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ORIGINAL ARTICLE

Immigration history of amphidromous species on a Greater Antillean island

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ABSTRACT

Aim To use molecular data to test for dispersal structuring in the immigration history of an amphidromous community on an island.

Location The Caribbean island of Puerto Rico.

Methods Mitochondrial DNA sequences were obtained from 11 amphidromous species, including shrimps, fish and a gastropod, sampled from throughout the island. The timing of population expansion (T_E) in each species was calculated using nucleotide variation and molecular clock dating methods. The order of species accumulation was then reconstructed (oldest to most recent estimate for T_E), and groups of species with non-overlapping estimates for T_E were identified. The temporal span and average immigration rate for each group were calculated and compared with expectations of two previously published models of island immigration [the 'dispersal-structured model of island recolonization' (Whittaker & Jones, *Oikos*, 1994, **69**, 524–529), which predicts short phases of rapid immigration followed by extended phases with relatively slow immigration rates; and the 'colonization window hypothesis' (Carine, *Taxon*, 2005, **54**, 895–903), which suggests that opportunities for island colonization are temporally constrained to discrete waves of colonization].

Results The molecular data indicated the immigration history of Puerto Rican amphidromous fauna from the late Pleistocene through the Holocene and identified two groups of species with non-overlapping estimates for T_E and one group that overlapped with the other two groups. The temporal span, average immigration rate and lack of discreteness between all three groups indicated a continuum of immigration rather than distinct phases of species arrivals.

Main conclusions This study did not support the expectations of the immigration models and suggested that amphidromous species from Puerto Rico comprise a single class of marine-based dispersers. The immigration sequence we report probably reflects a recolonization chronology in this community, in keeping with the notion of species turnover through time. Four areas of future research into the immigration history of amphidromous species on islands are identified, and indicated the possibility that equilibrium processes govern long-term community change in amphidromous biota on islands.

Keywords

Amphidromy, colonization window, demographic expansion, dispersal structuring, equilibrium biogeography, freshwater recolonization, island biogeography, marine dispersal, Puerto Rico.

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INTRODUCTION

The arrival of species to islands has long interested biogeographers (e.g. Darwin, 1859; MacArthur & Wilson, 1967). Some classical studies in island biogeography have examined immigration by experimentally defaunating small islands, or by capitalizing on the sterilization of islands by natural disturbance, and monitoring the subsequent arrival of species

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(Simberloff & Wilson, 1969; Whittaker & Jones, 1994). For example, patterns of plant immigration to Rakata Island (Krakatau group, Indonesia) following its sterilization in 1883 by a series of volcanic eruptions showed distinct phases of recolonization in terms of the dispersal mode of species (i.e. oceanic dispersal, wind-borne dispersal or hitchhiking within dispersing animals) and rates of species accumulation, giving rise to the 'dispersal-structured model (DSM) of island recolonization' (Whittaker & Jones, 1994; Whittaker & Fernández-Palacios, 2007). The 'colonization window hypothesis' (CWH; Carine, 2005) is an alternative hypothesis, which suggests that opportunities for island colonization are temporally constrained to discrete waves of colonization, such as the waves of plant colonization to the Macaronesian islands that were associated with land bridges during historical periods of lowered sea levels (Carine, 2005; Kim *et al.*, 2008). Although many studies have examined the immigration history of islands over ecological time-scales (i.e. <100 years, Heaney, 2000), other studies have used molecular data to reconstruct immigration histories over much longer temporal scales (see Emerson, 2002). These studies have indicated the sequence of islands colonized by a given taxon (e.g. Clegg *et al.*, 2002; Hormiga *et al.*, 2003; Page *et al.*, 2005; Garb & Gillespie, 2006; Gillespie *et al.*, 2008), the sequence of species arriving on a given island (e.g. Juan *et al.*, 1996; Parent & Crespi, 2006), and long-term changes in rates of immigration arising from deterministic, abiotic factors (e.g. Ricklefs & Bermingham, 2001). The reconciliation of models of species accumulation on islands, such as the DSM and CWH, across ecological and evolutionary time-scales is an area of island biogeography to which molecular genetic analysis can contribute (Emerson, 2002).

Various components of island stream faunas, including fish, decapod crustaceans and gastropods, undertake obligate amphidromous migration whereby larvae are released in freshwater reaches, drift downstream to marine or estuarine habitats, and then migrate upstream as post-larvae to freshwater adult habitats (McDowall, 2004, 2007). Therefore, amphidromous species have clearly defined abilities for marine dispersal. In the DSM, the rate of recolonization facilitated by oceanic dispersal is rapid in Phase 1 of the model and then declines steadily through Phases 2 and 3 (Whittaker & Fernández-Palacios, 2007). Factors influencing this decline include variation among species in their ability for oceanic dispersal (i.e. rapid immigration for good dispersers followed by a reduced rate of immigration for poorer dispersers), exhaustion of species in the source pool of potential arrivals, and reduced habitat or niche availability on the island (Whittaker & Fernández-Palacios, 2007). Phases 1 and 2 of plant recolonization to Rakata Island comprised relatively short time intervals (i.e. <25 years), whereas Phase 3 covered a relatively extended period of time (i.e. >60 years), reflecting the stochastic and slow rate of immigration by poor dispersers later in succession (Whittaker & Jones, 1994). Although some population genetic studies indicate that amphidromous species have equal and well-developed abilities for among-river (within-island) marine dispersal (e.g. Cook *et al.*, 2008a, 2009), dispersal limitation is a fundamental determinant of biodiversity patterns in island stream communities, including for amphidromous species (Covich, 2006). Whether amphidromy represents a single class of dispersal over ecological and evolutionary time-scales is therefore a key question in freshwater island biogeography. If amphidromous species differ in their abilities for large-scale oceanic dispersal, long-term patterns of arrival to an island may contain signatures of dispersal structuring, such as relatively short phases of rapid immigration followed by extended phases with relatively slow immigration rates as predicted by the DSM. Alternatively, if the molecular data indicate discrete periods of immigration that do not differ in their immigration rate, then temporal constraints on immigration, such as those predicted by the CWH, may suggest the importance of historical landscape processes on dispersal limitation.

In this study we used mitochondrial DNA (mtDNA) data from 11 amphidromous species from Puerto Rico, including shrimps, fish and a snail, to estimate the timing of the most recent population expansion (T_E) in each species and to test for dispersal structuring in the immigration history of this community. We first discriminated between contemporaneous and non-contemporaneous estimates for T_E, as the former would probably reflect population growth by pre-existing populations following bottlenecks associated with abiotic factors (e.g. disturbance) whereas the latter would probably reflect demographic change following founder events associated with species-specific immigration to the island. We then determined if the expectations of the DSM (i.e. short phases of rapid immigration followed by extended phases with relatively slow immigration rates) or of the CWH (i.e. discrete phases of immigration that did not differ in their immigration rate) were reflected in the molecular data for this community.

MATERIALS AND METHODS

The sampling design follows that presented by Cook *et al.* (2008a, 2009) and includes three marine regions (Atlantic Ocean, Mona Passage and Caribbean Sea), each with three rivers, spanning the entirety of the island (Fig. 1). The species we assayed include representatives of all amphidromous higher taxa (i.e. caridean shrimp – Crustacea: Decapoda; gobiid fishes – Osteichthys: Perciformes; and snails – Mollusca: Gastropoda). Although our samples also contained *Potimirum mexicana* (Decapoda: Atyidae) and two additional *Macrobrachium* species (Decapoda: Palamonidae), sample sizes for these species (i.e. $n < 10$ per taxon for the whole island) were too small to make a valid comparison with the 11 taxa we examined. Although not all 11 species were represented in all rivers, all species were sampled in at least two regions, with most species being sampled in all three regional areas, meaning that a broad geographical area was sampled for each species (Table 1). Population genetic analyses indicate that all species have continuous population structures among rivers in Puerto Rico (Cook *et al.*, 2008a, 2009); thus, samples from through-

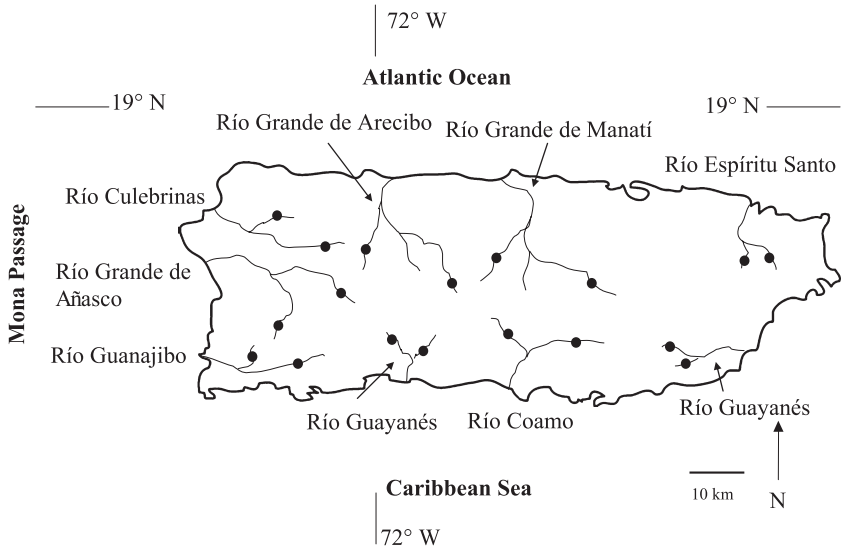

Figure 1 Map of Puerto Rico showing locations, rivers and regions sampled.

out the island were pooled for demographic analysis and the data for each species reflected island-scale molecular variation. Sequences of the cytochrome *c* subunit I (COI) mtDNA gene were amplified, aligned and edited for the invertebrates as described in Cook *et al.* (2008a, 2009), and aligned and edited fragments of the ATPase 6 and 8 mtDNA gene for the gobiid fish were obtained as described in Cook *et al.* (2007).

The population demographic parameters D (Tajima, 1989), F_S (Fu, 1997) and R_2 (Ramos-Onsins & Rozas, 2002) were calculated for each species in DnaSP (Rozas *et al.*, 2003), using 10,000 coalescent simulations with the observed number of segregating sites. Significantly negative values of F_S and D, and significantly positive R_2-values indicate a genetic pattern expected under population growth. Mismatch distribution analyses (MDAs; Rogers & Harpending, 1992), which test patterns of nucleotide variation against a null model expected under a sudden population expansion, were also implemented in Arlequin (Schneider *et al.*, 2000) using 10,000 bootstrap replicates. MDA calculates various population parameters, such as the raggedness index (r; Rogers & Harpending, 1992), with significantly ragged populations having stable demographic histories and non-significantly ragged populations having sudden population growth. For data distributed according to a sudden population expansion model (i.e. non-significant r indices), MDA calculates lower- and upper-confidence bounds using nonparametric bootstrapping for the additional parameters tau (τ; Li, 1977), which is an index of time since population expansion, and theta-0 (θ_0) and theta-1 (θ_1), which are the pre- and post-expansion values for the mutation parameter $2N\mu$, where N is the effective female population size and μ is the mutation rate per nucleotide per generation (i.e. $\theta_1 - \theta_0$ is indicative of the magnitude of effective female population growth, with effective population size defined as the reciprocal of the probability that two individuals have the same mother; Rogers, 1995).

No species were significantly ragged, and the various population demographic parameters indicated demographic expansions (see Results and Table 1); thus, the time of population expansion (T_E) for each species, including the 95% lower- and upper-bound estimates, were calculated by rearranging the formula $\tau = 2\mu t$, where μ is the mutation rate per nucleotide per generation, and t is time in generations (Li, 1977; Rogers & Harpending, 1992). Thus, $t = \tau/2\mu$, where μ is the mutation rate multiplied by the number of base pairs in the DNA fragment divided by 1,000,000. The sequence divergence rates of 1.4% per million years (Myr^{-1}) (Knowlton & Weigt, 1998) for the decapod COI sequences, 1.8% Myr^{-1} for the gastropod COI sequences (Wilke & Pfenninger, 2002) and 1.3% Myr^{-1} for the goby ATPase sequences (Bermingham *et al.*, 1997) were converted to mutation rates by dividing by 2, as divergence rates are double mutation rates. For example, the point estimate of the population expansion in *Atya scabra* was calculated: t in generations $= 2.13/((1.4/2 \times 596)/1{,}000{,}000)$, and converted to time in years (i.e. T_E) by multiplying by 2 (see Cook *et al.*, 2008a for assumptions on generation times in these fauna).

The order of species accumulation was reconstructed whereby the oldest expansion event (i.e. largest value for T_E) corresponded to one species on the island ($S = 1$), through to the most recent expansion event corresponding to all species on the island ($S = 11$). Groups of species with non-overlapping estimates for T_E were identified, and the temporal span of each group was determined using the oldest and most recent point estimates of T_E and dividing by the number of species in the group to give an average immigration rate for each group.

RESULTS

Mitochondrial DNA sequence data contained signatures of population expansions in all species, although the magnitude of demographic change varied considerably among species (less than one-fold increases to over three-and-a-half-fold increases; Table 1). The molecular data indicated the immigration history of Puerto Rican amphidromous fauna from the

Table 1 Species and sample sizes and population demographic parameters for each species. *P*-values are in parentheses, and significant values ($\alpha = 0.05$) are in bold.

Species	*n*	*D*	F_S	R_2	*r*	τ	θ_0	θ_1	GenBank accession numbers
Crustacea: Decapoda: Atyidae (atyid shrimp)									
*Atya lanipes** Holthuis, 1963	773/185/8/3	**−2.683 (<0.001)**	**−65.712 (<0.001)**	**0.012 (<0.001)**	0.186 (0.630)	0.714	0.000	0.771	EU005053–EU005083
*Atya scabra** (Leach, 1815)	596/225/9/3	**−2.005 (<0.001)**	**−201.469 (<0.001)**	**0.032 (0.003)**	0.006 (0.601)	2.130	7.059	4,026.250	EU005084–EU005224
*Atya innocuous** (Herbst, 1792)	777/48/4/2	−0.811 (0.222)	**−11.990 (0.005)**	0.081 (0.227)	0.012 (0.223)	8.936	0.000	87.930	EU005036–EU005052
Micratya sp.	756/104/5/3	0.457 (0.749)	**−20.418 (<0.001)**	**0.091 (<0.001)**	0.015 (0.640)	8.668	0.002	15.579	FJ348828–FJ348931
Micratya poeyi (Guérin-Méneville, 1855)	775/52/5/3	−2.133 (0.002)	**−11.918 (<0.001)**	**0.106 (<0.001)**	0.089 (0.603)	0.694	0.000	256.992	FJ348779–FJ348827
Crustacea: Decapoda: Xiphocarididae (long-faced shrimp)									
*Xiphocaris elongata** (Guérin-Méneville, 1856)	768/66/5/3	**−2.139 (0.003)**	**−73.964 (<0.001)**	**0.036 (<0.001)**	0.006 (0.724)	8.502	0.003	175.938	EU004940–EU005000
Crustacea: Decapoda: Palaemonidae (long-armed river prawn)									
*Macrobrachium faustinum** (de Saussure, 1857)	708/71/7/3	**−2.487 (<0.001)**	**−45.119 (<0.001)**	**0.021 (<0.001)**	0.049 (0.546)	1.571	0.000	7.245	EU005001–EU005035
Actinopterygii: Perciformes: Gobiidae (gobies)									
Sicydium sp.	657/40/5/2	−1.264 (0.085)	**−16.292 (<0.001)**	**0.110 (<0.001)**	0.021 (0.378)	5.430	0.003	53.994	FJ348976 – FJ349015
Sicydium buscki Evermann and Clark, 1906	657/80/5/2	**−2.215 (0.001)**	**−61.918 (<0.001)**	**0.096 (<0.001)**	0.026 (0.350)	3.631	0.003	6,655.000	FJ349016–FJ349095
Sicydium punctatum Perugia, 1896	657/34/4/3	**−2.504 (<0.001)**	**−11.636 (0.002)**	**0.114 (<0.001)**	0.030 (0.280)	2.252	0.000	19.609	FJ348742–FJ348775
Mollusca: Gastropoda: Neritidae (amphidromous snail)									
Neritina virginea (Linnaeus, 1758)	354/44/2/2	−1.835 (0.012)	**−15.194 (<0.001)**	**0.108 (<0.001)**	0.033 (0.350)	4.623	0.003	12.839	FJ348932–FJ348975

n, number of base pairs of DNA fragment/individuals/rivers/regions sampled; *D*, Tajima's *D*; F_S, Fu's F_S; R_2, Ramos-Onsins & Rozas' R_2; *r*, Rogers & Harpending's raggedness index; τ, tau, an index of time since population expansion expressed in units of mutational time; θ_0 and θ_1, pre- and post- expansion values for the mutation parameter (i.e. $2N\mu$, where *N* is the effective female population size and μ is the mutation rate per gene per generation).

*Results from Cook *et al.* (2008a).

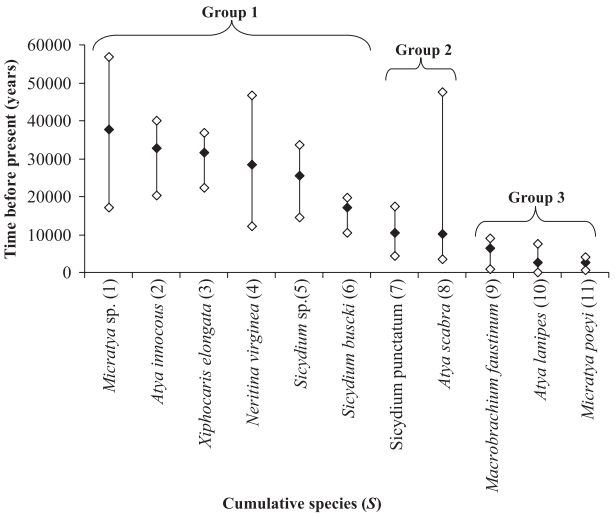

Figure 2 Cumulative number of species (S) plotted as a function of timing of expansion (T_E), showing the point estimate for the time of expansion for each species (solid diamonds) and 95% lower- and upper-confidence bounds (open diamonds). Three groups of species are indicated, with Groups 1 and 3 having T_E estimates that do not overlap.

late Pleistocene through the Holocene and show non-overlapping estimates of expansion time for some species-pair combinations, including between some species within the genera *Atya* and *Micratya* (Fig. 2). Three groupings of species were identified (Fig. 2): Group 1, which contained species with T_E estimates that did not overlap with Group 3; Group 2, which contained species with T_E estimates that overlapped with both Groups 1 and 3; and Group 3, which contained species with T_E estimates that did not overlap with Group 1. Group 1 spanned approximately 46,359 years and contained eight species, yielding an average immigration rate of one species every 5795 years; Group 2 spanned approximately 15,715 years and contained two species, giving an immigration rate of one species every 7857 years; and Group 3 spanned 8427 years and contained three species, giving an average immigration rate of one species every 2809 years. The higher taxa that were represented by more than a single species (i.e. shrimp and fish) were not contained within only a single grouping (Fig. 2).

DISCUSSION

The molecular data indicate non-contemporaneous population expansions in the species we considered in this study, including two groups of species (Groups 1 and 3) with non-overlapping estimates for the timing of population growth. This suggests that patterns of demographic change in these species were not associated with population growth following bottlenecks in pre-existing populations (i.e. a consequence of disturbances such as hurricanes, tsunamis, volcanoes), as abiotic forcing would have facilitated contemporaneous estimates for T_E. Instead, the results suggest species-specific estimates for the timing of founder events associated with immigration to Puerto Rico throughout the Quaternary.

Two of the three species in Group 3 (*Atya lanipes* and *Micratya poeyi*) had extremely low levels of genetic variation (e.g. nucleotide diversity, π, is an order of magnitude lower than that for all other species, Cook *et al.*, 2008a, 2009), raising the potential for selective sweeps to be a determinant of patterns of nucleotide variation. This would invalidate the conclusion of non-contemporaneous population growth, although the use of unlinked nuclear gene sequences in future studies would enable patterns of nucleotide variation resulting from demographic changes or selective sweeps to be disentangled. However, the third species in Group 3 (*Macrobrachium faustinum*) had levels of genetic variation similar to those of all species in Groups 1 and 2 (Cook *et al.*, 2008a, 2009), indicating that species without impoverished genetic diversity can also have recent estimates for T_E. Furthermore, an earlier study suggested that taxon cycling, which is a biotic process of species turnover and community change (Ricklefs & Bermingham, 2002), explains the patterns of nucleotide variation in *A. lanipes* (i.e. secondary expansion and the recolonization of Puerto Rico following historical regional decline, Cook *et al.*, 2008a). Interestingly, *A. lanipes* is the most morphologically and ecologically distinct species within *Atya* (Hobbs & Hart, 1982). These types of distinctive characteristics are expected for species undergoing secondary expansions and recent immigration to new habitats within taxon cycles (Wilson, 1961; Erwin, 1981; Ricklefs & Bermingham, 2002). In contrast, the genus *Micratya* contains only a single described taxon (*Micratya poeyi*), whereas a recent phylogenetic study indicated two cryptic species from Puerto Rico within the genus (Page *et al.*, 2008). It would be interesting to determine if these morphologically cryptic species have diverged in aspects of their ecology (e.g. habitat utilization and distribution), as expected for closely related species interacting in taxon cycles (Ricklefs & Bermingham, 2002). Such patterns of habitat differentiation between closely related species have been shown for *A. lanipes* and other *Atya* species in the West Indies (Chace & Hobbs, 1969) and for *A. innocuous* and *A. scabra* (and among congeners of *Macrobrachium*) on the Lesser Antillean island Basse Terre, Guadeloupe (Fièvet *et al.*, 2001).

The expectations of brief phases of rapid immigration followed by relatively long phases of slow immigration, as described in the DSM, or of discrete phases of immigration, as predicted by the CWH, were not evident in the molecular data for the Puerto Rican amphidromous community. Instead, the groupings of species with similar estimates for T_E indicated a relatively long period of more ancient immigration followed by a relatively brief period of more recent immigration. Furthermore, estimates of T_E for species in Group 2 overlapped with T_E estimates for species within Groups 1 and 3, indicating a continuum of immigration to the island by amphidromous species, rather than distinct phases of species arrivals as expected under the DSM and CWH. Although dispersal limitation is a fundamental determinant of biodiversity patterns in insular stream communities (Covich, 2006), the

results of this study indicate that amphidromy represents a single class of marine dispersal. Molecular assessments of immigration histories of other amphidromous communities on other islands, especially highly isolated oceanic islands, would facilitate further examination of the prospect for dispersal structuring and multiple dispersal classes within amphidromous biota.

The Puerto Rican freshwater (i.e. non-amphidromous) crab *Epilobocera sinuatifrons* probably colonized the island by rafting (Rodríguez & López, 2003) and is thus a stream species with a strikingly different potential for marine-based dispersal in comparison to amphidromous species. In contrast to population patterns shown for the amphidromous species (Cook *et al.*, 2008a, 2009), molecular data for the freshwater crab indicate significant population structuring among rivers on the island (Cook *et al.*, 2008b). Population subdivision confounds the types of island-scale demographic analyses used in this study, and therefore would make results for an island-scale analysis invalid and not comparable with results for the amphidromous species, precluding the inclusion of molecular data for *E. sinuatifrons* in this study. However, stream insects with adult flight are often genetically continuous among stream systems over scales comparable to the scale of our study (Hughes, 2007; Wilcock *et al.*, 2007; Chaput-Bardy *et al.*, 2008). It would be interesting to juxtapose molecular analyses of the immigration history of stream insects on Puerto Rico (which would reflect the wind-borne dispersal aspect of the DSM) with patterns in the immigration history of amphidromous biota we report here. Such analyses would contribute to a broader understanding of the island biogeography of insular freshwater communities. It would also be interesting to compare wind-borne immigration by adult stream insects with the wind-borne dispersal of plants as described in the DSM (Whittaker & Jones, 1994; Whittaker & Fernández-Palacios, 2007).

Spatial and temporal scales are critical issues to consider when reconstructing the immigration histories of biotas on islands (Whittaker, 2000; Whittaker *et al.*, 2008). The molecular signatures we report extend back to only the mid-Pleistocene; thus, they are unlikely to reflect initial arrival to the island by its amphidromous biota. Instead, they probably reflect a recolonization chronology in keeping with the notion of species turnover through time and broadly suggest an equilibrium process of community change, as described in MacArthur & Wilson's (1967) theory of island biogeography and more recent theories in island biogeography (e.g. the general dynamic theory of oceanic island biogeography; Whittaker *et al.*, 2008). However, it is unlikely for equilibrium biogeography to be maintained throughout the total evolutionary history of a community (Heaney, 2000) or the history of an island (Whittaker *et al.*, 2008), and other studies have suggested non-equilibrium immigration histories in some island biotas (Whittaker, 1995; Ricklefs & Bermingham, 2001). More ancient processes, such as those occurring during the Miocene, when many of these species originated and underwent morphological divergence from their progenitors (Page *et al.*, 2008), and more recent processes, such as source–sink population dynamics in shrimp populations in response to disturbance (Greathouse *et al.*, 2005; Covich *et al.*, 2006), are suggestive of non-equilibrium dynamics at larger and smaller temporal scales, and at smaller spatial scales than the 'island scale' that our molecular data reflect (e.g. at river or river-reach scales; Covich, 2006).

This study indicates four areas for future research. First, our analyses used only a single mtDNA marker for each species, meaning that selective sweeps cannot be disregarded as potential influences on patterns of nucleotide variation, particularly for *A. lanipes* and *Micratya poeyi*. Future studies using unlinked nuclear gene sequences would enable discrimination between patterns of nucleotide variation resulting from demographic processes or selective sweeps. Second, our analyses used within-island molecular variation to examine the immigration history of an amphidromous community. Calculating the timing and frequency of immigration using coalescent-based modelling at among-island scales would be a complementary approach to the method we used in this study for using molecular data to reconstruct the immigration history of island species. Third, our analysis was focused on detecting dispersal structuring in the amphidromous biota. Extending the analysis to include aquatic insects would enable analysis of dispersal structuring in stream species that have ocean- versus wind-borne dispersal mechanisms. Finally, it would be interesting to explore further our suggestion that amphidromous communities represent biotic systems that align with equilibrium theories of species turnover and island biogeography. Continued research into the immigration history of amphidromous and aquatic insect species on other islands, including on highly isolated oceanic islands, would facilitate the generation of more general knowledge about the immigration history and biogeography of lotic species on islands.

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