma)	progression rule?	multiple species per island or volcano?	adaptive radiation?	source
Mammalia	rice rats (<i>Oryzomys</i> , <i>Nesoryzomys</i> , <i>Megaoryzomys</i>)	at least 8	no	3?	North, Central, and South America	?	?	?	on Santa Cruz, Isabela and Fernandina	no	Clark (1984)
Reptilia	Galápagos giant tortoise (<i>Geochelone nigra</i>)	15 (11 extant)	yes	1	South America	1.5–2.0	6.0–12.0	yes	on Santa Cruz and Isabela	may be	Caccone <i>et al.</i> (1999, 2002), Beheregaray <i>et al.</i> (2004), Russello <i>et al.</i> (2005) and Ciofi <i>et al.</i> (2006)
	lava lizards (<i>Microlophus</i>)	9	yes	2	South America	1.4 [#]	10.2* 2.0–2.7 ^{#,a} 3.6–4.0 ^{#,b}	yes	no, one island and one species	no	*Wright (1983), Lopez <i>et al.</i> (1992) #Benavides <i>et al.</i> (2007)
	snakes (<i>Philodryas</i> , <i>Alsophis</i>)	3	no	3?	South America and Caribbean	?	?	?	yes	?	Thomas (1997) and Grehan (2001)
	leaf-toed geckos (<i>Phyllodactylus</i>)	6	yes	3?	South America	?	8.9	yes	on San Cristóbal only	no	Wright (1983)
	marine (<i>Amblyrhynchus cristatus</i>) and land (<i>Conolophus spp.</i>) iguanas	1 (marine) 2 (land)	yes	1?	South America	> 10	< 2	yes	land iguana: on V. Wolf (Isabela)	may be	Wyles & Sarich (1983), Rassmann (1997), S. Glaberman <i>et al.</i> 2005–2008 (unpublished data), G. Gentile, <i>et al.</i> 2005–2008 (unpublished data) and S. Steinfartz <i>et al.</i> 2005–2008 (unpublished data)

(Continued.)

Table 2. (Continued.)

class	taxa	number of species or subspecies	phylogeny available?	number of colonization events	geographical origin	time of initial divergence within Galápagos (Ma)	divergence time with closest extant lineage (Ma)	progression rule?	multiple species per island or volcano?	adaptive radiation?	source
Aves	Darwin's finches (<i>Geospiza</i> , <i>Camarhynchus</i> , <i>Cactospiza</i> , <i>Platyspiza</i> , <i>Certhidea</i>)	14	yes	1	South America/ Caribbean	1.6	2.0–2.3	no	yes	yes	Sato <i>et al.</i> (2001), Burns <i>et al.</i> (2002) and Petren <i>et al.</i> (2005)
	mockingbirds (<i>Nesomimus</i>)	4	yes	1	North America/ Caribbean	?	0.6–5.5	yes	no	no	Arbogast <i>et al.</i> (2006)
Insecta	<i>Galagete</i>	12	yes	1	South America	2.9–3.7	?	no	yes	no	Schmitz <i>et al.</i> (2007)
	microlepidoptera										
	<i>Galapaganus</i> weevils	10	yes	1	South America	10.7–12.1	7.2	no	yes	no	Sequeira <i>et al.</i> (2000)
	<i>Stomion</i> darklings	12	yes	1	?	?	?	?	yes	no	Finston & Peck (1997, 2004)
	<i>Ammophorus</i>	12	no	2?	South America	?	?	?	yes	?	Peck (2006)
	<i>Philatis</i>	20	no	1	South America?	?	?	?	yes	?	Peck (2001)
	<i>Scaphytopius</i>	17	no	2?	?	?	?	?	yes	?	Peck (2001)
	<i>Oliarus</i>	12	no	1	?	?	?	?	yes	?	Peck (2001)
	<i>Pterostichus</i>	12	no	2?	South America?	?	?			?	Desender <i>et al.</i> (1992) and Peck (2006)
	<i>Dagbertus</i>	?	on Santa Cruz, San- tiago and Isabela	5	?	?	?			?	Peck (2001)
	<i>Blapstinus</i>	?	yes	3?	South America?	?	?			?	Peck (2006)
Gastropoda	<i>Bulimulus</i> land snails	?	yes	1	South America	?	?			yes	Breure (1979) and Parent & Crespi (2006)
		yes	yes								

^a*Microlophus* 'Eastern radiation'.
^b*Microlophus* 'Western Radiation'.

represent the direct ancestor, which could have been, and perhaps was, a now extinct lineage of mainland giant tortoises. Thus, the date of the oldest divergence within the Galápagos lineage probably provides a more accurate estimate of the minimum time since colonization. The oldest node within the Galápagos tortoise radiation is a little more recent than the oldest islands and the molecular divergence time for the southern Isabela clade is less than 500 000 years, which agrees with estimates of the island's age (Naumann & Geist 2000; Caccone *et al.* 2002; Beheregaray *et al.* 2003b, 2004).

Data from cytochrome *b* mitochondrial DNA (mtDNA) sequences indicate a time for the divergence of the land and marine iguana lineages of less than 10 Ma (Rassmann *et al.* 1997), which precedes the origin of the emerged islands. This suggests that they first colonized the now submerged islands and then colonized the current islands as they emerged. Genetic work on both land and marine iguanas is revisiting this dating (S. Glaberman, D. Lanterbecq, S. Steinfartz, C. Marquez, K. Dion, T. Hanley, A. Caccone 2005–2008, unpublished data; G. Gentile, M. Milinkovitch, A. Fabiani, C. Marquez, H. L. Snell, H. M. Snell & W. Tapia 2005–2008, unpublished data), which was based on an overall mtDNA rate of 2% Myr⁻¹ extrapolated from bovid data.

Colonization of the Galápagos by ancestors of Darwin's finches has been estimated at 1.6–2.3 Ma (Sato *et al.* 2001), well within the age of the present islands.

Galapaganus beetles are estimated to have diverged from their closest living, mainland relative over 7 Ma, based on both an intrinsic (Sequeira *et al.* 2008) and extrinsic clock (Sequeira *et al.* 2000). However, most DNA derived estimates of the timing of interisland colonization and within-island diversification are consistent with the geological formation of the islands (Sequeira *et al.* 2008). The earliest divergence time within the endemic Galápagos lepidopteran *Galagete* radiation was estimated at 3.3 Ma, within the time that the present islands were available for colonization (Schmitz *et al.* 2007).

For other Galápagos lineages, it is not possible to estimate the time of divergence from their closest relatives because there is no reliable molecular clock for the taxonomic group and/or genes in question (Parent & Crespi 2006), or the relevant continental biota is so poorly known that their close relatives cannot be identified (table 2). Another possibility is that the closest extant relative outside the archipelago does not necessarily represent the direct ancestor of the insular lineage, which could be extinct (Emerson 2002).

4. TIMING AND SEQUENCE OF COLONIZATION AND SPECIATION

The sequence of colonization and speciation within the archipelago can be inferred by comparing phylogenetic information on a lineage with the geological ages of the islands. The most commonly predicted and tested colonization scenario is a movement from old to young islands, suggesting that successful intraarchipelago colonization is more likely to occur on recently formed

islands with unoccupied niches (Brooks & McLennan 1991). This pattern, often referred to as the progression rule (Wagner & Funk 1995), has been observed in a range of lineages and island systems (Fleischer *et al.* 1998; Juan *et al.* 2000). On Galápagos, this implies a diversification sequence from southeast to northwest, paralleling the geological formation of the islands. The Galápagos archipelago is formed by geographical clusters of islands of similar age (White *et al.* 1993) and therefore if the progression rule applies, species formation should also occur in 'clusters' and not necessarily match perfectly the sequence from old to young islands.

The historical biogeographical scenarios proposed for Galápagos endemic organisms based on phylogenetic hypotheses suggest inconsistent relationships between population diversification and island formation across lineages. The Galápagos giant tortoises lineage is among the best-studied cases of diversification on the islands, with species-level phylogenetic analyses based on multiple mtDNA markers (Caccone *et al.* 1999, 2002), as well as population level demographic history and population structure analyses based on both mtDNA (Beheregaray *et al.* 2004; Russello *et al.* 2007a) and several microsatellite markers (Beheregaray *et al.* 2003a,b; Ciofi *et al.* 2006). Although the lineage of giant tortoises does not follow a strict linear migration from older to younger islands, the species-level phylogenetic pattern uncovered from mtDNA data suggests that giant tortoises diversified approximately in parallel to island geological formation (Caccone *et al.* 2002; figure 1b). Furthermore, estimation of population-level genetic diversity, population divergence and recent demographic history of Galápagos giant tortoises based on mtDNA revealed a pattern of lineage sorting consistent with the temporal formation of the archipelago (Beheregaray *et al.* 2004). Indeed, tortoise species from older islands have exclusively endemic haplotypes that define divergent monophyletic clades, whereas taxa from younger islands (Isabela, in particular) have haplotypes shared among lineages on different volcanoes and which exhibit a recent history of coalescence (Beheregaray *et al.* 2004). One of the two lineages of Galápagos lava lizards has also diversified in concordance with the geological formation of island clusters of similar age (Kizirian *et al.* 2004).

In a population genetic study of 22 populations of marine iguanas (*Amblyrhynchus cristatus*), Rassmann *et al.* (1997) found that the mtDNA cytochrome *b* marker had a signature of population differentiation concordant with geographical isolation of populations across the archipelago. However, data from three nuclear microsatellite loci indicated relatively high levels of gene exchange among populations (mean $F_{ST}=0.1$), contradicting the mtDNA pattern. This discrepancy was suggested as being due to sex-biased dispersal, with higher interpopulation dispersal in males than females (Rassmann *et al.* 1997). A current analysis of the population structure of marine iguanas based on 13 microsatellite loci, however, depicts a very different picture in which most island populations represent different genetic clusters (Steinfartz *et al.* 2007; S. Steinfartz, D. Lanterbecq, C. Marquez & A. Caccone 2005–2008, unpublished data). A companion analysis using mtDNA control region data reveals

three main mtDNA lineages, as follows: one on the eastern and central islands, one restricted to the northern and western islands and one that spans from east to west (S. Glaberman, D. Lanterbecq, S. Steinfartz, C. Marquez, K. Dion, T. Hanley & A. Caccone 2005–2008, unpublished data). The evolutionary relationships among these groups are unclear owing to shallow levels of divergence, as in the cytochrome *b* data. Thus, the patterns of island colonization are not as well defined as for the tortoises. It is clear, however, that the lineage occupying the northern and western regions of the archipelago is the product of a recent expansion based on a unimodal distribution of pairwise differences between individuals as well as a high abundance of low-frequency haplotypes. This conclusion fits with the overall younger age of the western islands.

Galápagos mocking birds were inferred to follow the progression rule (Arbogast *et al.* 2006). By contrast, Darwin's finches show limited evidence of diversification closely associated with the geological formation of the islands. Grant & Grant (2008) suggested that the radiation of finches unfolded with an increase of types of species with change in climate and increased habitat diversity, associated with an increased number of islands. However, there is no clear evidence suggesting that the number of islands has increased through time. Nevertheless, divergence time within this lineage is not associated with the age of the islands where the species are found, perhaps a result of considerable interisland dispersal.

A progression rule pattern has been inferred for Galápagos bulimulid land snails (Parent & Crespi 2006; figure 1c). By contrast, Galápagos flightless weevils (genus *Galapaganus*) do not follow the progression rule. Phylogenies based on mtDNA (Sequeira *et al.* 2008) or mtDNA combined with nDNA (Sequeira *et al.* 2008) indicate that colonization and diversification in this lineage are linked to geological history in a more complex scenario. For example, *Galapaganus williamsi*, which occurs only on Isabela, coalesces at the deepest node of the phylogeny, while species from the oldest islands of Española and San Cristobal are shallower in the phylogenetic tree. The Microlepidoptera genus *Galagete* (12 species) is another example in which the progression rule fails to explain phylogeographical patterns of diversification. Species connecting at the deepest node are not found on the oldest islands and the sequence of colonization and speciation does not follow the geological formation of the islands, but rather a stochastic colonization scenario (Schmitz *et al.* 2007).

In general, the diversification sequence in Galápagos terrestrial faunal groups seems to follow the progression rule, with the more vagile lineages constituting the exception (Galápagos finches, *Galagete* lepidopterans and *Galapaganus* weevils).

5. THE GEOGRAPHICAL MODE OF SPECIATION

In an insular context, speciation can happen between or within islands. If colonization rate between islands is high and individuals interbreed among island populations, these populations will effectively be part of the same gene pool. However, ongoing but low levels of gene flow do not constrain local adaptations of

Darwin's finch (Petren *et al.* 2005) or lava lizard (Jordan *et al.* 2005) populations on islets peripheral to a main island. Lineages that have recently colonized the islands might not have had the time to differentiate within the archipelago. The Galápagos hawk is thought to have diverged from its continental sister clade less than 300 000 years ago, and populations from different islands are genetically very similar (Bollmer *et al.* 2006). However, mitochondrial and minisatellite data indicate a general pattern of rapid population expansion followed by genetic isolation of hawk populations, suggesting that this lineage is in the earliest stages of further divergence (Bollmer *et al.* 2006). Genetic analysis of the Galápagos hawk's ischnoceran louse may shed further light on the cryptic evolutionary history of its host (Whiteman *et al.* 2007).

(a) Speciation between islands

If colonization rate between islands is low, one would expect to find a pattern of genetic structuring among island populations, potentially leading to differentiated species that are single island endemics. Rassmann *et al.* (1997) initially proposed that marine iguana populations across the archipelago showed very little divergence but ongoing work suggests that most island populations have considerable levels of genetic differentiation (S. Steinfartz, D. Lanterbecq, C. Marquez & A. Caccone 2005–2008, unpublished data). Galápagos giant tortoises have diverged to form 15 taxa, 11 of which are extant. Their taxonomic status is still in flux. Some authors consider them different subspecies (Pritchard 1996), while others refer to them as species owing to their genetic distinctiveness (Powell & Caccone 2006; Russello *et al.* 2007a). Española, San Cristobal, Pinzón, Santiago and Pinta each has only one named species; San Cristobal had two distinct populations but one is now extinct (Caccone *et al.* 2002; Russello *et al.* 2007a). Isolation among islands has promoted speciation in the two independent lineages of lava lizards (Kizirian *et al.* 2004; Benavides *et al.* 2007). Using microsatellite markers, Jordan & Snell (2008) have tested the hypothesis that genetic drift in isolation has caused the differentiation of Galápagos lava lizards on 12 islets that were probably connected to the larger island of Santa Cruz during the Late Pleistocene. They found strong genetic differentiation among island populations, a positive correlation of genetic diversity with island size, no relationship between genetic and geographical distance and a strong negative correlation between heterozygosity and measures of genetic differentiation. They concluded that overwater dispersal is rare and further differentiation of lava lizards may be prevented by island fusion during periods of lower sea level. The land iguanas (Snell *et al.* 1984; Rassmann 1997) and the mocking birds (Arbogast *et al.* 2006) also have at most one species per island, but the relative contributions of selection and drift to differentiation remain unclear. Recent work on the two Galápagos land iguanas, *Conolophus subcristatus* and *Conolophus pallidus* (G. Gentile, M. Milinkovitch, A. Fabiani, C. Marquez, H. L. Snell, H. M. Snell & W. Tapia 2008–2008, unpublished data), based on mtDNA

sequence data, confirms the genetic discontinuities between the populations of *C. subcristatus* from the western (Fernandina and Isabela) and central (Santa Cruz, Baltra, Seymour and Plaza Sur) islands. This pattern seems to parallel that of their sister taxon, the marine iguanas, in which there is clear genetic differentiation between eastern and western islands (S. Glaberman, D. Lanterbecq, S. Steinfartz, C. Marquez, K. Dion, T. Hanley & A. Caccone 2005–2008, unpublished data; S. Steinfartz, D. Lanterbecq, C. Marquez & A. Caccone 2005–2008, unpublished data). The level of differentiation between the two *C. subcristatus* groups is only slightly lower than that between the two species (*C. subcristatus* and *C. pallidus*).

Darwin's finches show limited evidence of speciation on different islands. The larger central islands contain largely the same suite of 9–10 species, many of which also occur on several smaller and peripheral islands (Grant 1999). Several phylogenetic analyses have revealed little resolution among six species of tree finches and five species of ground finches (Freeland & Boag 1999; Sato *et al.* 2001; Petren *et al.* 2005; figure 1*d*). A combination of factors is probably responsible for this, including the recent origin of many species, the homogenizing effects of hybridization (Grant *et al.* 2004) and interisland dispersal (Petren *et al.* 2005). Allopatric speciation has been inferred between the small (*Geospiza scandens*) and large (*Geospiza conirostris*) cactus finches, although both populations of large cactus finches are more closely related genetically to different populations of small cactus finches than they are to one another. The warbler finches (*Certhidea olivacea* and *Certhidea fusca*) were believed to be the same species, until studies showed different subsets of islands to harbour two different species that are more genetically distinct than any other species in the entire group (Petren *et al.* 1999; Tonnis *et al.* 2005). There is pronounced morphological divergence between-island populations of several species of Darwin's finches. Some of these differences are paralleled by substantial genetic differences (*Geospiza difficilis*, *G. scandens*/*G. conirostris*), while in other cases, genetic differences are minimal or are not correlated with morphological or geographical divergence (*Geospiza fortis*/*Geospiza magnirostris*; Petren *et al.* 1999, 2005). Recent studies suggest interisland movements of Darwin's finches may not be as rare as previously suspected (Petren *et al.* 2005; Tonnis *et al.* 2005). Morphological differences among island populations may therefore not be as much evidence of isolation from gene flow as previously thought, but rather evidence of differing selective regimes and local adaptation in the presence of gene flow. Theoretically, low levels of gene exchange may promote local adaptation under some conditions (Whitlock & Phillips 2000). The warbler finches (*C. fusca* and *C. olivacea*) appear to conform to an allopatric mode of speciation, being clearly separated on different subsets of islands. However, the occurrence of some very widely distributed *C. fusca* haplotypes suggests that speciation was not driven by geographical isolation and limited dispersal. Other factors, such as habitat or natural selection against immigrants, may have limited genetic exchange and allowed speciation to occur (Tonnis *et al.* 2005).

Terrestrial invertebrates often have low dispersal ability (especially flightless groups), so single island endemics would be expected. The flightless beetle genus *Neoryctes* includes four single island endemic species, each restricted to the moist highland zone of the island on which it occurs (Cook *et al.* 1995). The microlepidopteran genus *Galagete* has a complex pattern of diversification. Some of the species are single-island endemics, others are found on multiple islands, and two occur on 10 and 11 islands (Schmitz *et al.* 2007). The inference of the geographical mode of speciation from the phylogeny is problematic, mainly owing to the wide distribution of most of its taxa. Little is known of the ecology of *Galagete* (Schmitz *et al.* 2007), which makes it difficult to infer ecological or habitat shifts.

In sum, patterns of speciation between islands tend largely to reflect a combination of dispersal capability and habitat suitability. Less vagile taxa show more pronounced genetic structure among island populations. They are more prone to longer periods of absence from suitable islands as a result of extinction. More vagile taxa show little differentiation among subsets of islands, but may be absent from islands with apparent suitable habitat. Several taxa show non-overlapping distributions among subsets of islands. In these cases, co-occurrence may be limited by dispersal, but also by the presence of other similar species. The possibility of occasional gene exchange between islands that would create loose evolutionary connections among differentiated populations remains largely unexplored.

(b) *Speciation within islands*

In addition to island isolation, other physical features of islands can influence the mode of diversification in an archipelago. Island area and elevation are positively correlated in many island groups and are prime determinants of moisture and island habitat diversity. Greater habitat diversity provides the potential for within-island diversification, but also increases the chances that a new colonist will find a suitable habitat. Once a particular lineage has colonized an island, it can speciate within that island either by adapting to different habitats, commonly referred to as ecological speciation (Schluter 2000), or by allopatric speciation if an island is large enough for populations to become isolated by geographical or topological means (volcanoes, barren lava, inhospitable habitat, etc.). The strength of the effect of island area depends not only on geography and topology but also on the dispersal ability of the organisms, being strongest for animals with low dispersal ability and specialized ecological requirements. The low dispersal ability of the giant tortoises is a good example, with four species on Isabela, one on each major volcano. Isabela probably started as separate island volcanoes that then merged. The volcanoes are now separated by lava fields, which are a formidable obstacle to tortoise movement. It is therefore possible that their populations were isolated for 400 000 years, and then experienced limited mixing (over the lava fields) for the past 100 000 years once the volcanoes were connected. mtDNA and nDNA data support the genetic distinctiveness of the three species living on

the central and northern volcanoes (Alcedo, Darwin, Wolf; [Caccone *et al.* 2002](#); [Beheregaray *et al.* 2004](#); [Ciofi *et al.* 2006](#), *in press*; [Russello *et al.* 2007a](#)). However, genetic divergence and similarities among populations on the southern volcanoes (Cerro Azul, Sierra Negra) do not support the taxonomic subdivisions ([Ciofi *et al.* 2006](#)) that were previously suggested based on morphology ([Fritts 1984](#); [Pritchard 1996](#)). The taxonomic assignment of tortoise populations on Santa Cruz has been contentious. There are at least three lineages that are as genetically distinct from each other as from lineages on other islands, being connected only through the deepest nodes in the molecularly based tree ([Russello *et al.* 2005](#)). Shell shape (domed versus saddlebacked carapace) is the most distinctive phenotypic difference among giant tortoise populations and has been associated with habitat differences. The ancestral state of this character in Galápagos is probably domed ([Caccone *et al.* 2002](#); [Russello *et al.* 2005](#)) and recent DNA data from extinct taxa suggest that the saddleback morphology arose independently more than once ([Russello *et al.* 2005](#); [Poulakakis *et al.* 2005–2008](#), unpublished data). However, the role of selection and developmental constraints in the diversification of Galápagos giant tortoises remains to be clearly determined. Research using novel field friendly three-dimensional imaging techniques and morphometric methods is addressing such issues ([Chiari *et al.* in press](#)).

Within-island divergence has been suggested as a mode of speciation for Darwin's finches. Divergence occurs along an elevational gradient in small ground finches on Santa Cruz ([Kleindorfer *et al.* 2006](#)). *Geospiza conirostris* on Genovesa showed an ephemeral tendency to mate assortatively according to similarities in beak shape and song ([Grant & Grant 1989](#)). Assortative mating according to beak size occurs within populations of medium ground finches on Santa Cruz, although this tendency appears to be significantly reduced by human activity ([Hendry *et al.* 2006](#)) and wet conditions, when competition is also presumably reduced ([Huber *et al.* 2007](#)). Sympatric speciation has yet to be convincingly demonstrated in birds on islands such as the Galápagos that are smaller than 10 000 km² ([Coyné & Price 2000](#)), and so it seems unlikely that any of these situations will result in complete speciation.

[Lack \(1947\)](#) proposed a model for within-island species build-up of Darwin's finches that relied on limited dispersal between islands to create initial differences in allopatry, followed by rare colonization, establishment of secondary contact and further differentiation in sympatry as a result of resource competition and character displacement. This model has in principle been adapted to account for faunal community build-up in a wide variety of systems including Galápagos taxa. Despite the apparent lack of isolation between finch populations on different islands ([Petren *et al.* 2005](#)), [Lack's](#) model of faunal build-up may still apply. Immigrants that normally interbreed with residents may on rare occasions form distinct, reproductively isolated populations, depending on environmental circumstances and the combination of traits possessed by immigrants and residents (e.g. [Grant & Grant 2008](#)).

In the beetle genus *Galapagamus*, diversification was within island on San Cristobal, one of the oldest islands, and within-island speciation could not be rejected for the Santa Cruz clade; in both cases, shifts to highland habitats seem to have evolved independently ([Sequeira *et al.* 2008](#)). Although this habitat shift is consistent with selection contributing to within-island diversification, it is not known whether it is associated with a corresponding adaptive shift in phenotype. Notably, [Sequeira *et al.* \(2008\)](#) inferred that speciation did not occur within the younger island of Isabela, where diversity is the result of between-island colonization. Similarly, [Parent & Crespi \(2006\)](#) found a combination of within- and between-island speciation in Galápagos bulimulid snails. Polyphyletic land snail assemblages were found on islands centrally located in space and time (Isabela, Santa Cruz, Pinzón, Santiago), whereas the more isolated islands of Española, San Cristobal and Floreana (again in both space and time) were occupied mostly by monophyletic assemblages resulting from within-island diversification. Some bulimulid species occur in sympatry and may have adapted to the different habitats where they occur ([Coppo & Glowacki 1983](#); [C. E. Parent & B. J. Crespi 2000–2005](#), unpublished data). However, the relative importance of drift and selection in within-island diversification of this group is not known.

The beetle genus *Stomion* has also diversified both within and between islands ([Finston & Peck 2004](#)). Each population contains only one morphospecies, and even on large islands such as Santa Cruz and Isabela where two or three species occur, they never occur in sympatry. [Finston & Peck \(2004\)](#) therefore suggested that speciation happened in allopatry. *Stomion* species have low vagility, even at very small local scales ([Finston *et al.* 1997](#)), which should promote micro-allopatric speciation, in agreement with the scenario proposed by [Finston & Peck \(2004\)](#). No evidence of ecological or morphological adaptation has been found in the genus ([Finston & Peck 1997, 2004](#)), strengthening the idea that diversification happens via micro-allopatric speciation within islands following between-island colonization. [Peck \(1990\)](#) has suggested that troglobites (cave-dwelling invertebrates) might provide good examples of diversification within islands. There are several examples of a cave-dwelling form that has a sister species living nearby outside the cave ([Peck 1990](#); [Peck & Finston 1993](#)), but without a molecular phylogeny we cannot tell how these species were formed.

In sum, the clearest cases of within-island speciation occur in taxa with low vagility and on large islands with diverse habitats. Isabela, with several volcanoes separated by recent lava flows, is especially conducive to within-island diversification. In some cases, subsets of taxa have found their way to other islands, making it more difficult to distinguish within-island speciation from multiple between-island speciation events. For more vagile taxa, speciation between islands seems more likely, given the extreme habitat differences among islands; but within-island processes are often difficult to rule out, and in either case, ecological specialization can play an important role.

(c) *Dynamics of species diversification*

The number of species on an island depends on speciation, colonization and extinction rates. The three processes are affected by biogeography (island area, elevation and insularity) and ecology (habitat diversity). However, the species diversity equilibrium is dynamic and changes through time because islands themselves change (Whittaker *et al.* 2008). Moreover, a delay is expected between the time an island becomes available for colonization and speciation, and the time equilibrium is reached. For example, Parent & Crespi (2006) found that the younger islands of Fernandina and Isabela had fewer land snail species than expected based on their area, elevation and insularity. Similarly, there are only two species of flightless *Galapaganus* beetles on Isabela, whereas San Cristobal, Santa Cruz and Floreana each has three species (Sequeira *et al.* 2008). By contrast, there are more species of the moth genus *Galagete* on Isabela and Fernandina (eight each) than on any of the older islands (Schmitz *et al.* 2007). This contrast among lineages might be a reflection of their different dispersal capacity or the stochasticity of interisland dispersal in some lineages.

Furthermore, the geographical configuration of the whole archipelago is dynamic, and there have been changes in island number, size and isolation due to sea-level variation on various time scales. On a short time scale (from now back to the Pleistocene), it appears that changes in sea levels created terrestrial avenues for gene flow during glacial periods that disappeared when sea levels rose. The effect this sea level change can have on species diversity on Galápagos has been relatively unexplored, but Jordan & Snell (2008) suggested that lava lizard diversity might have increased if islands had been isolated for longer periods. Environmental changes over the short term can influence the evolutionary trajectory of species (Grant 1999), so it is also likely that longer term climate changes have had an important effect on the evolution and extinction of species that remains largely unknown. A sobering example comes from a recent study on El Niño effects on levels of genetic diversity in Galápagos marine iguanas (Steinfartz *et al.* 2007), in which even species with large population sizes may suffer dramatic collapses in genetic diversity when populations are subject to frequent and possibly recurrent environmentally devastating events.

6. FUTURE PROSPECTS FOR EVOLUTIONARY RESEARCH ON GALÁPAGOS ISLANDS

Despite the large volume of evolutionary research that has been undertaken in Galápagos, several species groups remain relatively unstudied in terms of diversification within Galápagos and their relationship to possible sources of colonists (table 2). Most phylogenetic studies of Galápagos organisms have been based on mtDNA, sometimes in combination with one or a few nuclear markers. Mitochondrial DNA has desirable properties for phylogenetic inference (Avice 2000), but the likelihood that a single locus reflects the history of species and populations decreases when divergence occurs rapidly and recently (Hudson & Coyne 2002), as for much of the diversification in the

Galápagos. Multilocus studies of sequence variation, such as intron locus variation (Edwards *et al.* 2007), offers some promise for providing more robust estimates of phylogenetic and phylogeographic divergence. However, in the only case in which they have been used, giant tortoises, they were not helpful (Caccone *et al.* 2004). For more vagile taxa such as winged insects and birds, multilocus microsatellites now offer a powerful means to estimate even low levels of gene flow, admixture and population divergence.

Ecology and habitat specialization can be critical factors in speciation both within and between islands. Phylogenetic studies can be broad but are limited in their ability to reveal speciation processes. The number of studies of natural history, ecology, evolution and behaviour is small and limited in scope. Field studies are limited spatially and temporally by logistics and funding. Thus a great deal remains to be revealed about speciation in Galápagos animals. One need only consider a single field research programme (Grant 1999; Grant & Grant 2008) to see the magnitude of contributions to the study of evolution and speciation that are possible.

7. CONSERVATION AND THE ROLE OF EVOLUTIONARY GENETICS IN GALÁPAGOS RESEARCH

While providing ecologists and evolutionary biologists with 'natural laboratories', island biotas are also very often in danger of going extinct. This is due both to their generally small population sizes associated with small geographical ranges, as well as to the relatively simple ecosystems they inhabit (which is why they are so valued by biologists). Island ecosystems are therefore particularly susceptible to catastrophic disturbances by invasive species. Understanding the phylogenetics and biogeography of island species allows greater insights into setting conservation priorities and enacting rational conservation policies, as illustrated in the examples below on Galápagos tortoises (Powell & Caccone 2008).

Phylogenetic analysis detected previously unrecognized taxa that deserve special conservation attention (Russello *et al.* 2005) and assigned individuals of unknown origin (zoo animals) to their correct location (Burns *et al.* 2003; Russello *et al.* 2007b). Such studies also allowed identification of genetic lineages in natural populations that were previously thought to be extinct or nearly extinct (Russello *et al.* 2007a; Poulakakis *et al.* 2005–2008, unpublished data). Understanding the genetics of endangered island biota may also aid in designing more rational recovery efforts such as captive breeding/repatriation programmes (Milinkovitch *et al.* 2004, 2007).

Over the last century, the human population of Galápagos has risen dramatically. Prior to 1900, fewer than 300 people lived in the islands (Lundh 2001). There are now nearly 30 000 residents on four inhabited islands and more than 130 000 visitors each year (Watkins & Cruz 2007). The human population boom has caused a marked increase in introduced species and diseases (Fessl & Tebbich 2002; Wikelski *et al.* 2004; Gottdenker *et al.* 2005). Several populations of birds have recently become

extinct (Grant 1999; Grant *et al.* 2005) and several species are now threatened or on the brink of extinction (e.g. Dvorak *et al.* 2004).

The near future will determine whether the Galápagos will provide a model for the deterioration of an island fauna in our time, or whether the brighter prospect of effective management and persistence will be realized so that future generations can continue to study the processes of evolution in action.

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