

The temporal dimension of marine speciation

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Abstract Speciation is a process that occurs over time and, as such, can only be fully understood in an explicitly temporal context. Here we discuss three major consequences of speciation's extended duration. First, the dynamism of environmental change indicates that nascent species may experience repeated changes in population size, genetic diversity, and geographic distribution during their evolution. The present characteristics of species therefore represents a static snapshot of a single time point in a species' highly dynamic history, and impedes inferences about the strength of selection or the geography of speciation. Second, the process of speciation is open ended—ecological divergence may evolve in the space of a few generations while the fixation of genetic differences and traits that limit outcrossing may require thousands to millions of years to occur. As a result, speciation is only fully recognized long after it occurs, and short-lived species are difficult to discern. Third, the extinction of species or of clades provides a simple, under-appreciated, mechanism for the genetic, biogeographic, and behavioral 'gaps' between extant species. Extinction also leads to the systematic underestimation of the frequency of speciation and the overestimation of the duration of species formation. Hence, it is no surprise that a full understanding of speciation has been difficult to achieve. The modern synthesis—which united genetics, development, ecology, biogeography, and paleontology—greatly advanced the study of evolution. Here we argue that a similarly synthetic approach must be taken to further our understanding of the origin of species.

Keywords Evolution · Oceans · Global change · Sea-level · Speciation rate · Paleontology

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Introduction

As a result of training and experience, I also habitually thought in four dimensions, time being the fourth and being particularly paleontological. Thus the aim of this book, which I think it accomplished, was to bring this dimension squarely, methodologically, into the study of evolutionary theory. (pg xvi & xxii)

George Gaylord Simpson, preface to the 1984 edition of *Tempo and Mode in Evolution*

The origin of species remains the “mystery of mysteries” after 150 years of research, despite much progress on the topic of evolution (Erwin and Anstey 1995; Coyne and Orr 2004). It has long been recognized that speciation, as the process by which populations become genetically isolated, works on both an ecological and a “deep time” geological timescale not fully captured by any single evolutionary discipline (Simpson 1944; Jablonski 2008; Reznick and Ricklefs 2009). Further, the length of time, frequently >100,000 years, and the geographic and biological scope of speciation are so large as to encompass considerable environmental diversity in both space and time. Modern evolutionary biologists can study the mechanisms and processes involved in the isolation of populations (Brooks and McLennan 1991; Coyne and Orr 2004), but they cannot predict whether currently isolated populations will ultimately give rise to species or regain genetic connectivity, and they struggle to scale experimental laboratory results to understand speciation in nature. Comparative phylogenetic approaches to speciation are stymied by the inability to detect young or incipient species or to account for the effects of extinctions (Hickerson et al. 2006; Quental and Marshall 2010). Paleontologists likewise are limited by their use of morphologically defined species and the temporal and spatial resolution of fossils (Purvis 2008), with the time-steps between fossil horizons often spanning more time than any given speciation event (Norris 1999).

Speciation involves the reproductive isolation of populations leading to the formation of new species. As the mechanisms leading to the genetic isolation of populations—biological and geographic isolating barriers—are strengthened or maintained through time, we are increasingly likely to recognize species-level groups [described by Hendry (2009) as ‘states’ in the speciation process]. Consequentially, studies of speciation typically investigate the biological processes leading to and maintaining reproductive isolation and the geography of speciation; rarely is the temporal dimension of speciation directly examined.

Here, we consider three consequences of the long time frame of speciation—the role of environmental variability, problems with recognizing incipient species, and the importance of extinction in speciation. First, wholesale environmental change can alter the genetic diversity, selective regime, and geographic isolation of populations (detailed below in ‘The Landscape of Marine Speciation’). Second, the duration of speciation also implies that short-lived, young species will often go unrecognized in the fossil and modern record due to under-sampling, morphospecies concepts, and the time necessary to accumulate genetic differences. Third, local and global extinction acts to increase the separation between groups of taxa by creating gaps in geographic ranges and reducing cross-breeding between nascent species. Extinction also increases the morphological and ecological distinctiveness of surviving species in our taxonomies. Historical contingency and environmental change—the set of events that have persistent effects on ecosystem structure and species characteristics—constantly shift the stage on which speciation occurs over time (Jackson et al. 2009).

In this paper, we focus primarily on speciation in the marine environment, due to the utility of marine fossils for addressing historical phenomena. Coastal basins can record evolutionary and ecological dynamics with high fidelity, although we are likely to always have problems resolving a detailed fossil record in rocky intertidal communities and other areas of net erosion (e.g. Baumgartner et al. 1992; Kidwell and Flessa 1995; Moy et al. 2002; Barron et al. 2009, 2010). High-resolution fossil records allow for the direct assessment of how the composition of communities and the ecology of species changed over time as well as of the tempo and pattern of evolution (Jackson and Cheetham 1999; Jackson and Williams 2004; Hadly et al. 2009). We can also reconstruct matching records of marine environmental evolution in great detail (e.g. Moy et al. 2002; Barron and Bukry 2007; Agnihotri et al. 2008). Together, marine fossil and environmental records provide a window for understanding the interaction between species and ecosystems under varying selective regimes (Dynesius and Jansson 2000; Jacobs et al. 2004; Guttal and Jayaprakash 2008; Lenton et al. 2008).

A historical view of speciation

Mechanisms and sequence of speciation

Species are typically discussed in the context of the *biological species concept*, which states that “Species are groups of interbreeding natural populations that are reproductively isolated from other such groups” (Mayr 1995, p. 5). Mayr defined the mechanisms of reproductive isolation as those biological processes involving “pre-zygotic” and “post-zygotic” barriers that restrict or prevent either fertilization or the development and reproductive viability of offspring, respectively (Mayr 1942; Coyne and Orr 2004). The restriction of isolating barriers to biological features of organisms—purposefully excluding geographic isolation—has been widely accepted by subsequent evolutionary biologists and shapes both the study and the perception of speciation.

Here we return to Dobzhansky’s original description of isolating barriers (Dobzhansky 1937) which includes both geographic and biological mechanisms (Fig. 1), as was recently revived by Sobel et al. (2010). The geographic and biological elements of speciation can be visualized as the changing balance of isolating mechanisms between two populations over time. In our example (Fig. 1), a population is genetically isolated at time t_0 by geography, which could result from processes like vicariant events or chance long-distance dispersal. At time t_{0+T} the population comes into sympatry with a close relative (geographic isolation is lost) and rapidly acquires pre-zygotic barriers to mating such as differences in ecology or mate-recognition systems. Later in our example, at time t_{0+2T} , the populations shift to a parapatric distribution (partial overlapping populations), with the strength of post-zygotic isolation gradually increasing through time. In the example (Fig. 1), environmental change could act as driver of variation along the geographic and pre-zygotic axes, forcing changes in species distributions and population sizes.

The relative strength of biological and geographical isolating mechanisms can vary over the course of speciation and between differing modes of speciation (Fig. 2). Figure 2a illustrates allopatric speciation as Mayr (1963) envisioned it where biological isolation (thin grey line) is always less than or equal to the isolation produced by the combined forces of biological and geographic isolating processes (thick grey line). In Fig. 2a, two populations become geographically isolated. During this period of geographic isolation, barriers to gene flow begin to accumulate. Gene flow is prevented during secondary

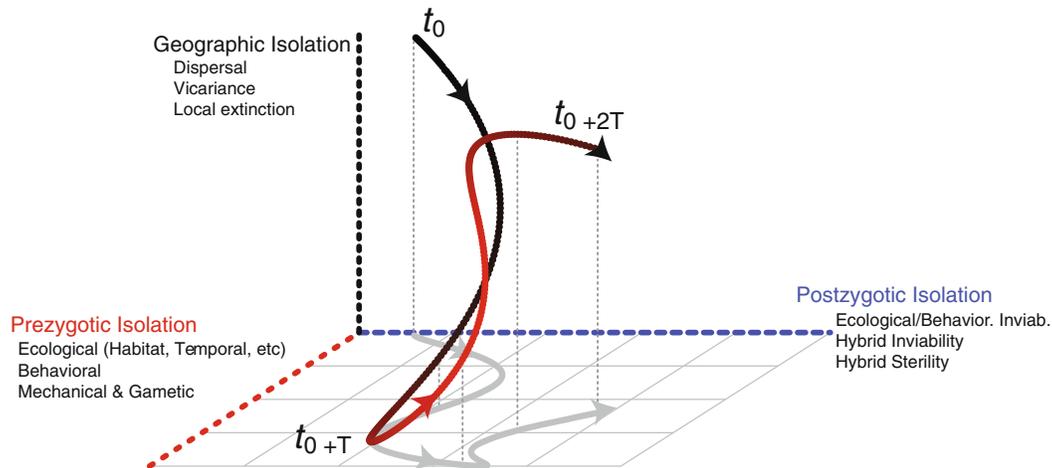


Fig. 1 Temporal variation in isolating barriers. Model of the shifting balance of mechanisms causing genetic isolation between two populations over time (*Heavy black line*). Biological isolating mechanisms include pre-zygotic and post-zygotic isolation (specific examples of each listed on figure). At time t_0 , gene flow is largely prevented by geographic isolation. Consideration of just biological isolation mechanisms (*grey shadow line*) gives a false impression that populations are relatively well connected at this time. Later times (t_{0+T} and t_{0+2T}) catch the evolving population in a state of sympatry and, later, parapatry with near relatives

sympatry of the two partially isolated populations by the rapid accumulation of pre- and post-zygotic barriers to speciation. Mayr recognized two species at the point where biological isolation (summed pre- and post-zygotic isolation) prevents appreciable gene flow (S_{bio}). However, if geographic barriers are included, the point of speciation (or no genetic exchange) occurs earlier (S_{total}). Figure 2b illustrates parapatric speciation, where genetic isolation is achieved early by a combination of geographic and biological isolation. Species may be slow to develop pre-zygotic barriers to hybridization if they remain in “splendid isolation” from near relatives, as illustrated by in Fig. 2b (thin grey solid line). Sympatric speciation necessitates the rapid accumulation biological barriers to mating in the absence of geographic isolation (Fig. 2c). Theoretically, speciation in sympatry readily occurs when sexual selection favors ecological adaptations that keep populations apart; in sympatry, pre-zygotic isolation is predicted to be fast relative to post-zygotic isolation. In all figures, the wide shaded band indicates the time needed between genetic isolation and the accumulation of genetic differences, allowing for the genetic recognition of species.

Extinction provides a historical mechanism that is not typically considered as a constructive force in speciation. However, from a historical perspective, extinction is a key source of species differences. As Raup (1994) puts it, “for an evolutionary biologist to ignore extinction is about as foolhardy as for a demographer to ignore mortality.” In the case of populations (local extinction), the removal of geographically, ecologically, sexually, or morphologically intermediate populations eliminates close relatives that are likely to be able to hybridize with a nascent species. At both the population-level and species-level (species extinction), the loss of intermediate groups makes those remaining appear more different (phylogenetically, ecologically, etc.). Thus, extinction creates the gaps and discontinuities between groups of organisms at the sub- to supraspecific level, and can explain “[t]he manifest tendency of life toward formation of discrete arrays...” (Dobzhansky 1937).

Consider the phylogeography of killer whales (Morin et al. 2010). Whole mitochondrial genomes show that killer whales can be subdivided into at least eight groups, four of which

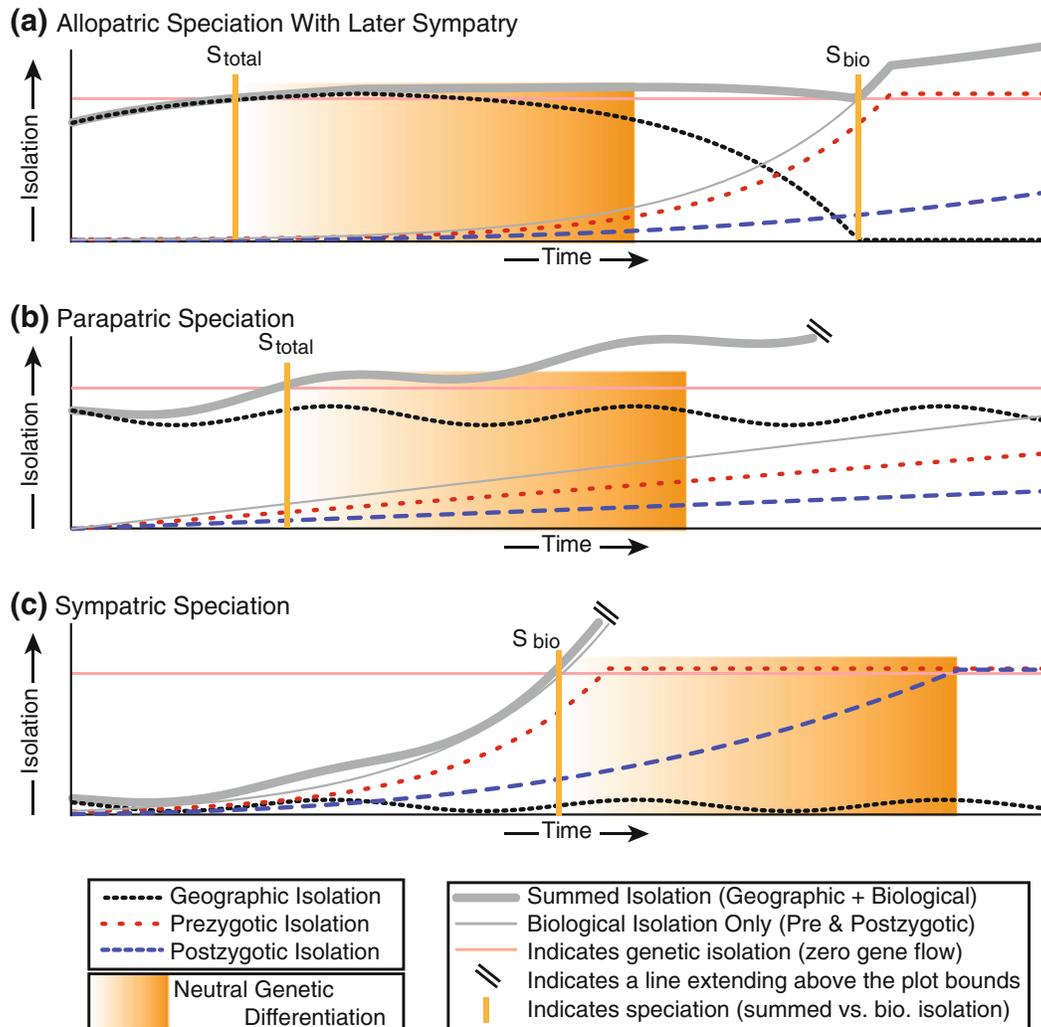


Fig. 2 Summed effect of isolation barriers. Models of **a** allopatric speciation **b** parapatric speciation, and **c** sympatric speciation as the summed effect of isolating mechanisms over time. Speciation, defined as the point of reproductive isolation (S_{total} , at the intersection of summed isolation—*thick grey line*—and zero gene exchange between two populations—*upper horizontal line*), occurs earlier in the time sequence when geography is isolating (**a**, **b**, *dotted black line*) than when biological mechanisms alone are considered (S_{bio} , *upper horizontal line*). Biological species (*vertical line* marked by S_{bio}) appear when biological isolation (*thin grey line*) intersects with and zero gene exchange between two populations (*upper horizontal line*). In some cases, like the parapatric model (**b**) shown, speciation is a drawn-out process due to the slow accumulation of genetic isolating factors

are currently given species-level status (Fig. 3a). These include populations that differ in their biogeography (inshore, offshore, Atlantic, Southern Ocean, etc.), morphology (coloration, body size), and behavior (hunting mammals, fish, living in pack ice, etc....) (Leduc et al. 2008; Morin et al. 2010). All the clades are typically quite small—several hundred to perhaps a few 1,000 individuals.

Were extinction to eliminate one or more of these genetically and behaviorally recognized killer whale clades what would be the result? The remaining clades, particularly sisters to the now extinct group, would appear to be more distinctive than they are now (Fig. 3b). There would be deeper genetic distinctions between the remaining groups. The apparent divergence times between the remaining sister groups would also grow (Monroe

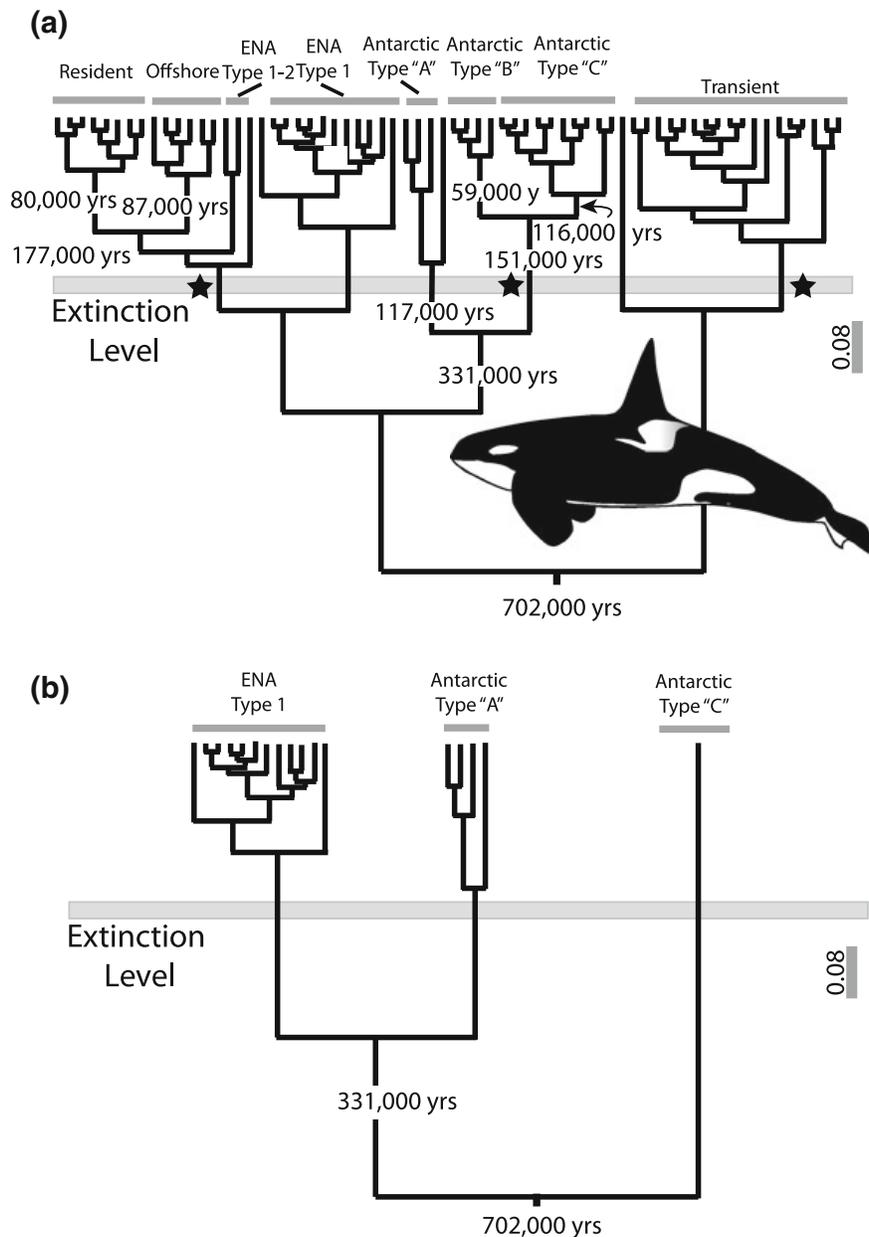


Fig. 3 Effect of extinction on the distinctiveness of populations. **a** Whole mitochondrial genome phylogeography of killer whales shows at least eight distinctive phylogenetic groups (Morin et al. 2010). Median times to the most recent common ancestor shown on some nodes. **b** Same phylogeography removing the clades in **a** marked with stars. Extinction creates long branch lengths and deep divisions between the remaining living groups. Geographic and ecological distinctions may also be amplified by extinction, increasing the likelihood that living groups will be recognized as species

and Bokma 2010). Their biogeography might include larger gaps. In short, we would be more likely to recognize the living clades as discrete species. These expectations match theoretical models of phylogenetic patterns (Rabosky 2010).

Although fossil data are useful for calibrating molecular phylogenies, a better fossil record is unlikely to completely fill in the missing data produced by extinction. The problem is that the determination of the geography and rates of speciation requires the

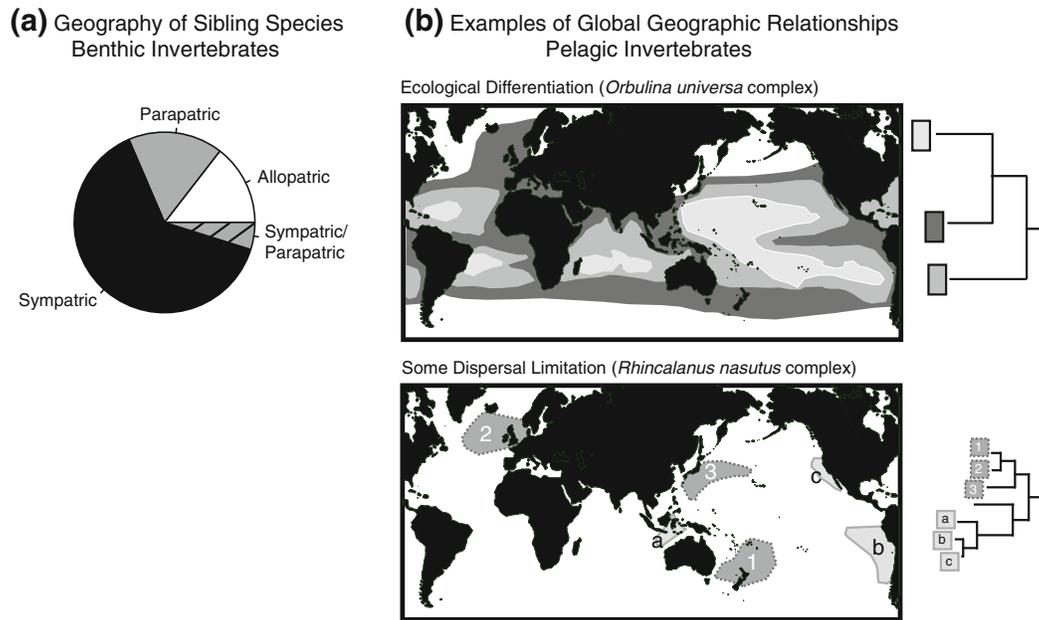


Fig. 4 Geography of marine speciation. **a** The geographic relationships of sibling species of benthic invertebrates taken from Knowlton (1993) round to 64% sympatric, 17% parapatric, 5% mixed sympatric/parapatric, and 15% allopatric among the 124 taxa studied. **b** Examples of global geographic relationships of pelagic invertebrates, including (**b, top panel**) ecological differentiation in the *Orbulina universa* complex after de Vargas et al. (1999) and (**b, bottom panel**) some evidence for dispersal limitation in the *Rhinocalanus nasutus* complex (Goetze 2003); branches in **b** schematized with letters and numbers for the sake of simplicity

reliable recognition of populations and species—particularly the number and geographic deployment of distinctive populations and nascent species within larger established species. If nascent species have small populations and look broadly like the numerically dominant species, the problem of recognizing speciation in fossils becomes large.

Geography of marine speciation

Allopatric speciation is typically considered the dominant geographic mode of speciation, given the relative ease of evolving unique ecological, behavioral, and sexual adaptations in the absence of gene flow. However, there is growing theoretical and empirical support for sympatric speciation (Dieckmann and Doebeli 1999; Gavrillets et al. 2000; Via 2001; Mallet et al. 2009; Crow et al. 2010; Elmer et al. 2010). In the marine realm, the primacy of allopatric speciation has long been questioned due to the relatively large ranges and high dispersal potential of marine species (Rapoport 1994; Kinlan and Gaines 2003; Palumbi 2004).

For instance, Knowlton's (1993) compilation of sibling species pairs supports the clear dominance of sympatric and parapatric speciation in benthic marine invertebrates (Fig. 4a). Knowlton noted the overwhelming dominance of sympatric sibling species pairs (64%) although she went on to argue that these may reflect a bias towards the detection of sibling species in sympatry rather than allopatry. More recently, cryptic species have been identified within many globally distributed marine taxa and provide examples of the varying role of geography in speciation. For example, one species of planktonic

foraminifera (*Orbulina universa*) was found to consist of three cryptic species separated by ecology into adjacent habitats on a global scale (Fig. 4b top; de Vargas et al. 1999). In another case, a species of copepod was found to harbor six cryptic species with evidence for geographic speciation (Fig. 4b bottom, specifically in the clade a–c; (Goetze 2003).

Numerous studies of dispersal and population genetics have shown evidence of geographic population structure and dispersal limitation (Palumbi and Warner 2003; Palumbi 2004). Gene flow within coastal taxa often shows evidence of dispersal-limitation by geographic and/or oceanographic barriers (Keever et al. 2009; Kelly and Palumbi 2010). Indeed, evidence for vicariant speciation also abounds in regions like the Isthmus of Panama and Baja California (Bernardi et al. 2003). Behavior appears to be an important factor driving the geographic structure in marine populations. For instance, population structure in sharks and whales may be driven by philopatry (Palumbi and Baker 1994; Heist et al. 1996; Pardini et al. 2001).

Differences in environmental preferences in closely related species can also result in very different geographic distribution patterns. Two sibling species of subtropical, open ocean copepods have distinctly different patterns of population connectivity in spite of being found throughout the world's oceans in highly similar habitats (Goetze 2005). Dispersal under different environmental conditions, sea levels, water mass proximity, and chance also contribute to marine species ranges and genetic structure (Brinton 1962; Benzie and Williams 1997; Palumbi et al. 1997; Benzie 1999). For example, species and population structure in the coastal, shallow-dwelling lemon shark, *Negaprion*, is correlated with distance along the 200 m isobath rather than by geographic proximity (Feldheim et al. 2001; Schultz et al. 2008).

Studies of speciation have often gotten caught up in debate about the importance of present-day geographic patterns (Butlin et al. 2008; Johannesson 2009), and may underappreciate the potential for large changes in biogeography during the course of speciation due to climatic shifts (Hewitt 2000a; Hofreiter and Stewart 2009). The abundance of marine cyptic taxa with overlapping distributions suggests that marine speciation may frequently proceed in a parapatric or sympatric mode as is seen along continental margins (Hellberg 1998). On the other hand, benthic invertebrates associated with islands commonly display evidence of allopatric or founder speciation (Paulay and Meyer 2002; Meyer et al. 2005; Frey 2010; Malay and Paulay 2010b) which, in some cases, developed secondarily into sympatric distributions (Paulay and Meyer 2002).

Time scale of speciation

How long does it take for populations to become recognizable as species? The timing of speciation can be described with two metrics: (1) the rate of *establishment of reproductive isolation by any given mechanism*, and (2) the *duration of the entire speciation process* (Fig. 5). For example, ecological differentiation can clearly be very fast—perhaps only 10 or 15 generations to establish partial reproductive separation (Schluter 2000; Hendry et al. 2007). Genetic, post-mating barriers are believed to develop more slowly—perhaps in several 1,000 generations, if at all (Gavrilets and Vose 2005). Most estimates of speciation rates suggest that species form over 100,000 years or even millions of years (Coyne and Orr 2004), although these are acknowledged upper limits based largely on time since divergence of sister species.

Estimates of speciation rates are commonly longer than the actual duration of speciation. Three problems with determining evolutionary rates are that:

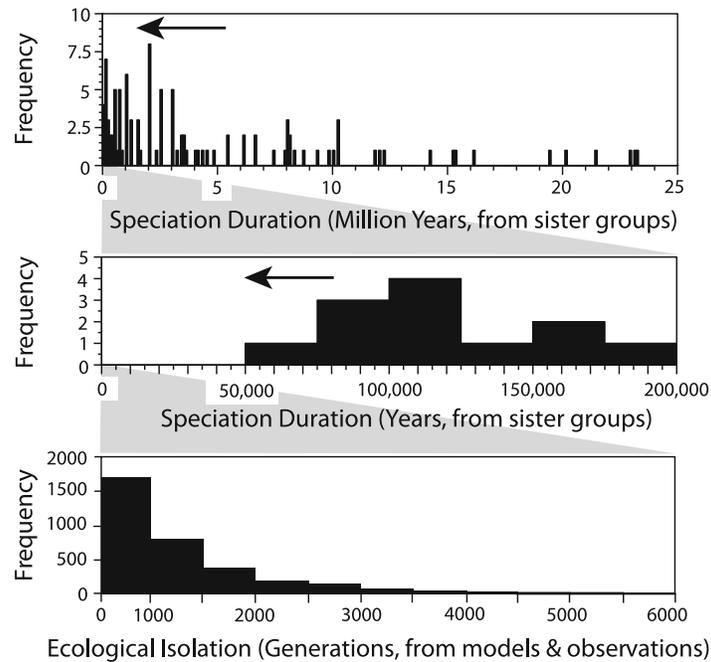


Fig. 5 Estimates of the duration of speciation. *Top and middle panels* present durations of speciation based upon divergence times of sister groups of marine taxa from recent molecular phylogenies (*top panel* in millions of years, *middle panel* in years). *Arrows* indicate that estimates are likely too long due to unrecognized extinction or inadequate sampling of living populations. *Bottom panel* shows estimates of the number of generations needed to acquire ecological isolation of populations based upon models and observations. Data derived from phylogenies of killer whales (Morin et al. 2010), sea stars (Foltz et al. 2008), neritid snails (Frey and Vermeij 2008), *Nacella* limpets (Gonzalez-Wevar et al. 2010), dolphins (Hare et al. 2002), hermit crabs (Malay and Paulay 2010a), and *Acar* bivalves (Marko and Moran 2009) as well as models (Gavrilets and Vose 2005) and observations (Hendry et al. 2007; Sadedin et al. 2009)

1. Modern species may not be recognized because they have not had the time to accumulate the genetic differences that are typically used to recognize species even though they are reproductively isolated and may have distinctive ecology, distributions and behavior.
2. We may fail to recognize actual sister-group relationships in molecular phylogenies because one of the sisters is extinct.
3. We may fail to recognize extinct sister groups because they were short-lived, had small populations, or were morphological indistinct.

For instance, it is likely that the duration of speciation is overestimated while the frequency of speciation (speciation events/time) is underestimated due to the presence of unrecognized cryptic species (Alizon et al. 2008). A study of geminate pairs of “sister taxa” of bivalves on either side of the Panama Isthmus showed that these species were actually composed of a series of cryptic species (Marko and Moran 2009), leading to the underestimation of the number and frequency of speciation events. Another example of the impact of incorrectly identified sister taxa on the study of speciation is the supposed Panamanian geminate pairs of seabass. These fish, upon molecular study, turned out to have nearest relatives in SE Asia—and apparently are not sister groups at all (Craig et al. 2007)! A paleontological issue for estimating the duration and frequency of speciation is the tendency to lump short-lived taxa into long-lived groups. This bias against recognition

of short-lived species is often compounded by low sampling resolution, small population size, and morphological similarity to more abundant taxa.

The *initial establishment of reproductive isolation* has been investigated with theory and with observation. Gavrillets and Vose (2005) investigated the formation of ecotypes in models of adaptive radiations and concluded that 98% of the time isolation was substantially established within 10,000 generations, and about 50% of model runs developed isolation within 1,000 generations (Fig. 5). These numbers are broadly in accord with the divergence times of ecotypes of the intertidal periwinkle, *Littorina*, which develop isolation between populations on exposed rocks and those in sheltered crevices in about 1,000 generations (Sadedin et al. 2009; Johannesson et al. 2010). Genetically isolated ecotypes are generally not recognized as species until they display some sort of persistence or accumulate a number of ecological, morphological, and behaviorally distinctive traits. However, given that the biological species concept is only defined for the present day, how long an ecotype must persist in order to be recognized as a species is an open question.

Conventionally, the *duration of full speciation* is estimated as the time since divergence of sibling species pairs, and is thought to range between approximately 80 thousand and 5.5-million years (Coyne and Orr 2004, p. 421, Table 12.1). In the ocean fossil record, morphological speciation of bryozoans, planktonic foraminifera, radiolarians, calcareous nanofossils, and diatoms has been documented to occur over 100,000 years to >1 million years (Jackson and Cheetham 1999; Norris 2000; Benton and Pearson 2001; Alizon et al. 2008). These durations are probably overestimates due to the presence of unrecognized sibling species (Alizon et al. 2008) and low-resolution sampling. For example, in a recent study, Hull and Norris (2009) showed that a species of planktonic foraminifera appears within a 44,000 year interval whereas previous studies (Malmgren et al. 1983) had suggested speciation required about 500,000 years. The difference in estimated duration reflects a previously unrecognized intermediate species that persists for at least 414,000 years.

Other examples of relatively rapid speciation are known from both fossils and genetic phylogenies. Meticulous study of Caribbean bryozoans using genetics and morphology reveals punctuated morphological shifts coincident with speciation, with species typically appearing in less than 160,000 years and then surviving for millions of years (Cheetham 1986; Jackson and Cheetham 1994). Analysis of the full mitochondrial phylogeny of killer whales (mentioned earlier, Fig. 3a) shows that several distinctive clades, recognized as species on the basis of genetics, behavior, ecology, and morphology, diverged from their sister groups as recently as 59,000 years ago (Morin et al. 2010). Of course, the actual duration of speciation must have been much shorter than this given that species persist after the speciation event. Classic examples of adaptive radiations document much faster rates of speciation, including the evolution of 500 cichlid species over 100,000 years in Lake Victoria (Kuraku and Meyer 2008).

Evidence for rapid speciation satisfies one of the criteria for the much debated pattern of punctuated equilibrium, the paleontological observation that speciation is commonly geologically rapid and is followed by “stasis” in which there is little or no directional morphological change (Eldredge and Gould 1972). Punctuated equilibrium was originally formulated to contrast with “anagenetic evolution” in which species are said to continually track environmental change leading to constant morphological evolution. Furthermore, the “punctuated” appearance of species in the fossil record was advanced as evidence for allopatric speciation on the theory that speciation would be nearly invisible in the geologic record until peripheral isolates became sufficiently well established to spread outside their place of origin (Eldredge and Gould 1972; Gould and Eldredge 1977). However, while the

“punctuated” pattern undoubtedly occurs (e.g. Kelley 1983; Cheetham 1986; Stanley and Yang 1987; Wei and Kennett 1988; Sorhannus 1990; Norris et al. 1996; Benton and Pearson 2001; Hull and Norris 2009), we are dubious about claims that the pattern of abrupt speciation and stasis reflects a specific evolutionary process. By our reckoning, all the classic modes of speciation—allopatry, parapatry and sympatry—operate on time scales that are compatible with the “rapid speciation” criterion of punctuated equilibrium as long as reproductive isolation, if not the emergence of full post-zygotic barriers to crossing, is established in the space of less than a few tens of thousands of years. Most geological examples of punctuated equilibrium are not sampled at temporal resolutions finer than 10,000–50,000 years and so are incapable of resolving most rates of speciation seen in this review.

The second claim of “stasis” in punctuated equilibrium suggests that species do not track environmental change with continuous morphological evolution after they appear (Eldredge and Gould 1972; Sheldon 1996; Hunt 2010; Monroe and Bokma 2010; Weiss 2011). There certainly are examples of stasis in the fossil record, but their significance for evolutionary process is also open to question (Monroe and Bokma 2010). Stasis could reflect homeostatic processes such as niche conservatism or stabilizing selection that restrict the range of evolutionary responses of species once they have evolved (as discussed by Monroe and Bokma 2010). However, stasis might also reflect conservatism of skeletal evolution while other traits evolve more rapidly.

Yet another possibility is that stasis represents an artifact of the failure to recognize a series of cryptic species. For example, we might be tempted to describe the 15 million year longevity of the foraminifer, *Orbulina*, as an example of stasis until we realize that this morphospecies is composed of at least three living cryptic taxa that diverge 6–12 million years ago (Morard et al. 2009), and additional fossil taxa that must have existed before 12 million years ago. It seems that *Orbulina* has continued to spin off new species through its history in defiance of the expectation of “stasis” even while remaining morphologically conservative as a clade. Hence, in a modern context, punctuated equilibrium is primarily important for denying that anagenesis is the dominant pattern of morphological evolution but neither the rate of species formation nor the processes that govern subsequent morphological stasis are uniquely described by any particular mechanism.

The landscape of marine speciation

The oceanic fossil record makes three key points for a discussion of speciation. First, the constancy of environmental change means that populations rarely see the same ecological context over their history of transformation into new species. Instead, speciation plays out amid a shifting fabric of community structure and environmental conditions. Second, climate cycles can force many incipient species through numerous environmental filters that affect their genetic structure and geographic distributions (Jacobs et al. 2004). For instance, population genetics provides evidence of recent bottlenecks related to Quaternary glaciations (Hewitt 2000b; Hoelzel et al. 2002; Schultz et al. 2008). Similarly, ancient DNA has revealed large changes in population size and distributions in Pleistocene mammals (Lister and Stuart 2008; Hofreiter and Stewart 2009), which are not captured by modern population genetic structure. Third, local and regional extinction is a common process, as is recognized by biogeographers (e.g., Gaston 1998). The extirpation of populations can lead to biogeographic range shifts, changes in genetic diversity, and the loss of sister taxa that are difficult to reconstruct from observations of living organisms.

A study of the evolution of Antarctic sea slugs (*Doris*) is a case in point (Wilson et al. 2009). These nudibranchs live on sponges and are found around the Antarctic continent, southern South America and islands in the Southern Ocean. Genetic assays show that there is considerable diversity in modern sympatric populations and that genetically distinctive clades can be widespread. Wilson et al. hypothesize that high local diversity developed through the repeated geographic isolation of populations due to Plio-Pleistocene glacial cycles in Antarctica. The current genetic diversity and distribution of distinctive clades of Antarctic nudibranchs are a product of a dynamic history of differentiation, dispersal and likely extinction as well.

The constancy of environmental change

Paleoclimatology and paleoecology record the dynamism of environmental change. The variability of the natural environment is illustrated in long, annually resolved climatologies from sediments in lakes and the ocean (Fig. 6). These records are based upon changes in sediment color that reflect changes in local rainfall and biological production. The lake record from coastal Ecuador (Fig. 6a) shows the well developed signature of +1,000 year bundles of frequent and intense El Niño cycles, particularly in the past 7,000 years (Moy et al. 2002). In contrast, the marine record from offshore Venezuela (Fig. 6b) shows that the last glacial period had much more variable climate than the comparatively stable last 10,000 years (Hughen et al. 2000). In a microevolutionary context, multiple effects of high frequency climatic oscillations have been observed Darwin's Finches, with El Niño cycles affecting mean beak morphology (Boag and Grant 1981), population isolation (Grant and Grant 1983), hybridization (Grant and Grant 1993), and character divergence (Grant and Grant 2006).

Climate variation, like that indicated in sediment cores (Fig. 6), is well known to have major effects on coastal and oceanic ecosystems. For example, historical observations of salmon runs along the west coast of North America demonstrate that fish abundance varies

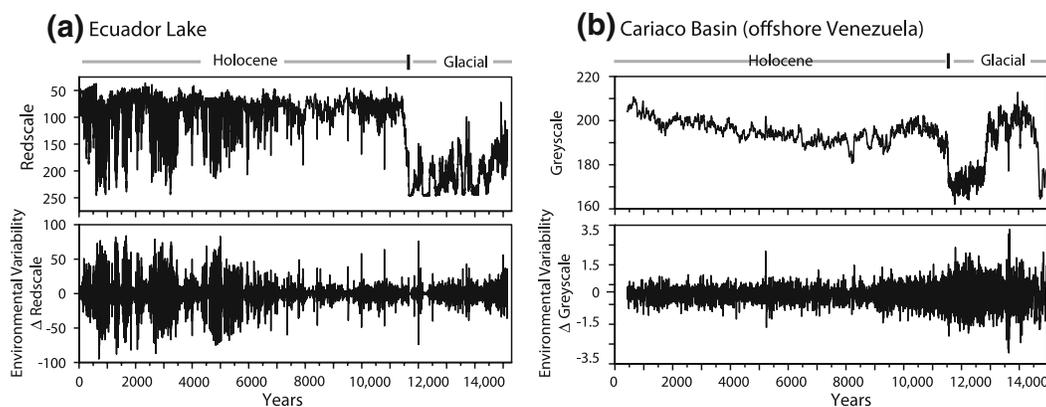


Fig. 6 Changes in annual to millennial environmental variability. Data for **a** an Ecuadorian lake (Moy et al. 2002), and **b** a marine basin off Venezuela (Hughen et al. 2000). Both records reflect changes in color of sediment cores over the past 15,000 years (*top panels*) that are due to variations in coastal climate, runoff, and land vegetation cover. Estimates of year-to-year variability in both settings are calculated (*lower panels*) by subtracting the color level from any given year from the previous year's color level. The Ecuador lake record reveals ~1,000 year long cycles of el Niño-driven variations in precipitation. The Venezuela record displays high inter-annual variation in climate variability (also reflecting coastal runoff) during the terminal phases of the last glacial period. Both records suggest that species must deal with substantial environmental heterogeneity over the 1,000's to 100,000's of years during which speciation takes place

on a multi-decadal cycle—the Pacific Decadal Oscillation (Mantua et al. 1997; Lehodey et al. 2006; Alheit and Bakun 2010). The Pacific Decadal Oscillation regulates the amount of runoff in coastal rivers that nurture young fish fry and also modulates the strength and location of upwelling that feed fish at sea. Decadal climate cycles can have significant impacts on recruitment and juvenile survivorship (Ruttenberg 2000). Indeed, climatological changes occur on ecologically relevant time scales and can produce abrupt “tipping-point” behavior in ecosystems (Hsieh et al. 2005; Lenton et al. 2008; Scheffer et al. 2009).

Decadal-scale climate changes are overlain on still longer climate oscillations from centuries to millennia and more. Studies of tree ring records, coral growth rates, and annually laminated marine sediments have illuminated the impact of century-scale climate change on marine ecosystems (Field et al. 2006; Cobb et al. 2008; Carilli et al. 2009, 2010; Nurhati et al. 2009). For instance, the abundance of fish scales in annually layered marine sediments show century-scale cycles in sardine and anchovy abundance off central California (Baumgartner et al. 1992). The cycles in fish abundance reflect regular, major changes in coastal ecosystems that play out on longer time scales than most ecological observations (MacCall 1996; Finney et al. 2010). Still longer-period orbital cycles (with time scales of 20,000 years or more) include major changes in sea level, with attendant shifts in the distribution and connectivity of coastal and benthic marine ecosystems (Dynesius and Jansson 2000; Jansson and Dynesius 2002). Together, climatic oscillations on decadal to millennial scales have the potential to alter all aspects of species’ selective regimes including ecology, behavior, and population size, resulting in the reinforcement or loss of incipient species (Siepielski et al. 2009).

Repeated cycles in habitat assembly and fragmentation

Speciation occurs on long enough time scales that processes of speciation encompass changes in habitat distribution due to orbitally forced climate change and sea level variations, like those during the Pleistocene (Fig. 7). During the last glacial maximum, sea level was 120 m lower than today (Miller et al. 2005; Peltier and Fairbanks 2006). In the Gulf of Mexico, the width of the modern inner shelf (down to 50 m water depth) is more than twice that of the shelf during a sea level drop of >50 m (Fig. 7a). Such sea level falls occur numerous times during each of the large glacial-interglacial cycles in the Pleistocene (Lambeck and Chappell 2001; Miller et al. 2005). An even larger reduction in shelf area accompanies the >100 m drop in sea level (Fig. 7a) during the last glacial maximum (~26,000 years ago; (Peltier and Fairbanks 2006). Similar reductions in shelf area are associated with sea level change in the southern Pacific (Hanebuth et al. 2009) as exemplified by the Gulf of Carpentaria between Australia and Papua New Guinea (Fig. 7b). Hence, it seems likely that coastal benthic communities have been exposed to large changes in habitat area, distributions, and connectivity on several 1,000-year time scales (Rocha 2003) that easily fall within the timescale of speciation.

A drop in sea level would expose the continental shelves, restricting most shallow marine benthic habitats to a narrow strip along the upper continental slope (Jacobs et al. 2004; Siddall et al. 2010) and eliminate populations whose range shifts are inhibited by geography (Grant and Bowen 2006). Atolls would lose their lagoons and reef systems would exchange their broad shelves for narrow, high-gradient margins. Estuaries and broad lowland wetlands would also be restricted to small patches on otherwise high gradient coastlines.

Such dramatic changes in the size of coastal habitats seem likely to have produced massive changes in population sizes and connectivity of benthic species (De Bruyn and

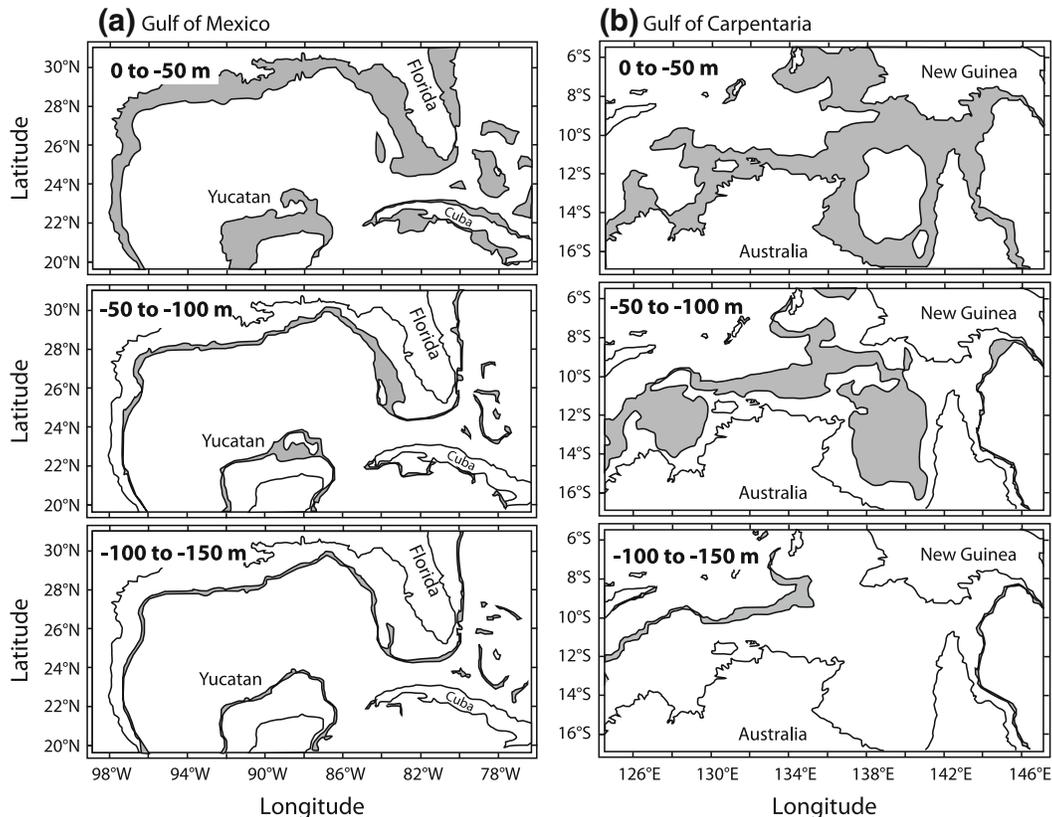


Fig. 7 Effects of sea level on habitat area of shallow marine taxa. **a** The Gulf of Mexico, and **b** the Gulf of Carpentaria. *Top panels* in **a** and **b** show present distribution of coastal areas less than 50 m depth. As sea level falls -50 m (*middle panels*) and -100 m (*bottom panels*), shallow marine habitat contracts dramatically to a thin strip along the continental margin. Sea level fell below -120 m during the full glacial periods during each of the last glacial stages. Frequent low sea level stands suggest that many coastal species interactions were confined to a narrow ribbon during 90% of the last 100,000 years. Bathymetric data from <http://iridl.ldeo.columbia.edu/SOURCES/WORLDBATH/bath/html+viewer?>

Mather 2007), particularly those restricted to disappearing habitats. Glacial cycles are also associated with major temperature variations including a $\sim 5^{\circ}\text{C}$ decrease in tropical sea surface temperatures during the last glacial maximum (Waelbroeck et al. 2009; Shakun and Carlson 2010). Hence, the narrow continental slope intertidal communities formed during sea level low stands would also have to accommodate considerable migration of species attempting to reach thermal optima (Maggs et al. 2008). The restriction of species migration to a few narrow corridors along continental margins is likely to have produced even more severe limitations on dispersal pathways than for most terrestrial organisms.

While speciation could occur during these climate cycles (Dawson and Hamner 2005; Foltz et al. 2008; Wilson et al. 2009), incipient species might also be hybridized out of existence during the next cycle. Indeed, Cronin (1985) and Cronin and Raymo (1997) hypothesized as much, arguing that the apparent lack of speciation in Pleistocene deep sea ostracodes was a reflection of repeated destruction of incipient species by climate cycles. Other studies have also found little Pleistocene amplification of evolutionary rates in rocky substrate faunas (Williams and Reid 2004) or coral reef fish (Rocha and Bowen 2008).

The superposition of different scales of climatic variation on species suggests that oceanic community structure can shift in taxonomic composition and dominance over the

history of any given species or speciation event. Species may repeatedly become assembled into “no-analog” communities when taxa that do not presently co-occur are brought together by environmental conditions which have no modern counterpart (Jackson and Williams 2004). Such non-analog communities are well known from late glacial forest and mammalian assemblages (Jackson and Williams 2004; Graham 2005) and oceanic microfossil assemblages (Cannariato et al. 1999; Mix et al. 1999; Kitamura 2004). The presence of non-analog assemblages suggests that the selective regimes of incipient species may repeatedly shift far out of observed modern conditions.

Indeed, analyses of community similarity in fossil plankton show that repeated climate cycles result in the iterative reassembly of oceanic communities with differing community structure (Fig. 8). For instance, we have long fossil records for a group of fossil calcareous algae—the discoasters—that show that oceanic communities repeatedly experienced a wide range of selective environments that only occasionally approached modern conditions. A 1 million year record from a North Atlantic drill core shows that the similarity of discoaster communities to the initial community structure ranged from almost identical (100% similar) to a similarity of just 40% (Fig. 8a, b, data from Chepstow-Lusty 1989). In addition, a comparison of discoaster community similarity in different oceanic sites shows that during some times community structure is nearly identical throughout the North Atlantic (Total cross-site pairwise similarity = 10, Fig. 8c) while at other times the same sites differed almost completely in community composition. These results echo those for a foraminiferal community where populations in the tropical North Atlantic were only rarely more than 85% similar to modern populations between 400 and 900 thousand years (Cullen and Curry 1997). This modest level of community repeatability suggests that the ecological landscape seen by incipient species can deviate significantly from modern configurations.

Does the discoaster record reflect a larger truth about the frequency of variability in marine ecosystem composition? There are few examples as long and continuous as open ocean microfossil records, but there is little question that many marine ecosystems are highly dynamic. Shell middens in coastal California, for example, show that invertebrate assemblages shifted from those dominated by hard substrate animals to infaunal sandy-bottom assemblages during the mid Holocene ~3,000 years ago (Graham et al. 2003). This ecological shift is interpreted as the result of rising sea level that initially created rocky or gravel-dominated coastal environments by trapping sand in flooded river channels. In contrast, there are some examples suggesting remarkable stability in community composition ranging from decadal scales (Rebstock 2001) to millennial (Pandolfi and Jackson 2006). For instance, Pandolfi and Jackson (2006) note that similar coral reef communities persisted across 220 thousand years, although there was variation in the relative abundance of the most dominant coral taxa.

Conclusions

Speciation is a historic process, and yet historical records have largely been left out of the modern explosion of research into the mechanisms of speciation. The core problem has been a failure to study speciation at the appropriate scale both from biological and paleontological perspectives. The historical dimension enters modern biology through the use of fossils to calibrate molecular phylogenies, but is typically neglected in studies that could benefit from estimates of paleogeographic distributions, population sizes and connectivity, and the frequency and amplitude of change in ecological interactions. Modern species and populations are a snapshot on a shifting evolutionary stage.

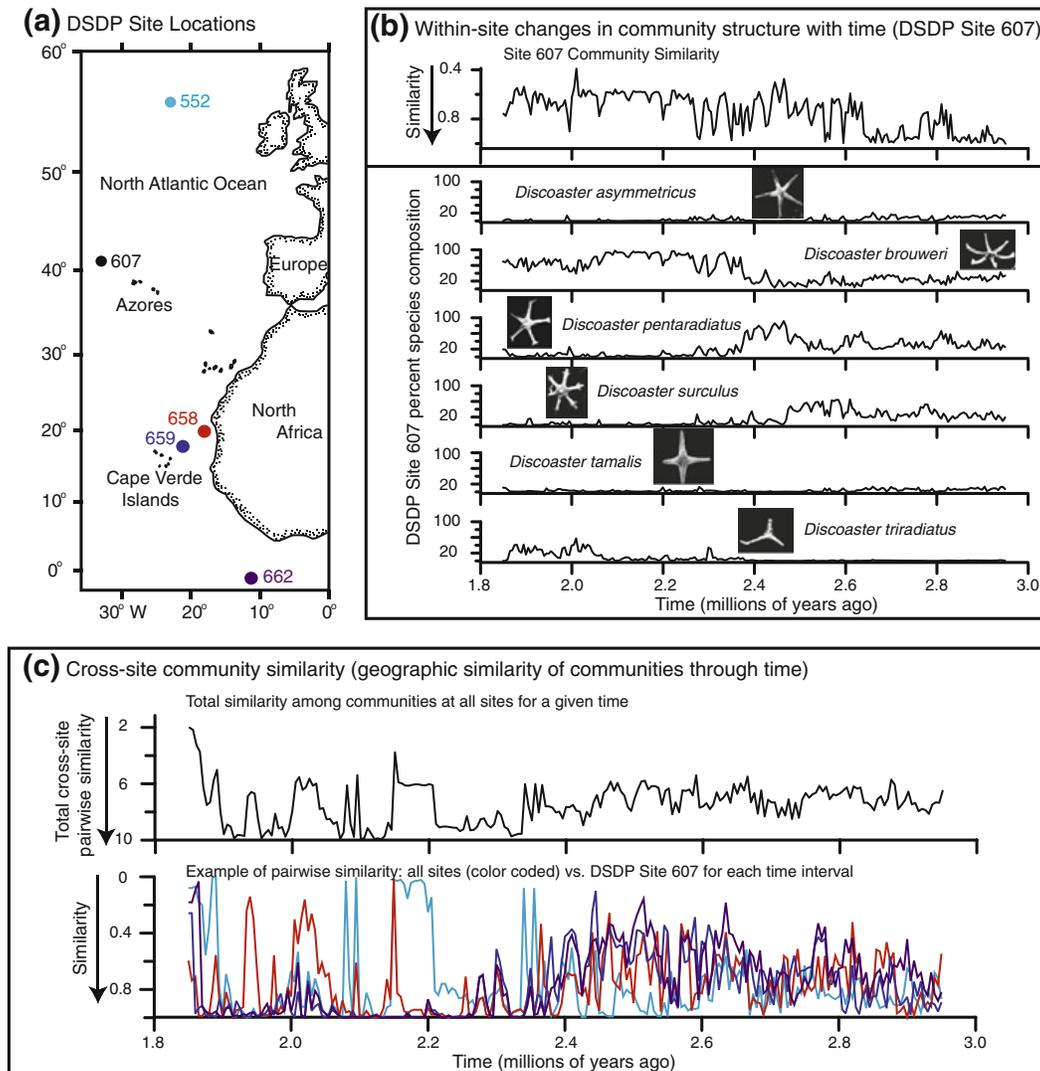


Fig. 8 Temporal and spatial variation in discoaster community structure. Discoaster community structure over 1-million years at six sites in the North Atlantic (data from Chepstow-Lusty et al. 1989). Similarity of communities at DSDP Site 607 (b) to the initial community—as measured by Morisita's index of community dissimilarity on relative abundance data—displays up to 60% differences in community structure. Individual species (b, lower six panels) show a wide range in community composition. The geographic deployment of communities across the North Atlantic also is highly variable (c). Differences in community similarity across sites was analyzed by a pairwise site comparison of community similarity (c)

Modern molecular phylogenies offer only a limited perspective on how speciation has occurred owing to the problems of extinction (Quental and Marshall 2009, 2010), unrecognized or un-sampled sibling species, past population dynamics and range shifts, among others. Notably, a recent quantitative, evolutionary model has incorporated oscillating environmental conditions (Colwell and Rangel 2010), but empirical tests and/or calibrations with the fossil record are needed. Paleobiologists (including us!), unfortunately have nearly always studied the fossil record from too coarse a temporal and spatial resolution to be of use in discerning the dynamics of speciation. It has been easy to dismiss the fossil record as uninformative of speciation mechanisms because paleobiologists have rarely

fully exploited the richness of their record. Yet the fossil record presents a rich tapestry of biogeography, ecology and morphology placed in an unrivaled temporal framework.

There are a variety of ways to incorporate a historical and a paleontological perspective into the study of speciation; developments we view as important to continued advances in the field of speciation research:

1. While all studies acknowledge the importance of history in generating modern phylogenies, the relative importance of this “history” is rarely rigorously incorporated and tested. Important advances could come from models that quantify the effects of variation in the rates of speciation and extinction on tree shape, and test specific hypotheses with the fossil and modern record. In addition, the quantitative combination of modern and fossil phylogenies offers the possibility to overcome limitations of each data type respectively (Purvis 2008). Many older models of tree shape assume “pure birth” or alternatively constant rates of speciation and extinction (approach and limitations discussed in Nee 2006; Purvis 2008, among others)—hardly realistic scenarios. A newer generation of Bayesian models allows for variations in rates of genetic evolution that could reflect variations in genetic mutation or extinction (e.g. Battistuzzi et al. 2010; Brown and Yang 2010; Drummond and Suchard 2010; Smedmark et al. 2010), and can be used to investigate the effects of varying rates of speciation and extinction on tree topology. We also advocate the use of models that explicitly incorporate ecological and environmental variation on evolution and speciation (Colwell and Rangel 2010; Shpak et al. 2010) to generate more realistic evolutionary hypotheses.
2. We could advance the integration of evolutionary rates, geographic patterns of divergence, and the significance of morphological and ecological evolution by comparing genetic phylogenies with fossils. While fossil data are commonly used to create calibration points in molecular phylogenies, it is rare to combine genetic inferences of species ecology or distribution with ecological or morphological data derived from fossils to evaluate speciation mechanisms. Well dated reef terraces (as in the uplifted reefs of New Guinea) or drill cores in atolls may achieve sufficient resolution to record evolutionary dynamics of shallow marine invertebrates like the bryozoans studied by Jackson and Cheetham (1999) and reef communities studied by Pandolfi and Jackson (2006) and (Pandolfi 1999).
3. The genetic calibration of morphological taxonomies typically used in the fossil record will also be useful to refine our understanding of divergence rates (Purvis 2008). As we have emphasized, divergence times and rates are subject to significant uncertainties in molecular phylogenies due to the presence of extinct sibling species. Paleontologists, while potentially better positioned to recognize extinct taxa, must grapple with the problem of recognizing closely related species whose species-level traits may not fossilize. In both cases, we need to refine our criteria for recognition of sibling taxa using inferences gained from studying the morphology and genetics of living relatives.
4. Fossil DNA provides extraordinary insight into the population variability of some terrestrial groups but has scarcely been investigated in marine environments. Potential materials that could be studied include vertebrate bones, fur, and feathers from archaeological middens or seal and seabird rookeries. Remains of whales and fur seals from old whaling/sealing stations or from museum collections offer the potential to reconstruct population structure before or during human exploitation. DNA analysis of Pleistocene deposits like penguin colonies could start to examine the effect of climate variation on genetic diversity in the marine realm. Studies of eggshells from penguin

- rookeries have already revealed major changes in tropic ecology (Emslie et al. 2007; Emslie and Patterson 2007).
5. The fossil record can also be used to explore evolutionary ecology on temporal and spatial scales relevant to the problem of speciation. The deep sea fossil record is increasingly capable of offering insights into speciation as well. The development, in recent decades, of orbitally tuned chronologies makes it possible to correlate events between different ocean basins at a resolution of a few 1,000 years even many millions of years ago (Lisiecki and Raymo 2005). Networks of deep sea cores with these refined time scales are now available to study population histories from the tropics to the polar ocean. New methodologies, such as trace-metal and light stable isotope geochemistry ($\delta^{18}\text{O}$, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$) now make it possible to deduce species ecology including trophic relationships, depth distributions, and symbiotic relationships (Norris 2000). Hence, paleontology has moved far beyond traditional morphological studies of speciation into biogeographic and ecological work tied to regional and global climatology.

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