

## Circulation Around Islands, Gene Flow, and Fisheries Management

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### ABSTRACT

La circulación oceánica alrededor de islas tiene influencia en la dispersión de larvas planctónicas y reclutamiento de juveniles a las islas, afectando a su vez las poblaciones de especies que se pescan. Se presentan seis modelos hidrográficos que pueden ejercer dichas influencias, a saber: (1) difusión en mares estratificados, (2) intrusiones de agua debido a oscilaciones de marea, (3) zona de convergencia estacional, (4) remolinos (eddies) acerca andose a las islas, pero que han sido generados cerca de éstas, (5) afloramientos generados cerca de la isla, (6) remolinos generados por la topografía de las islas. Si la dispersión de larvas planctónicas y el reclutamiento post-larval están sincronizados con los patrones de circulación que proveen para la mezcla de aguas oceánicas y neríticas, entonces, el flujo genético a través de las islas deberá ser mayor que aquellos sitios en donde no exista tal sincronización. Por lo tanto, la administración pesquera exitosa deberá variar de isla en isla, dependiendo en parte de estos patrones.

### INTRODUCTION

Oceanic circulation around an island is strongly influenced by the local boundary between land and sea. The development of hydrodynamic features, the length of time they persist around islands, and the extent they reach in space will affect the transport of marine organisms, including eggs and larvae (Norcross and Shaw, 1984), as well as the aquatic ecosystem. The purpose of this paper is to examine some features associated with circulation around islands and to consider how they might influence the distribution and evolution of nearshore marine organisms.

The distribution of planktonic marine organisms around islands often follows a decreasing gradient with distance from shore similar to that found near the coastlines of most continents. This pattern has been called the "island mass effect" (Doty and Oguri, 1956) and has been used as a model of distribution for organisms around islands (Gilmartin and Revelante, 1974; Hargraves *et al.*, 1970; Sander, 1981; Sander and Steven, 1973) as well as near land masses (*e.g.*, Anderson and Roff, 1980; Motoda *et al.*, 1978). The island mass effect has been frequently observed (Corredor *et al.*, 1984; Gordan, 1971; Sheldon *et al.*, 1972; Sourmia and Ricard, 1975; Walters, 1976; Wiebe *et al.*, 1975), and recent work has been directed toward identifying its specific hydrodynamics (El-Sayed and Weber, 1980; Sander, 1981). Biological patterns more complex and varied than decreasing offshore gradients are common, however, and because the

distribution of species is influenced by individual responses to the environment as well as by the immediate hydrographic history (McKelvie, 1985), island effect gradients may be overridden (Gunderson *et al.*, 1972). For instance, zooplankton may show an inshore-offshore gradient (Sander and Steven, 1973; Sette, 1955) or may not (*e.g.*, King and Hida, 1954). Likewise, fish larvae may be distributed uniformly to distances up to 12 km from islands, may be more abundant nearshore, or may be more abundant offshore, depending on species and production of pelagic (offshore) or nonpelagic eggs (Leis and Miller, 1976). Further, vertical migration can lead to spatial patterns quite different from those that would arise from passive responses to hydrography (*e.g.*, Anderson and Stolzenback, 1985). Herein we focus on the hydrodynamic patterns only.

The degree to which circulation retains planktonic larvae around islands may determine the local abundance of benthic and neritic biota and also affect the large-scale distribution patterns and the genetic structure of local populations (Figure 1). At one extreme, all gametes or larvae released by adults are transported away from the island by ocean currents, and all recruits to the local population arrive from an up-current source (Figure 1A). At the other extreme,

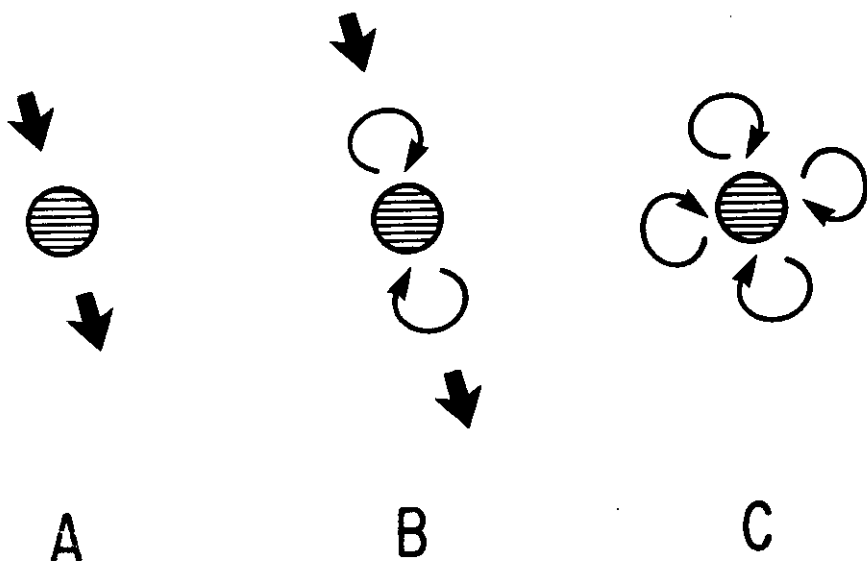


Figure 1. Possible dispersal patterns around oceanic islands. (A) Total dispersal. All larvae released near the island are advected away; all recruits come from upstream sources. (B) "Golden mean." Some larvae released by island adults are retained nearshore and some recruits originate from these larvae; other larvae and recruits follow pattern A. (C) Total retention. All larvae released by island adults are retained in local waters; all recruits originate from these larvae.

all recruits to an island are offspring of endogenous populations (Figure 1C). A continuum extends between these extremes, with some recruits originating from the island and others recruited from elsewhere (Figure 1B). The intermediate pattern could occur when anomalous events interrupt typical circulation as well as when typical circulation includes both retention and dispersal mechanisms.

We will begin by reviewing features that influence larval dispersal. Next we will discuss implications of larval transport for the biogeography and genetic structure of island populations. Finally, we present a testable hypothesis designed to reveal whether a coupling exists between the scales of hydrodynamic features and the temporal and spatial spawning patterns of insular marine fauna.

#### MODELS OF CIRCULATION AROUND ISLANDS

Hydrodynamic processes around islands can be understood by measuring temperature, salinity, and current velocity. Also, holoplankton and phytoplankton may act as scalar indicators of such processes (Gower *et al.*, 1980) and aid in the interpretation of physical data: *e.g.*, on spatial scales of approximately 40 m, phytoplankton chlorophyll behaves as a dye even though phytoplankton are actively growing (Denman and Powell, 1984). The examples we discuss are drawn as if from data acquired near-synoptically by ships and by remote sensors on aircraft or satellites.

Six models of circulation around islands and its potential impact on larval dispersion and retention are presented (Figure 2). Model 1 acts as a reference for the others. It depicts an island in a stratified sea that has minimal effect on the ocean circulation around it, *e.g.*, Bermuda, with a slow, steady flow from the west and a deeper thermocline on the southern side of the island than on the northern (Hogg, 1972). (An anomaly on the northwestern corner of the island is omitted in our model for the purpose of simplification.) The effect of this interaction between ocean and island on plankton distribution should be exactly the same as a gradient normal to the coast as described by Doty and Oguri (1956). Nutrient enrichment from the island (whether caused by runoff, tidal and wind mixing of shallow water, or trapping and gradual release of nutrients by benthic algae) will "diffuse" away from the island (Okubo, 1971). The resulting pattern of increased productivity around the island could be either symmetric or asymmetric depending on whether a slow, steady flow persists. Such patterns have been described around Oahu, Hawaii (Doty and Oguri, 1956), the Marquesas (Jones, 1962), Barbados (Sander and Steven, 1973), Bermuda (Sheldon *et al.*, 1972), and islands in the Caribbean (Corredor *et al.*, 1984). Passive planktonic larvae would also "diffuse" away from the island under similar circumstances. In the absence of mean flow, the number of larvae remaining near the island would depend on the initial concentration and the diffusivity coefficient, but if the swimming ability of larvae increased during growth and development, then some might actively swim back to the island. The major caution regarding data demonstrating this model is that values averaged over time may suggest diffusion whereas the pattern is actually due to a sequence of hydrodynamic events.

The remaining models are of hydrodynamic features that tend either to restrict or to enhance mixing between neritic and pelagic waters. Horizontal mixing is restricted when fronts are established between the two water masses

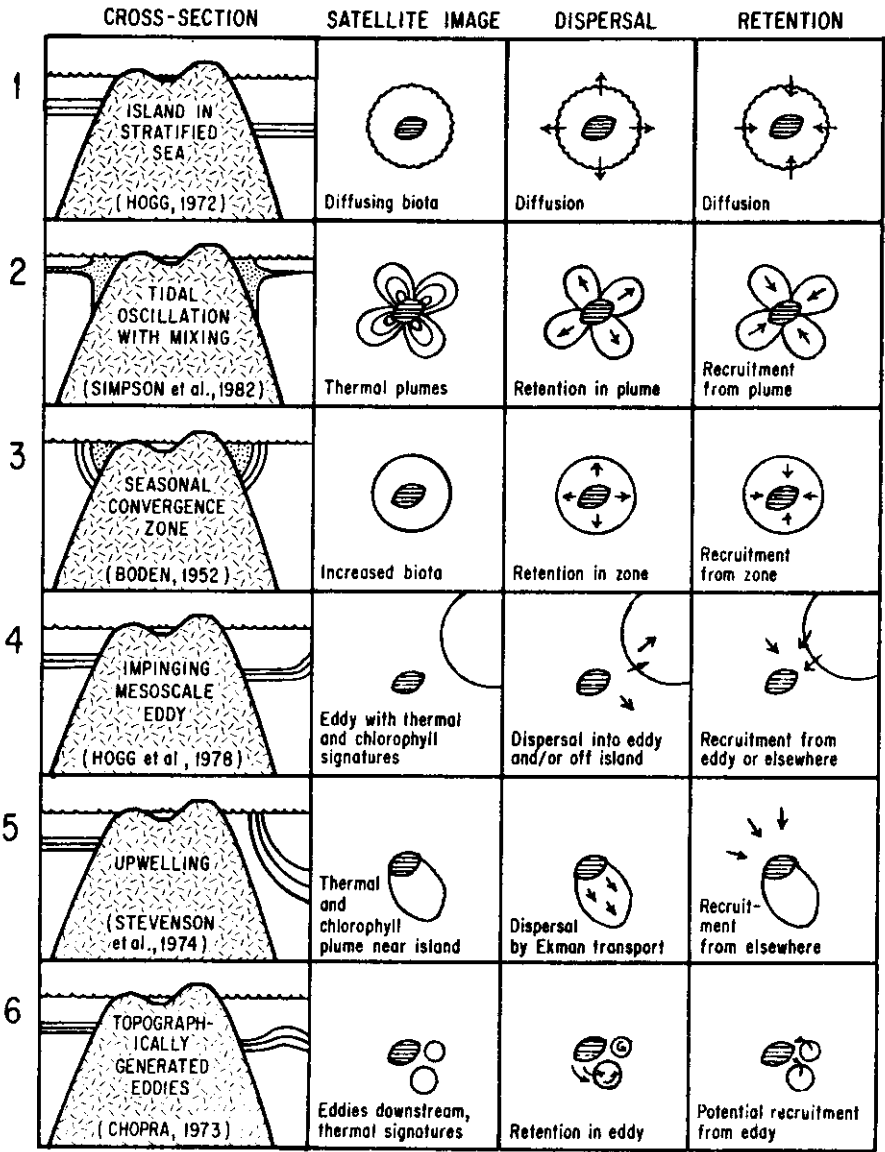


Figure 2. Models of island mass effects and their impacts on larval dispersion. See text for details.

and is enhanced by processes that move neritic water offshore or by cross-frontal mixing.

Model 2 illustrates an effect found around islands on continental shelves (Simpson *et al.*, 1982; Townsend *et al.*, 1983) created when bottom topography interferes with flow, and as a result oscillatory motion becomes rotational (Pingree and Maddock, 1985). Here, depending on the relationship of tidal current velocity to water depth, plumes may be established, enhancing mixing within neritic waters but restricting the mixing between neritic and oceanic waters except along the pycnocline (Pingree and Maddock, 1979). Such tidal plumes, which may last for several days, have been observed by satellite (Simpson *et al.*, 1982). The effect has not been demonstrated around islands in the open ocean, and, because of its dependence on the ratio of depth and tidal velocity, is of little significance there. For larvae from islands in shallow seas, however, the presence of tidal plumes could mean retention and could increase the likelihood of local recruitment.

In Model 3, a seasonal convergence zone (Boden, 1952), which resembles a "retrograde" shelf front in the temperature profile (Mooers *et al.*, 1978), can effectively separate a well mixed zone of nearshore water from open ocean water. The zone is established because density gradients set up cyclonic or anticyclonic circulation patterns depending on local conditions (Uda and Ishino, 1958; von Arx, 1948 and 1954). Around Bermuda, high water temperatures in the summer create low densities in the lagoon. Lagoon water flows outward in an anticyclonic pattern until it reaches the 23.50 sigma-t isopycnic (Boden, 1952). There the water sinks, mixes with water from the open ocean, and flows back into the lagoon along the reef bottom. The 23.50 sigma-t isopycnic represents the region of convergence. The circulation pattern retains insular waters nearshore in the summer (Boden, 1952). Similar circulation patterns have been described within atolls (von Arx, 1948, 1954; Uda and Ishino, 1958) but have not been investigated recently. Seasonal patterns of this kind could enhance retention of larvae during critical periods in their planktonic development. When the front breaks down, larvae may already have metamorphosed into a benthic form or may be capable of swimming to juvenile habitats.

In Model 4, a mesoscale eddy impinges on island waters. This eddy originated away from the island, in the Gulf Stream, for instance. The hydrographic effects created by its presence include high-velocity, longshore currents between the eddy and the island (Hogg *et al.*, 1978) and the possible advection of island water into the eddy system. Cross-frontal advection has been shown for an eddy in the California Current (Haury, 1984) and for cold core (Wiebe and Flierl, 1983) and warm core (Wroblewski and Cheney, 1984) Gulf Stream rings. Larvae from three water masses— shelf, slope, and Sargasso Sea — have been entrained in Gulf Stream warm core rings (Flierl and Wroblewski, 1985; Wroblewski and Cheney, 1984), and eddies off California (Johnson, 1971) and Australia (McWilliams and Phillips, 1983) appear to be important to lobster larvae dispersal. A mesoscale eddy near an oceanic island potentially can:

1. Deposit developed larvae from off-island sources into island waters.
2. Disperse larvae to or away from the island in high-velocity shear currents.
3. Entrain insular larvae, either retaining them near the island or dispersing them away when the eddy moves on.

In Model 5, wind-induced upwelling occurs on the down-current side of an island. As early as 1933, upwelling was suggested as a mechanism that would contribute to coral reef productivity (Orr, 1933), and plumes of increased productivity due to upwelling have been shown on satellite images of the Galapagos Islands (Feldman *et al.*, 1984). Upwelled water may not penetrate reef waters (Brandon, 1973); the upwelling circulation pattern tends to advect water away from land by Ekman transport (*e.g.*, Stevenson *et al.*, 1974). Larvae released in upwelled waters therefore would tend to be carried away from the island in an upwelling plume.

In Model 6, downstream eddies with turbulent mixing of neritic and oceanic waters are created when persistent laminar flow is interrupted by an obstacle (Barkley, 1972; LaFond and LaFond, 1971; White, 1971), as often occurs near the Hawaiian Islands (reviewed by Chopra, 1973) and as may occur near Barbados (Emery, 1972). These eddies could retain larvae from the island (*e.g.*, Lobel and Robinson, 1983) or from sources up-current of the island, depending on where the eddies were formed (Hamner and Hauri, 1981). The temporal duration of such eddies depends on their energy; near Hawaii they dissipate in approximately two months while moving away from the islands at a translational velocity of about 6 cm/s (Chopra, 1973). Dispersal and retention will depend on cross-frontal mixing processes that advect larvae into and out of the eddy (Flierl and Wroblewski, 1985) as well as on the extent to which larvae are able to escape by swimming.

In summary, each model of ocean interaction with an island creates a dynamic pattern, which in turn affects the dispersal and retention of planktonic larvae. Retention of larvae in island waters may be associated with the events that restrict mixing between neritic and oceanic waters (Models 2 and 3: tidal plumes and seasonal convergence). Dispersal away from the island may be associated with the events that enhance mixing (Models 4 and 5: currents associated with an impinging mesoscale eddy and Ekman transport associated with upwelling). Either retention or dispersal, or both, may occur when neritic and oceanic waters are mixed but the mixed water mass is retained near the island (Model 6). More than one of these hydrodynamic events may occur simultaneously during the planktonic life of a cohort of larvae. For instance, local upwelling may occur on one side of the island while turbulent eddies occur on the other. In addition, a single event could act both to disperse and retain larvae, depending on the time of larval release, physical events, and the length of larval life relative to hydrographic events. Finally, a cohort of larvae could be subjected to many of these events during its planktonic phase, or to just one such event. The larval dispersal history of the island population will be evident in its genetic structure.

#### ISLAND BIOGEOGRAPHY, GENETIC STRUCTURE, AND EVOLUTION

Endemism is a special case of biogeography, genetic structure, and evolutionary patterns, and it is instructive to examine endemism with respect to oceanic islands. Factors influencing the degree of endemism on islands include:

1. Age of the island.
2. Geologic history affecting the island such as changes in sea level, climate, and circulation patterns.

3. Ecological constraints affecting physiological responses and tolerances of the organisms (Scheltema, 1986).
4. Life histories of island species, especially the dispersal characteristics of their larval stages (planktonic, non-planktonic, etc.).

For present purposes it can be assumed that the ecological conditions for perpetuation of the species are met. Of the remaining factors, the only factor that can be measured on a time scale shorter than eons is the life histories of island species and this factor needs to be examined with respect to the interplay between circulation patterns around islands and the dispersal and retention of eggs and larvae. A high degree of endemism on an island indicates that species have not overcome barriers to distribution whereas low endemism suggests that they have done so.

On the left end of the continuum in Figure 1 are conditions that lead to the dispersal of larvae away from the islands and the recruitment of juveniles from up-current sources, high gene flow among populations and over evolutionary time, low speciation rates, and widespread distribution (Scheltema, 1978). It is assumed that species with a wide geographic range necessarily have a gene flow great enough to offset differentiation by genetic drift (Scheltema, 1986). Hydrodynamic events in the ocean environment determine the rate of arrival of new recruits, not the reproductive output of local stock. Situations where success of larvae in the pelagic environment, rather than initial size of the larval pool, is critical to recruitment have been described by the early survival hypothesis of Hjort (1914) and the match-mismatch hypothesis of Cushing (1972). If larvae are dispersed away from the island and never return, the island population would be unlikely to develop new species because natural selection would act on genes constantly removed from the island. The high gene flow into the island would keep the population gene pool similar to its upstream sources. Endemism would not occur.

On the right hand side of the continuum (Figure 1) conditions have selected for the evolution of reproductive patterns that lead to the retention of larvae near islands, the recruitment of juveniles from these larvae, low gene flow, and the potential for speciation and consequent endemism. Recruitment rates will depend largely on size of the island stock (Ricker, 1954). The low gene flow to the island would keep the population gene pool distinct from its upstream sources; endemism could occur.

Examples approximating the conditions at both ends of the continuum can be found among oceanic islands. The islands of Bermuda may represent conditions toward the left end and the Hawaiian Islands, the right end.

The 22 small islands of Bermuda lie in the western North Atlantic, at 32° N, within the North Atlantic gyre, and within the "Gulf Stream ring corridor" where cold core rings dominate the circulation (Richardson, 1983), but not within or adjacent to the Gulf Stream itself. In 1975, during a nine-month period that included both breeding and recruitment seasons for many species (April—September), four Gulf Stream rings affected Bermuda waters (Hogg *et al.*, 1978). Although a seasonal convergence zone may occur around Bermuda (Boden, 1952), retaining larvae in local waters, the possibility clearly exists for recruitment from Gulf Stream rings, depending on the proportion of viable recruits delivered on the rings. Endemism is low in Bermuda among species with planktonic larvae (Briggs, 1976). Recruitment to Bermuda on irregularly occurring Gulf Stream rings would be expected, and such an irregularity appears

in the gastropod record of local extinctions and recoveries (Abbott and Jensen, 1967).

For species with short plankton periods, the role of rings in dispersal may not be very important, and endemism may develop over time. For example, electrophoretic-genetic data for the gastropod, *Strombus gigas*, indicates restricted gene flow between Caribbean and Bermuda populations (Berg *et al.*, 1983 and 1985). Also, for species with very long plankton periods, larvae dispersed away from the island may contribute to populations whose genes ultimately return to Bermuda. For example, the spiny lobster, *Panulirus argus*, has a planktonic life of approximately one year (Farmer *et al.*, 1989), a period of time that would allow wide dispersal within the Gulf Stream recirculation system.

Many coral reef species are endemic to the Hawaiian Islands (Banner, 1953; Kay, 1967; Lobel and Robinson, 1986). The Hawaiian Islands are located within the North Pacific gyre, extending from SE to NW between 18° N to about 29° N. Because they lie within the influence of trade winds, topographically generated eddies frequently are found in their wakes. Endemism suggests local recruitment and Hawaii's eddies may play a role in keeping planktonic larvae near the islands (Lobel and Robinson, 1983, 1986). Introduced species, however, have spread to other islands in the archipelago (Barlow, 1981) and inter-island dispersal evidently can occur. Many reef fish species have two annual peaks of spawning (*e.g.*, Munroe *et al.*, 1973), and in Hawaii these coincide with periods of weak currents and the presence of eddies. These fish continue to spawn throughout the year, however, and the possibility of both widely and locally dispersed larvae in varying proportions is possible (Barlow, 1981; Sale *et al.*, 1984). Thus, for some reef species, at least, the Hawaiian Archipelago seems to lie toward the right end of the continuum (Figure 1), with spawning strategies keyed to hydrographic features that tend to retain local larvae.

Clearly, whether larvae are widely or locally dispersed will depend on how reproductive patterns are linked to temporal and spatial scales of hydrographic changes. The linkage of scales is critical (Denman and Powell, 1984; Legendre and Demers, 1984; Tett and Edwards, 1984; Yentsch and Yentsch, 1984). Only those biological activities that are synchronized with, shorter in duration than, and smaller in size than a hydrographic event will be affected by that event (Denman and Powell, 1984; Legendre and Demers, 1984). For example, differences in temperature over a few vertical centimeters (Gregg and Sanford, 1980) may influence the rate of nutrient uptake of phytoplankton but will not affect the respiration of large fish. A mesoscale eddy hovering near an island for two months may retain larvae until they are ready to metamorphose if their planktonic phase is less than two months in duration, but cannot retain longer-lived larvae. Similarly, spatial and temporal patterns of larval release must also coincide with the presence of an eddy.

It is possible to formulate a null hypothesis in which hydrodynamic forces control larval dispersion, gene flow, and biogeographic distribution independent of patterns of release of larvae. The hypothesis can be stated in either of two ways:

1. Hydrodynamic features that tend either to restrict mixing between nearshore and oceanic waters or to trap mixed water near an island will retain larvae, resulting in low gene flow and species endemism.



2. Hydrographic effects that tend to enhance mixing between nearshore and oceanic waters will disperse larvae away from an island, resulting in high gene flow and a low degree of endemism.

Because each island exhibits its own hydrodynamic features, the null hypothesis can be tested by comparing islands inhabited by species demonstrating similar reproductive patterns but affected by different hydrodynamic events. Likewise, one could compare islands affected by similar hydrodynamics but inhabited by species with different reproductive patterns. A comparison of genetic structures of local populations, of larval recruits, and of plausible donor populations could lead to four possible scenarios that entail high gene flow:

1. High gene flow associated with no particular reproductive pattern but with hydrodynamic features that enhance mixing between neritic and oceanic waters would support the null hypothesis.
2. High gene flow associated with particular reproductive patterns but with either hydrodynamic features that enhance mixing or hydrodynamic features that reduce mixing between neritic and oceanic waters, or both, would not support the null hypothesis.
3. High gene flow associated with particular reproductive patterns and only with hydrodynamic features that reduce mixing between neritic and oceanic waters would falsify the null hypothesis.
4. High gene flow associated with particular reproductive patterns and with hydrodynamic features that enhance mixing between neritic and oceanic waters would neither support nor falsify the null hypothesis but would suggest a tight linkage between reproductive patterns and hydrodynamic processes. Analogous scenarios could be developed for low gene flows.

A rigorous test of the interaction between hydrodynamic features around islands and reproductive strategies would entail synoptic sampling of larvae from ships, detection of hydrodynamic events by satellite remote sensing, and the determination of the electrophoretic-genetic composition of larvae, island adults, and adults from up-current and down-current populations. Such a test would greatly enhance our understanding of biogeographic and evolutionary patterns.

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