doi:10.1111/evo.13030

Ephemeral ecological speciation and the latitudinal biodiversity gradient

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Received February 10, 2016
Accepted July 29, 2016

The richness of biodiversity in the tropics compared to high-latitude parts of the world forms one of the most globally conspicuous patterns in biology, and yet few hypotheses aim to explain this phenomenon in terms of explicit microevolutionary mechanisms of speciation and extinction. We link population genetic processes of selection and adaptation to speciation and extinction by way of their interaction with environmental factors to drive global scale macroecological patterns. High-latitude regions are both cradle and grave with respect to species diversification. In particular, we point to a conceptual equivalence of "environmental harshness" and "hard selection" as eco-evolutionary drivers of local adaptation and ecological speciation. By describing how ecological speciation likely occurs more readily at high latitudes, with such nascent species especially prone to extinction by fusion, we derive the ephemeral ecological speciation hypothesis as an integrative mechanistic explanation for latitudinal gradients in species turnover and the net accumulation of biodiversity.

KEY WORDS: Adaptation, biodiversity, extinction, latitude, speciation.

The Enigma: Higher Tropical Diversity, Higher Temperate Speciation and Extinction

Species richness provides a convenient and ubiquitous metric of biodiversity as a simple summary of the net outcome of the give-and-take between speciation and extinction. One of the oldest recognized patterns of species richness is the latitudinal gradient in biodiversity, such that more species are known from lower tropical latitudes than from higher latitudes outside the tropics (Wallace 1878; Fischer 1960; Pianka 1966; Hillebrand 2004). Why *do* the tropics have more species? One possibility is that net rates of diversification are greater in tropical latitudes (Mittelbach et al. 2007). However, this does not appear to be true in general (Schluter 2016) and only recently is it emerging that rates of both speciation and extinction might commonly be lower in the tropics (Weir and Schluter 2007; Botero et al. 2014; Rolland et al. 2014; Weir 2014; Schluter 2016). And why might speciation and extinction rates both be elevated at high latitudes? We propose that the ephemeral nature of nascent species generated by adaptive divergence, ecological speciation, provides a key and underexplored element to the answer.

Both Darwin and Wallace posited that latitudinal differences in species richness reflect a promoting influence of extensive biotic interactions in the tropics combined with a limiting influence of harsh climate toward more extreme temperate zones (Darwin 1859; Wallace 1878). This intuitive thinking persisted until the modern synthesis when effort was devoted to determining more precisely the factors underlying this relationship. Much subsequent evolutionary research on the latitudinal biodiversity gradient has focused on explanations for differential net diversification rates, for which there are many nonmutually exclusive possibilities. This large literature is well-reviewed (Chown and Gaston 2000; Willig et al. 2003; Hillebrand 2004; Mittelbach et al. 2007; Mannion et al. 2014; Fine 2015; Schluter 2016), so here we simply note that factors other than diversification rate per se also may contribute, including the temporal duration, geographic extent, and species carrying capacity of tropical versus nontropical regions. With these broad-scale views of diversification in mind, how do population processes ultimately generate such patterns of biodiversity given that population genetic microevolution is the sandbox of speciation?

We aim here to better connect latitudinal species gradients with the microevolutionary basis to speciation and extinction, in terms of ideas about how genetics and selection operate as underlying components of diversification. The ideas that we present are not usually set side-by-side to consider how they interconnect, despite being individually uncontroversial. Given accumulating evidence that the tropics experience lower rates of both speciation and extinction (Weir and Schluter 2007; Botero et al. 2014; Pyron 2014; Weir 2014; Sánchez-Ramírez et al. 2015; Schluter 2016), we argue that an explicit melding of ideas about the mechanistic causes of species origination and extinction with biogeographic differences between low- and high-latitude regions would help to integrate a variety of seemingly disjointed patterns with the intuition of the founding fathers of evolutionary biology.

Ecological Speciation, Population Genetics, and the Ephemerality of Nascent Species

Biologists identify species as those groups that are fully reproductively isolated, "good" species, and those who are distinct yet incompletely isolated populations ("nascent" species). That is, the genetic distinctiveness of nascent species has not yet been fully locked in by intrinsic reproductive isolation (Coyne and Orr 2004; Nosil 2012). Nascent species, in our view, represent close sibling lineages, generally accepted to be distinct evolutionary entities, often having arisen from adaptive divergence and recent cessation of gene flow. In some taxonomic traditions there would be no distinction between nascent and good species, in other traditions nascent species could be termed distinct races or subspecies. Nascent species will often result as an accident of geographic isolation, but whether they experience equivalent or divergent selection pressures relative to their progenitors will depend on local circumstances. Reproductive isolation may be incomplete or dependent on environmental interactions to manifest, and even genetically intrinsic isolating barriers may be polymorphic (Cutter 2012). It is inevitable that accepted distinct species will include those that are incompletely isolated, given the continuum of reproductive isolation in the speciation process (Dobzhansky 1940; Wu 2001; Feder et al. 2012; Singhal and Moritz 2013). It is not inevitable, however, that nascent species will persist.

Although both nascent and fully reproductively isolated "good" species will be subject to traditional notions of extinction (i.e., failure of population persistence), nascent species are uniquely susceptible to an additional mode of extinction: population fusion (Harper et al. 1961; Lewis 1962; Futuyma 1987, 2010; Rhymer and Simberloff 1996; Seehausen 2006; Seehausen et al. 2008). The sensitivity of nascent species to such collapse through hybridization is inherent to "ephemeral" and "protracted" speciation models, and represents an important factor in understanding diversification rates through time (Etienne and Rosindell 2012; Rosenblum et al. 2012; Dynesius and Jansson 2014; Etienne et al. 2014). Indeed, a substantial literature now documents such resorption of nascent species across diverse organisms, from plants to invertebrates to vertebrates (Table 1) (Levin et al. 1996; Rhymer and Simberloff 1996; Gilman and Behm 2011). Given that extinction by fusion happens, might species that arise through some modes of speciation be especially vulnerable to it? Nascent species formed through ecological speciation, in particular, exhibit several characteristics that can predispose them to extinction by fusion.

Ecological speciation is a major process underlying the production of new species (Rundle and Nosil 2005; Schluter 2009; Sobel et al. 2010). In this process, distinct eco-environmental circumstances foster adaptation through divergent selection on the descendants of an ancestral population; the divergent selection then leads to reproductive isolation between descendant lineages, owing to genotype by environment interactions that disfavor intermediate phenotypes. That is, the diverging populations experience environment-dependent, extrinsic, reproductive isolation as a consequence of local adaptation. Let us now consider some factors that promote or restrain ecological speciation before turning to how these factors pertain to extinction by fusion and intersect with latitudinal features.

Local adaptation can proceed most rapidly when it operates on genetic variation that is preexisting, with additive effects, and controlled by many genes from the progenitor population, and when gene flow is constrained between daughter populations (Barrett and Schluter 2008; Orr and Unckless 2008; Pritchard and Di Rienzo 2010). These circumstances relate closely to what happens under ecological speciation through adaptive divergence. Specifically, we expect F1 hybrids between nascent "ecological" species to have reduced fitness in either parental environment (Rundle and Nosil 2005), which ought to reflect at least partial additivity of genetic effects (or epistasis involving dominant interactions). Local adaptation will commonly be polygenic in its genetic basis (Orr 2005; Pritchard and Di Rienzo 2010), which means that ecological mismatches of genotypes could extend into later generation hybrids (Arnegard et al. 2014). However, polygenic selection often results in adaptation by shifting allele frequencies at many loci rather than fixation of alleles at single loci (Chevin and Hospital 2008; Pritchard et al. 2010). This occurs, in part, because even strong overall selection gets partitioned into much weaker selection coefficients on each individual contributing locus (Latta 1998; Le Corre and Kremer 2003; Gavrilets and Vose 2005). Subsequent alterations of selective pressures, however, can easily reverse those phenotypic changes with such a genetic architecture to adaptation. Consequently, we should expect that nascent ecological species (1) may often arise from selection on preexisting additive genetic variation (Schluter and Conte 2009), (2) are partially reproductively isolated and so may

Table 1. Examples of ecological change and the ephemerality of speciation.

Study system	Scenario	Region	References
Stickleback fish (*Gasterosteus*)	Increased turbidity from crayfish colonization may have led to breakdown of premating isolation	British Columbia, Canada	Gow et al. (2006), Taylor et al. (2006), Behm et al. (2010), Lackey and Boughman (2013), Keagy et al. (2016)
Cichlid fish (*Haplochromis*)	Eutrophication-induced turbidity disrupts signaling and assortative mating	Central African Great Lakes	Seehausen et al. (1997)
Megrim flatfish (*Lepidorhombus*)	Reduced spawning habitat due to oil spill may have reduced assortative mating	Atlantic Spain	Crego-Prieto et al. (2012)
Trout fish (*Oncorhynchus*)	Anthropogenic disturbance possibly facilitates hybridization	British Columbia, Canada	Bettles et al. (2005)
Darter fish (*Etheostoma*)	Unknown basis to hybridization	Central United States	Halas and Simons (2014)
Alpine whitefish (*Coregonus*)	Eutrophication-induced breakdown of reproductive isolation	Switzerland	Vonlanthen et al. (2012)
Whitefish (*Coregonus*)	Invasion of fish competitor-induced diet shift and breakdown of reproductive isolation	Norway	Bhat et al. (2014)
Pupfish (*Cyprinodon*)	Anthropogenically induced secondary contact resulted in rapid hybridization	Texas	Echelle and Connor (1989)
Darwin's finches (*Geospiza*)	Climatic and environmental changes facilitate hybridization	Galapagos Islands, Ecuador	Grant and Grant (1993), Grant et al. (2004)
Mallard ducks (*Anas*)	Agricultural habitat loss and introduction of sibling species led to hybridization	New Zealand	Rhymer et al. (1994)
Scincid lizards (*Plestiodon*)	Parallel evolution of body size and secondary contact of populations enabled hybridization	California	Richmond and Jockusch (2007)
Tiger salamanders (*Ambystoma*)	Hybridization with introduced species in anthropogenically modified habitats yielded hybrid vigor	California	Fitzpatrick and Shaffer (2007a, 2007b)
Wolves (*Canis*)	Habitat changes facilitated hybridization	Southern United States	Wayne and Jenks (1991)
Crayfish (*Orconectes*)	Anthropogenically induced secondary contact resulted in hybridization and competitive superiority of hybrids	Wisconsin	Perry et al. (2001)
Honeybee (*Apis*)	Hybridization of subspecies in their nonnative range	Mexico	Clarke et al. (2002)
Wild radish (*Raphanus*)	Parental species in introduced range replaced by hybrids owing to reproductive and colonizing superiority	California	Hegde et al. (2006)
Stripeseed (*Piriqueta*)	High fitness of hybrid genotypes contributes to an expanding hybrid zone	Florida	Martin and Cruzan (1999)

have the potential to or continue to experience substantial gene flow (Nosil et al. 2009; Feder et al. 2012), and (3) will have diverged recently and so will share much ancestral polymorphism.

The maintenance of nascent ecological species as genetically distinct requires the constant vigilance of divergent selection, favoring local adaptation in the face of the possibility that the homogenizing force of immigration and dispersal pressure will dominate (Schluter and Conte 2009; Gray and Goddard 2012). For nascent species to persist as distinct thus requires the corresponding persistence of divergent selection that outweighs gene flow until genetically "intrinsic" reproductive barriers accumulate, for example, as negatively epistatic Dobzhansky–Muller incompatibilities (DMIs) (Dobzhansky 1936; Muller 1942; Orr and Turelli 2001). Environmentally induced shifts in the strength and direction of selection do occur in the wild, with the strongest shifts for traits that experience the strongest selection (Siepielski et al. 2009; Morrissey and Hadfield 2012). Such shifts can reconnect separated populations with gene flow through greater migration and altered selective regimes on both the populations themselves and hybrid individuals. Consequently, young ecological species will be especially susceptible to ecological perturbations that disrupt the regimes of divergent selection and dispersal because they could lead to hybridization and fusion back into a single population genetic entity (Nosil et al. 2009). Theory shows that divergence through sexual selection from standing variation also is susceptible to population fusion (Servedio and Burger 2014). Sometimes termed "reverse speciation" (Seehausen 2006) or "extinction by hybridization" (Rhymer and Simberloff 1996), this resorption is a natural counterpart of ecological speciation, made explicit in ephemeral macrospeciation models (Etienne and Rosindell 2012; Rosenblum et al. 2012; Etienne et al. 2014).

Even if local adaptation does produce allele fixation from historical genetic variability, these ancestrally- polymorphic alleles will be less likely to create intrinsic reproductive incompatibilities in the form of DMIs than will new derived, population-specific mutations (Orr 1995). Eventually, however, when adaptation makes use of new mutational input, a genetic architecture comprising fewer loci with larger individual effects can emerge (Yeaman and Whitlock 2011); although given the short time-frame of nascent species' origins, any new fixed mutations may be uncommon. Selection in the progenitor population would have made it unlikely that ancestrally polymorphic alleles will produce negatively epistatic interactions that might provide the basis to DMIs (Orr 1995; Coyne et al. 2000), despite being possible (Phillips and Johnson 1998; Corbett-Detig et al. 2013). Consequently, reproductive isolation of nascent ecological species will depend more on extrinsic genotype–environment interactions than on intrinsic genotype–genotype interactions. This conceptual limitation in creating intrinsic isolating barriers for divergent selection on standing variation likely is an important contributor to the common failure of experimental evolution studies to yield intrinsic reproductive isolation (Coyne and Orr 2004; Kawecki et al. 2012). When adaptation does involve selection on new mutations, then certainly ecological speciation would promote intrinsic reproductive isolation. Altogether, these aspects of the genetic architecture of ecological species formation make such nascent species especially susceptible to resorption in the event of environmental change that perturbs selection regimes. Nascent species formed by any mode of speciation can be subject to extinction by fusion, but we propose that lineages formed through ecological speciation will be especially prone to ephemerality as a result of the genetic architecture of divergent adaptation and changes in selective regimes.

Natural Selection and the Geography of Ephemerality

Are some geographic regions predisposed to rapid and repeated ecological speciation? If so, then lineages that exist in these regions would be similarly predisposed to being ephemeral. Regions prone to ecological speciation would be those that frequently experience the creation of distinct ecological circumstances that spurs directional selection along different axes. High-latitude parts of the world are likely to provide just these circumstances. Continual directional selection will press on peripheral populations that experience marginal habitat conditions proximate to the edge of a species range at high latitudes. When paired with restricted gene flow, selection on such peripheral populations can drive divergence to create nascent species (Mayr 1954; Lewis 1962; Garcia-Ramos and Kirkpatrick 1997).

Studies in recent years have demonstrated that greater environmental harshness may be the key factor that fosters higher speciation rates in some groups (Botero et al. 2014; Weir 2014; Schluter 2016). This association between speciation rate and harshness could arise for several reasons. Climate cycles and more expansive "ecological opportunities" in high-latitude parts of the world make them particularly favorable to ecological speciation by facilitating the evolution of niche separation (Jansson and Dynesius 2002; Weir and Schluter 2004; Gavrilets and Vose 2005; Schluter 2016). We view ecological opportunity in this context as the manifestation of environmental changes that erase parts of communities, creating resource underutilization and thus permitting subsequent invasion and exploitation (Schluter 2000; Levin 2004). Recurrent environmental change and harshness at high latitudes may make adaptation to abiotic factors more important than in low latitudes (Schemske et al. 2009). We also expect high latitudes to experience more frequent wide-scale, major environmental perturbations. Consequently, the time lag between rapid adaptive divergence and the erratic incidence of extinction (both by fusion and by failure of populations to persist) will result in species richness far from equilibrium for substantial periods of time following such major perturbations (Stephens and Wiens 2003; Weir and Price 2011). Any diversity-dependent dampening of speciation rates, for example, owing to niche packing, will exert weaker effects on rates of speciation in such regions of greater ecological opportunity (Ricklefs 2010; Etienne and Haegeman 2012; Rabosky 2013). Despite the role of temporal stability in favoring species accumulation in the tropics to contribute to the latitudinal biodiversity gradient (Stephens and Wiens 2003), this factor would not in itself explain higher rates of species origination at high latitudes. These factors ought to promote high species origination rates at high latitudes through ecological speciation despite lower overall species richness.

And yet, it is an old notion that populations at their range margins suffer elevated extinction rates that may counteract even potent directional selection and speciation (Lewis 1962; Gavrilets et al. 2000). Although local extinctions in a fragmented landscape of populations can create migration discontinuities to facilitate divergence, they also present an elevated overall extinction risk. Also working against diversification, the same dynamism of environmental conditions and community composition at high latitudes could interrupt divergent selection pressures, inducing premature “secondary contact” that could lead to population merger and collapse of nascent species. Climate cycles that drive range shifts also can create isolated refugia and lead to divergence in allopatry to form nascent species (Hewitt 1999; Weir and Schluter 2004; Hoskin et al. 2011), creating the opportunity for extinction by fusion upon secondary contact during climate reversals (Dynesius and Jansson 2000; Barnosky 2005). In short, the same factor that facilitates the onset of ecological speciation, environmental change, also operates to perturb selection regimes and, in so doing, fosters the onset of secondary contact between nascent species that can induce resorption and extinction. To the extent that ecological speciation is a disproportionately important process governing high speciation rates at high latitudes owing to environmental dynamism, we should also expect such lineages to be subject to high rates of extinction by fusion and that this will constrain net diversification especially strongly at high latitudes.

How does this key characteristic of “environmental harshness” translate into the genetic process of adaptation? That is, what happens when variable and extreme conditions that confer density-independent mortality of individuals and the extirpation of subpopulations are more likely to be experienced by lineages at higher latitudes (Cracraft 1985; Levin 2004; Botero et al. 2014)? Viewed from a population genetic perspective of the adaptation process operating on fragmented and peripheral populations at range margins, these are exactly the conditions that lead to “hard selection” on traits (Wallace 1975; Saccheri and Hanski 2006). This contrasts with “soft selection” at the other end of the spectrum (i.e., hard viability selection vs. soft fecundity selection) in which extreme trait values confer fitness advantage or disadvantage via competition irrespective of their absolute values (Wallace 1975; Saccheri and Hanski 2006). We suggest that the extent of environmental harshness and the hardness of selection naturally represent, respectively, ecological and evolutionary perspectives of the same issue.

Regions with ecological opportunity might be predisposed toward colonization by ecological generalists (Jansson and Dynesius 2002), which provides prime real estate for subsequent divergent selection and specialization. The evolution of specialization through local adaptation and population divergence will arise more readily when adaptation operates through hard selection than when selection is soft, by virtue of a more complex adaptive landscape (Christiansen 1975; Van Tienderen 1991; Ronce and Kirkpatrick 2001). As a result, when hard selection predominates over soft selection, we might anticipate that it will promote ecological speciation through the evolution of locally adapted specialists. This is not to say, however, that soft selection plays no role in these environments because competition can be an important means of retaining adaptive differentiation in the ecological speciation process. Regardless, hard selection also more easily leads to extinction compared to when density-dependent “soft” selection predominates (Gomulkiewicz and Holt 1995; Garcia-Ramos and Kirkpatrick 1997). This situation of hard selection through environmental harshness is likely to pervade higher latitudes more so than low latitudes, and consequently to promote both ecological speciation and ephemerality more strongly at high latitudes.

The Ephemeral Ecological Speciation Hypothesis

We propose that the ephemerality of nascent species that ecological speciation generates through divergent selection contributes a microevolutionary, process-oriented view of the latitudinal biodiversity gradient. We hypothesize that organisms in high latitudes will experience higher rates both of speciation by divergent ecological selection and of extinction by fusion, even if nonfusion extinction rates are uniform. Disproportionate environmental harshness at high latitudes fosters ecological opportunity and adaptive divergence subject to “hard” selection, but these same vicissitudes of nature also trigger hybridization and species resorption. The ephemerality of nascent species through their extinction by fusion represents an underexplored and underappreciated component of the diversification process and ecological speciation in particular. Consequently, we expect high latitudes to exhibit greater species turnover because they experience both faster speciation and a higher effective extinction rate than in the tropics, potentially exacerbated by elevated traditional extinction from the failure of small and isolated populations of nascent species to persist near dynamic ecological extremes (Allee and Bowen 1932; Lewis 1962). The net diversification rate could thus be similar across latitudes or even higher in latitudes closer to the poles, as indicated by some of the latest analyses (Weir and Schluter 2007; Botero et al. 2014; Rolland et al. 2014; Weir 2014; Schluter 2016).

Strictly speaking, the ephemeral ecological speciation hypothesis appeals not to latitude per se, but to those geographic and climatic drivers that generate environmental harshness, ecological opportunity, and divergent local adaptation through "hard" selection (Fig. 1). It draws on some of the classic conclusions of Mayr (1954) and Lewis (1962), with respect to speciation and extinction near species range margins, and of Wallace (1878) and Fischer (1960), in terms of the process of speciation and extinction across large latitudinal scales. We emphasize the mechanistic connections between environment, population genetics, ecological speciation, and extinction by fusion for nascent species as important means of meting out macroecological pattern. That is, especially high extinction rates associated with rapid ecological speciation in the dynamic and harsh high latitudes make it "cradle and grave" for species, a perspective reinterpreted from the viewpoint of high-latitude regions relative to the viewpoint of the tropics as a "museum" of accumulated biodiversity that has been "spared destruction" (Stebbins 1974; Chown and Gaston 2000).

The drivers of species origination, ephemerality, and extinction that involve nascent species operate on a shallower time-scale than often is considered in global analyses of biodiversity. Unfortunately, analyses with deep phylogenetic depths may mask the signatures of causal drivers of species origination, especially if they also correlate with extinction (Phillimore et al. 2006; Kraaijeveld et al. 2011; Botero et al. 2014); latitudinal differences in deep clades also are more likely to reflect differences in expected equilibrium species richness (Cardillo et al. 2005). Moreover, the seasonal dynamism at high latitudes of relevance to environmental harshness and ecological speciation is a relatively recent phenomenon on geologic timescales (Schluter 2016). Nascent species are unlikely to register in the fossil record as distinct forms, so their extinction will simply result in a pattern of a "failure to speciate" (Rabosky 2013). Nascent species do, however, log in our assessment of extant biodiversity and so can be evaluated in molecular phylogenetic tests of speciation rates (Martin and Tewksbury 2008; Botero et al. 2014; Weir 2014). Consequently, we propose that the greatest signal relevant to the ecological speciation hypothesis will occur near phylogenetic tips rather than in very deep portions of phylogenies, making sister- and subspecies analysis most appropriate (Cardillo et al. 2005; Weir and Schluter 2007; Botero et al. 2014; Weir 2014). Analysis of recent phylogenetic time depths, however, raises its own complications. The issue of ancestral polymorphism and species tree inference become all the more pertinent for inferring the timing and rates of speciation for recent and rapid divergence of lineages (Burbrink and Pyron 2011; Cutter 2013).

In turn, the effect of time–depth on inferences about speciation and extinction rates might contribute to heterogeneity among higher taxa. For example, the molecular divergence between frog species often greatly exceeds that of birds (Avise et al. 1998), suggesting that birds might generate a stronger signal of the role of ecological speciation and ephemerality in producing the latitudinal biodiversity gradient. Indeed, unlike birds (Gaston and Blackburn 1996; Hawkins et al. 2006; Weir and Schluter 2007; Botero et al. 2014; Rolland et al. 2014; Weir 2014), hylid frogs show little evidence for a latitudinal contribution to rates of diversification (Wiens et al. 2006).

The ephemeral ecological speciation hypothesis makes a number of predictions that may be tested by phylogenetic, population genetic, and experimental means (Table 2). Intrinsic to its logic is that species origination and extinction rates will be greater in higher latitudes, despite the lower overall species richness. This contrasts with inverted expectations of speciation and extinction rates under some other hypotheses (Fischer 1960; Rohde 1992; Rosenzweig 1992; Mittelbach et al. 2007; Schemske et al. 2009; Fine 2015). As a consequence, sister species at high latitudes ought to share a more recent common ancestor than low-latitude sister species, also leading to a greater incidence of incomplete lineage sorting and residual ancestral polymorphism in high-latitude species. The prevalence of recent divergence and nascent species distinctiveness requiring chronic divergent selection ought to yield sister species at high latitudes more often exhibiting incomplete intrinsic reproductive isolation. Combined with the consequences of ancestral polymorphism for molecular phylogenetics (Cutter 2013; Hahn and Nakhleh 2016), "problem groups" with taxonomic confusion or hybrid swarms might also occur disproportionately in high latitudes (Grant and Grant 1992). The stochasticity of high turnover for nascent species at high latitudes might also produce phylogenies with greater phylogenetic imbalance and heterogeneity in the length of terminal branches as some lineages radiate and others collapse.

We have hypothesized that divergent ecological selection underpins speciation disproportionately at high latitudes, so, by extension, speciation mediated by other means ought to prevail in the tropics. Namely, these other means include so-called "mutation order" speciation driven by genetic conflict (Rice 1998; Presgraves 2010; Crespi and Nosil 2013), sexual selection (Ritchie 2007; Kraaijeveld et al. 2011; Maan and Seehausen 2011; Wagner et al. 2012; Mendelson et al. 2014), or genetic divergence of allopatric populations adapting independently to common environmental features via parallel directional selection or stabilizing selection (Mani and Clarke 1990; Barton 2001; Wiens 2004; Schluter 2009; Nosil and Flaxman 2010; Hua and Wiens 2013;

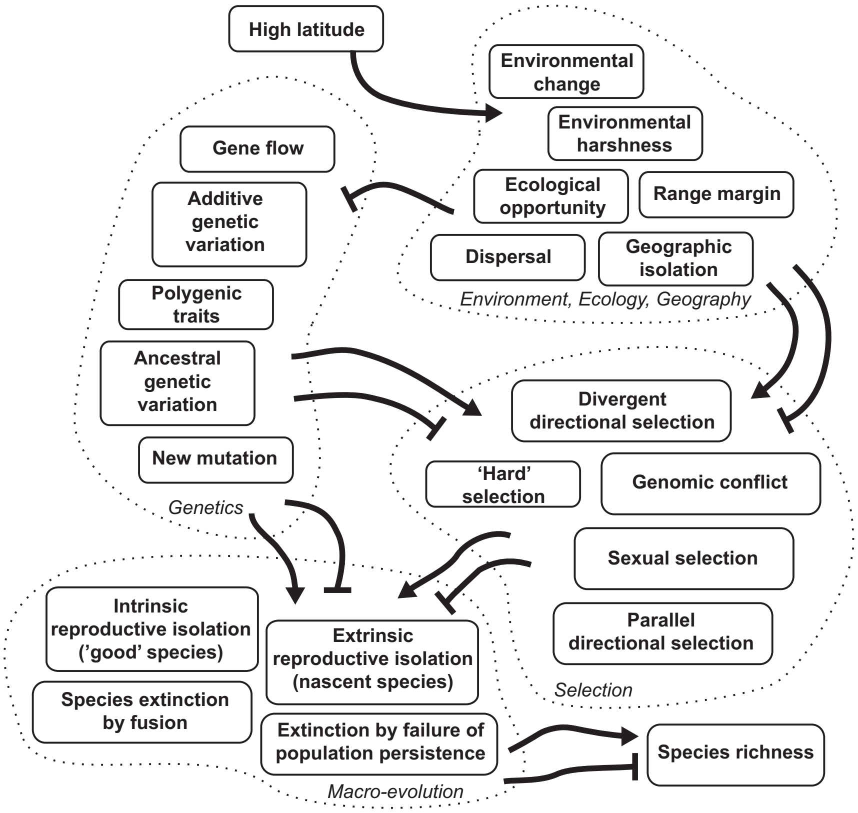

Figure 1. **The link between latitude and species richness pass through diverse microevolutionary biotic and abiotic factors. The relative strengths of positive (arrow) and negative (bar) connections among specific factors will determine the overall species richness of a region, including environmental, ecological and geographic factors, population genetic factors, modes of selection, and the macroevolutionary processes of species origination and extinction.**

Anderson and Harmon 2014). There does not appear to be much evidence for or against latitudinal gradients in the incidence of these modes of speciation, however, warranting further investigation. We do not deny an important role of ecological speciation in low latitudes, as classic examples of adaptive radiations in Darwin's finches and rift-lake cichlids attest (Schluter 2000), but nevertheless hypothesize an outsized overall contribution of this mode of speciation at high latitudes. Reciprocally, factors that foster ecological speciation also could facilitate "mutation order" speciation under some circumstances. The ephemeral ecological speciation hypothesis provides a microevolutionary process-oriented view of how speciation and extinction rates can vary predictably with latitude by connecting genetic mechanisms of the diversification process to selection and ecological, environmental, and geographic factors.

Simulations of Biodiversity: The Good, the Nascent, and the Ephemeral

The verbal logic that we have presented, while based on analytical insights in parts, would benefit from a more quantitative consideration. We developed and applied a modified implementation, with faster run-time, of the protracted birth–death (PBD) model of Etienne and colleagues (Etienne and Rosindell 2012; Lambert et al. 2015) allowing complete lineage extinction as well as linking nascent and fully reproductively isolated lineages (Fig. 2). The code is available as an R package at: https://github.com/jeremycg/protractedbirthdeath. We traced over time the numbers of extant "good" species that are reproductively isolated from all other lineages, "nascent" species that have incomplete reproductive isolation from some other lineages, as well as extinctions for these two classes of lineages (Fig. 2). To connect to the ephemeral ecological speciation hypothesis, we envision low latitudes as being represented by lower rates of species origination (principally the rate at which nascent species can themselves speciate λ_3, but also the speciation rate of "good" species λ_1) and extinction of nascent species (μ_2); higher values of these parameters correspond to more prevalent ecological speciation and ephemerality of nascent species at high latitudes (Fig. 2).

As a control, the broad outcomes of these simulations are largely intuitive: as speciation rates increase, so does species richness (Fig. S1). Similarly, higher extinction rates reduce species richness (Fig. S1). Species richness is more sensitive to changes

Table 2. **Predictions of the ephemeral ecological speciation hypothesis for the latitudinal biodiversity gradient.**

Prediction	Logic	Possible violations
Higher speciation rate at high latitudes	More prevalent speciation by divergent ecological selection	If low latitudes have prevalent speciation by sexual selection or genetic conflict; if widespread ecological generalists tend not to diversify
Higher extinction rate at high latitudes	More prevalent extinction by fusion and failure to persist	If widespread ecological generalists with low propensity for extinction dominate high latitudes
More recent common ancestor of sister species at high latitudes	Higher rate of ecological speciation at high latitudes	If ecological speciation prevalence does not correlate with latitude
More prevalent incomplete lineage sorting and shared ancestral polymorphism between sister species at high latitudes	Recent divergence leaves insufficient time for genealogical coalescence across the genome	If close sister species are not more common at high latitudes
Higher variance in time to common ancestor among sister species pairs at high latitudes	Greater lineage turnover at high latitudes	If extinction rates are greater at low latitudes
More phylogenetic imbalance for high-latitude clades	Heterogeneous loss and expansion of lineages with higher rates of speciation and extinction	If extinction and speciation is random with respect to adaptive innovations
Greater prevalence of species swarms at high latitudes	Hybridization upon secondary contact of incompletely isolated lineages facilitated by environmental dynamism	If isolated lineages fail to expand to create secondary contact
Greater prevalence of incomplete intrinsic reproductive isolation between species pairs at high latitudes	Genotype–environment interactions required for species cohesion at early stages of ecological speciation	If ecological speciation prevalence does not correlate with latitude
Greater requirement for divergent ecological selection to maintain species in high latitudes (vs. sexual selection, genetic conflict, “mutation-order” divergence)	Ecological speciation requires persistent divergent selection	If ecological speciation prevalence does not correlate with latitude
Extrinsic barriers in reproductive isolation more important in high latitudes	Consistent ecologically divergent selection among lineages drives ecological speciation	If ecological speciation prevalence does not correlate with latitude

in rates of speciation and extinction for “nascent” species than for “good” species when the speciation completion rate is low (λ_2 in Figs. 2 and 3; Fig. S1).

Our key questions relate to differences in species richness that follow from differing relative rates of nascent species origin or loss, so we probed relative rates of speciation and extinction in detail (Fig. 3). The region of parameter space corresponding to high relative rates of birth and death of nascent species loosely represents high-latitude conditions under the ephemeral ecological speciation hypothesis (top row of Fig. 3), whereas low, tropical latitude conditions are approximated by lower relative rates of these parameters (bottom row of Fig. 3). A broad region of parameter space can yield patterns consistent with a latitudinal gradient in biodiversity, resulting from an ephemeral ecological speciation process with disproportionately higher extinction (and speciation) rates for nascent species in high latitudes. Most of the parameter space that would produce a gradient in species richness also has a gradient in net diversification rate. However, even keeping the overall difference in speciation and extinction rates constant can lead to a pattern comparable to a latitudinal gradient in diversity. For example, conditions mimicking low latitudes show greater species richness than high latitudes when $\lambda_1 = 0.7$ in Figure 3A compared to $\lambda_1 = 0.4$ in Figure 3C for a given value of the speciation completion rate λ_2 (i.e., $(\lambda_1 - \mu_1) + (\lambda_3 - \mu_2) =$

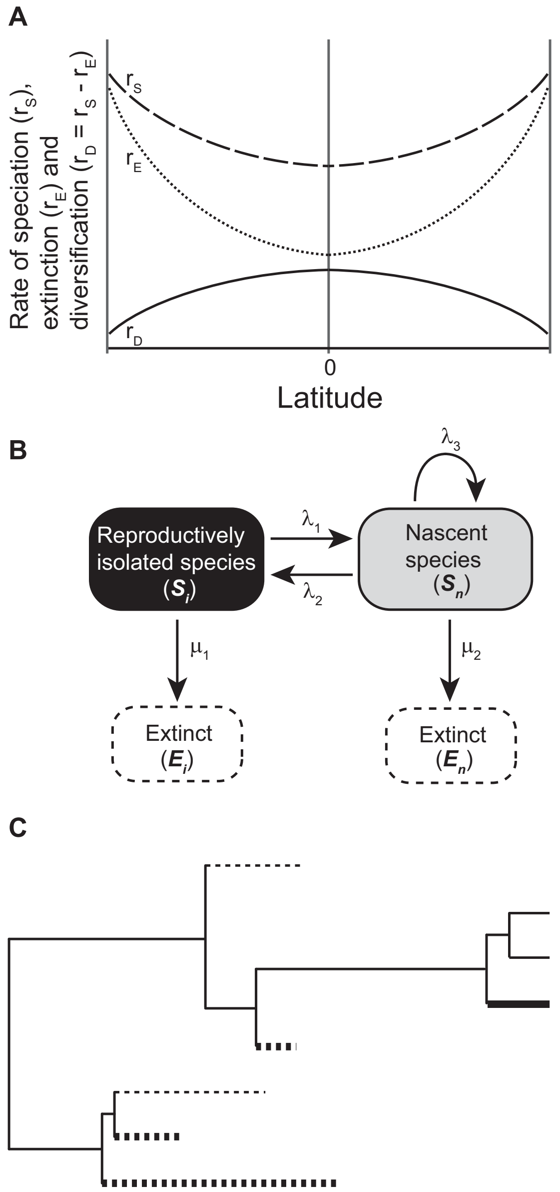

Figure 2. A greater diversification rate (r_D) in the tropics could occur despite higher rates of both speciation (r_S) and extinction (r_E) toward higher nontropical latitudes (A). (B) Diagram depicting the protracted birth–death model used in simulations of diversification (Etienne and Rosindell 2012; Lambert et al. 2015), incorporating separate rates of extinction and of new species origin for reproductively isolated (μ_1, λ_1) and nascent (μ_2, λ_3) lineages and a third rate capturing the rate of accumulation of reproductive isolation of nascent lineages (λ_2). (C) An example phylogeny for three extant species from eight total lineages in a protracted birth–death diversification simulation; dashed terminal branches indicate extinct species, thin terminal branches indicate "nascent" species, thick terminal branches indicate "good" species. Simulation code is available as an R package at: https://github.com/jeremycg/protractedbirthdeath.

0.3 for both high- and low-latitude simulated conditions). By contrast, an equivalent boost to species origination from nascent species would generate a biodiversity countergradient ($\lambda_3 = 0.7$ in Fig. 3B compared to $\lambda_3 = 0.4$ in Fig. 3D), indicating that total species richness and the sign of the biodiversity gradient is sensitive to the cause of the diversification gradient. These simulations of the diversification process lend further credence to the notion that relative rates of species origin and loss, incorporating explicitly the ephemeral nature of nascent species, can provide a crucial key to understanding latitudinal gradients of biodiversity.

Further Considerations

ARE SPECIES ORIGINATION RATES TRULY HIGHER AT HIGH LATITUDES?

The ephemeral ecological speciation hypothesis supposes ecological speciation to be a disproportionate mode of speciation at high latitudes, and there is good reason to expect ecological speciation to often yield higher rates of species origination than other modes (Schluter 2000; Nosil 2012). However, it must be recognized that sexual selection and genomic conflict also have the potential to drive rapid accumulation of reproductive isolation independently of ecological divergence, though they can work in concert with ecological factors (Seehausen et al. 1997; Rice 1998; Gavrilets 2000; Panhuis et al. 2001; Crespi and Nosil 2013). Also, hybridization between species can itself lead to the origin of new biological species rather than to extinction by fusion, as documented especially well in plants (Stebbins 1974; Rieseberg et al. 1996; Nolte and Tautz 2010). All of these processes could counteract latitudinal trends of ecological speciation in some taxa. More important and general than the prediction regarding speciation rates, however, is the expectation of higher extinction rates at high latitudes caused, in part, by species ephemerality through extinction by fusion. Modes of speciation not involving divergent ecological selection are generally not expected to yield such a prediction about extinction, except over long timescales, for example, if one were to presume predominance of speciation modes involving parallel or stabilizing selection of allopatric populations that yield times to complete speciation so long as to be interrupted at high latitudes by climate cycles. With the limited number of studies convincingly demonstrating accelerated rates of both speciation and extinction at high latitudes (Weir and Schluter 2007; Botero et al. 2014; Pyron 2014; Weir 2014; Sánchez-Ramírez et al. 2015; Schluter 2016), clearly further empirical study is needed in this area. Contrasts of longitudinal gradients in environmental factors and of persistent versus regularly perturbed systems, such as atoll series and elevation gradients, or invasive species might also provide useful empirical microcosms.

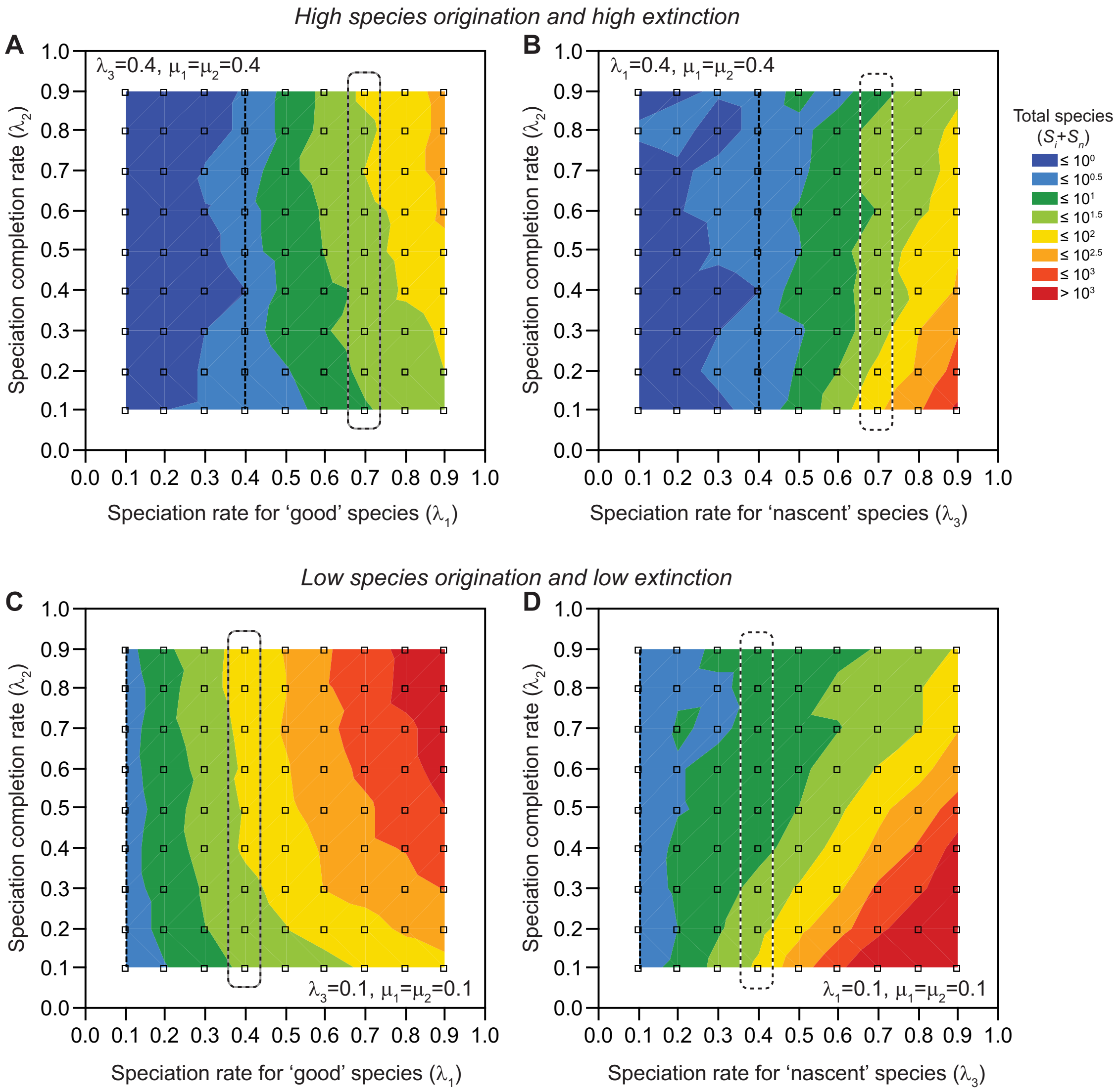

Figure 3. **Changes in diversity as a function of rates of origination (λ_1 and λ_3) and completion (λ_2) of reproductively isolated "good" species (A, C) and of "nascent" species (B, D). Higher speciation or lower extinction rates individually lead to greater species richness, but species richness is greatest in regions of parameter space where rates of speciation and extinction are both low (A and B cf. C and D). Species richness is more sensitive to changes in nascent species extinction and origination when speciation completion rates are low. Panels A and B mimic high-latitude regions, with high rates of both species origin and extinction; panels C and D mimic low-latitude regions. Vertical dashed lines indicate equivalent parameter combinations for panels in each row. Regions encircled by dashed lines indicate equivalent shifts in speciation rate for "good" species or for "nascent" species all of which yield $(\lambda_1 - \mu_1) + (\lambda_3 - \mu_2) = 0.3$, but have contrasting effects on total species richness (see main text). Results are shown for equal rates of extinction for good and nascent species; higher extinction rates for nascent species shift the species richness toward lower values (Fig. S1). Squares in each contour plot represent the average of 50 simulations of the protracted birth–death model for the corresponding parameter values. Simulations were carried out with speciation and extinction rates in units per species per million years, limited to a maximum of 10^5 taxa over a span of 15 million years. We have used the term "nascent species" in preference to "incipient species" to avoid any implication of inevitability to the speciation process.**

GENETICALLY INTRINSIC INCOMPATIBILITY ACCUMULATION

Because the rate at which species accumulate intrinsic barriers to interbreeding appears uncorrelated with net diversification rates (Rabosky and Matute 2013), it is therefore more plausible that cumulative biodiversity patterns will instead reflect rates of nascent species origination and of extinction (Fig. 3). Although postzygotic reproductive isolation might accumulate more rapidly in low-latitude *Drosophila* (Yukilevich 2013), this rate appears not to limit net diversification (Rabosky and Matute 2013). In contrast to flies, however, the time to sympatry of sister lineages occurs more rapidly at high latitudes in birds, possibly implicating more rapid accumulation of genetically intrinsic reproductive isolation at high latitudes (Weir and Price 2011).

Differences in the relative role of ecological versus "mutation order" speciation with latitude could contribute to latitudinal trends in the accumulation of intrinsic reproductive isolation. In principle, it is possible to perform phylogenetic contrasts of temperate and tropical lineages to test for differences in the accumulation of intrinsic reproductive incompatibilities (Moyle and Payseur 2009; Wang et al. 2013), or to apply comparative methods to lineages hypothesized to have diverged via ecological speciation versus "mutation order" speciation. Such tests could further disentangle the factors that contribute to geographic trends in the evolution of intrinsic reproductive isolation.

DIVERSITY-DEPENDENT DIVERSIFICATION

Elevated rates of ecological speciation at high latitudes also can be considered in the context of diversity-dependent diversification, in which net diversification rates decline over time as more species occupy a region (Ricklefs 2010; Etienne and Haegeman 2012; Rabosky 2013). However, rather than implying that high latitudes have an intrinsically lower "carrying capacity" of species numbers (Ricklefs 2009), in the context of the ephemeral ecological speciation hypothesis, a diversity-dependent interpretation of extant species richness could instead reflect high latitude regions comprising communities farther away from the "carrying capacity" (Weir and Price 2011). The possibility of lower net diversification rates at high latitudes (Mittelbach et al. 2007), however, would argue against this interpretation. Perhaps higher ecological speciation rates at high latitudes might represent a signature of diversity-dependence, owing to ecological opportunities being less fully exploited in high-latitude regions.

INTEGRATING MICRO- AND MACROEVOLUTION

By connecting evolutionary theory for populations to macroevolutionary patterns of species richness, the ephemeral ecological speciation hypothesis motivates further integration of phylogenetic comparisons and population genetics (Kisel et al. 2012; Leffler et al. 2012; Araújo and Costa-Pereira 2013; Cutter 2013; Hahn and Nakhleh 2016). What factors lead a species to retain hyperdiversity as a single population genetic entity rather than speciating to split into multiple independent evolutionary lineages (Cutter et al. 2013)? Answering this kind of question should benefit from exploring diversification at micro- and macroevolutionary levels simultaneously. Whether a lineage diversifies or not also relates to the problem of understanding the evolution of phenotypic plasticity and of habitat specialist versus generalist life histories, as these features can exert both promoting and restricting roles in speciation and extinction (Ronce and Kirkpatrick 2001; Thibert-Plante and Hendry 2011).

Why might some groups of organisms not conform to the expectations of the ephemeral ecological speciation hypothesis? Some life histories will be inherently less conducive to ecological speciation regardless of latitudinal position because the ability of divergent selection to make populations distinct depends on vagility being high enough to colonize new habitat but low enough to avoid homogenization by gene flow. Alternatively, low latitudes might actually be richer in relevant sources of divergent selection for some groups, especially those like parasites that are subject to especially strong biotic coevolutionary interactions (Schemske et al. 2009; Ricklefs 2010), perhaps accelerating ecological speciation at low latitudes in some cases.

MACROECOLOGICAL PATTERN AND PROCESS

The dynamics of speciation and extinction also may generate differential macroecological community patterns in a consistent trend with latitude. In particular, the shape of species richness-abundance distributions (RADs), which enjoy widespread use in ecology (McGill et al. 2007), may be sensitive to the diversification process (Rosindell et al. 2010). Should high and low latitude regions yield different RAD curves, it could implicate disproportionate roles of distinct mechanisms governing species richness and permit tests of alternative theories of community structure (McGill et al. 2007). Indeed, different modes of speciation generate distinct relationships between RADs and phylogenetic tree shape (Davies et al. 2011). For example, decreasing RAD evenness or an excess of rare species toward high latitudes could conceivably reflect environmental harshness, ephemeral nascent species (transients), increased colonization, or temporal distance to equilibrium richness (Gray et al. 1979; Hubbell 1979; Magurran and Henderson 2003; McGill et al. 2007).

Concluding Remarks

Among the most globally conspicuous patterns in biology is the relative richness of biodiversity in the tropics compared to high-latitude parts of the world. We propose that latitudinal disparity in the relative prevalence of ecological speciation, induced by environmental and geographic drivers, provides a key evolutionary mechanism that accelerates rates of both speciation and extinction at high latitudes. High latitude regions are both cradle and grave with respect to diversification processes. In particular, the special susceptibility of nascent species formed through divergent natural selection to extinction by fusion motivates this ephemeral ecological speciation hypothesis. We have integrated the role of factors such as environmental harshness and ecological opportunity with population genetic notions about adaptation and the hardness of selection as mechanisms governing the evolution of reproductive isolation and extinction by fusion. The ephemeral ecological speciation hypothesis provides a microevolutionary process-oriented view of how speciation and extinction rates can vary predictably with latitude by connecting genetic mechanisms of the diversification process to selection and ecological, environmental, and geographic factors.

ACKNOWLEDGMENTS

This study was inspired by the Atwood Lecture delivered by D. Schluter at the 2014 Atwood Colloquium in Ecology and Evolution at the University of Toronto. We are grateful to J. Weir, L. Mahler, and D. Schluter for their constructive comments. ADC is supported by a Canada Research Chair and the Natural Sciences and Engineering Research Council of Canada. ADC designed the study, performed and analyzed simulation output, and wrote the manuscript. JCG implemented and ran simulations, and contributed to writing the manuscript.

DATA ARCHIVING

The doi for our data is doi: 10.5061/dryad.734v9

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Associate Editor: J. Boughman
Handling Editor: R. Shaw

Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Figure S1. Changes in diversity as a function of rates of origination (λ_1) and extinction (μ_1) of reproductively isolated "good"' species (A–C) and as a function of rates of origination (λ_3) and extinction (μ_2) of "nascent" species (D–F).