

Speciation reversal and biodiversity dynamics with hybridization in changing environments

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Abstract

A considerable fraction of the world's biodiversity is of recent evolutionary origin and has evolved as a by-product of, and is maintained by, divergent adaptation in heterogeneous environments. Conservationists have paid attention to genetic homogenization caused by human-induced translocations (e.g. biological invasions and stocking), and to the importance of environmental heterogeneity for the ecological coexistence of species. However, far less attention has been paid to the consequences of loss of environmental heterogeneity to the genetic coexistence of sympatric species. Our review of empirical observations and our theoretical considerations on the causes and consequences of interspecific hybridization suggest that a loss of environmental heterogeneity causes a loss of biodiversity through increased genetic admixture, effectively reversing speciation. Loss of heterogeneity relaxes divergent selection and removes ecological barriers to gene flow between divergently adapted species, promoting interspecific introgressive hybridization. Since heterogeneity of natural environments is rapidly deteriorating in most biomes, the evolutionary ecology of speciation reversal ought to be fully integrated into conservation biology.

Keywords: biodiversity, conservation, extinction, hybrid speciation, hybridization, speciation reversal

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Introduction

Predicting the effects of environmental changes on dynamics of biodiversity is perhaps one of the most pressing issues for ecologists and evolutionary biologists (McKinney & Drake 1998; Sala *et al.* 2000; Buckley & Roughgarden 2004; Thomas *et al.* 2004). A considerable fraction of the world's biodiversity is of recent evolutionary origin, and is the legacy of divergent adaptation in heterogeneous environments (Rundle & Nosil 2005). This includes locally adapted allopatric populations, genetically differentiated and ecologically maintained sympatric and parapatric ecotypes or incipient species, and perhaps the majority of closely related species (Coyne & Orr 2004). Divergent adaptation of plant and animal populations can also trigger further evolutionary diver-

sification if they are used as hosts by herbivorous insects and parasites, contributing significantly to global biodiversity (Price 1980; Bush & Butlin 2001).

The importance of habitat heterogeneity for the ecological maintenance of species richness is well rooted in community ecology (Tilman 1994; Rosenzweig 1995) and in island biogeography (MacArthur & Wilson 1967; Buckley 1982), and it is empirically strongly supported (Rosenzweig 1995; Ricklefs & Lovette 1999). It is also a cornerstone of conservation management (Mora *et al.* 2006). In evolutionary genetics, ever since the classical work of Wright on the genetic structure of populations, the impact of spatial and temporal heterogeneity of environments for the maintenance of genetic polymorphisms under selection has been a central theme (Wright 1951; Hedrick 1986). However, both theory and conservation practice have rarely addressed the effects of environmental heterogeneity on both species and genetic diversity simultaneously (but see Vellend 2003, 2004).

When ecologically driven speciation is common (Coyne & Orr 2004), an evolutionary continuum is formed from the

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adaptive genetic polymorphism within a species to the diversity among closely related species (Skulason & Smith 1995; Schluter 2000). Across this continuum, fertility barriers are weak and gene flow between species is barred mainly by divergent selection and correspondingly diverging mating preferences. Between such species, there is often a low level of gene flow, through which selection may promote the exchange of beneficial genetic variants while counteracting gene exchange at loci that maintain divergent adaptation of species in a shared heterogeneous environment (Wu 2001). To the extent that species boundaries are maintained by divergent adaptation, a loss of environmental heterogeneity may be expected to cause a sudden collapse of biodiversity.

Introgressive hybridization is best recognized in conservation biology as a cause of extinction brought about by species translocations or by the removal of dispersal barriers, bringing previously allopatric species into secondary contact [i.e. causing a loss of β -diversity (difference in species composition between localities) and γ -diversity (total species richness across all localities); Rhymer & Simberloff 1996; Allendorf *et al.* 2001]. On the other hand, genetic admixture of historically sympatric or parapatric species as a consequence of reduced heterogeneity in their shared environment [i.e. causing a loss of α -diversity (species richness within a single locality)] has been rarely recognized as a major cause of biodiversity erosion.

Impacts of human activities on natural environments are common in most biomes, and often make them more homogenous by, for example, simplifying habitat structure, fertilizing oligotrophic patches, or simplifying the diversity of signalling pathways (Candolin *et al.* 2006; Hendry *et al.* 2006; Seehausen 2006). We predict that, where genetic differentiation between species is maintained by adaptive evolution that is driven by heterogeneous environments, even a temporary loss of heterogeneity will bring a system to a new steady state with much reduced biodiversity.

To scrutinize this general prediction, this paper has two main parts: (i) a review of empirical case studies about the environment-dependent, ecological and evolutionary outcomes of interspecific hybridization, and (ii) the development of a simple mathematical model for biodiversity dynamics incorporating hybridization. We first discuss conceptual issues on the causes and outcomes of introgressive hybridization, then review published empirical examples, formulate the model, and finally discuss the vulnerability of biodiversity to the scenario described by our general prediction.

Concept notes

Hybridization plays dual roles in biodiversity dynamics. On one hand, it may contribute to an increase in species numbers by enhancing evolutionary potential through

elevation of genetic variability and introduction of novel gene combinations (Arnold 2006). On the other hand, hybridization may affect species numbers downward by collapsing existing species and constraining speciation by continuously breaking down incipient linkage disequilibria between genetic loci (Felsenstein 1981; Kirkpatrick & Ravigne 2002). More importantly, which role hybridization will play is context-dependent, influenced by the ecological background where it occurs. We look in more details into these context-dependent dual roles of hybridization by drawing upon theory of ecological and hybrid speciation. Here we consider biodiversity dynamics at a spatial scale across which hybridization can happen via spontaneous movements of organisms (i.e. not via anthropogenic translocations).

Ecological speciation is caused by adaptive divergence between populations or morphs within populations in response to divergent or disruptive selection (Skulason & Smith 1995; Schluter 2000; Coyne & Orr 2004; Rundle & Nosil 2005). During this process, gene flow between diverging populations or morphs becomes reduced either because trait divergence pleiotropically reduces gene flow (by-product speciation; Rundle & Nosil 2005), or because selection acts against migrants or intermediate phenotypes, that are ecologically less successful than extreme phenotypes (Rundle & Nosil 2005). Such reproductive isolation between divergent populations is induced by prezygotic (mate choice) and extrinsic (ecological) postzygotic mechanisms, in the absence of intrinsic postzygotic hybrid dysfunction. Heterogeneous environments provide alternative ecological niches and promote divergent adaptation, favouring the evolution of assortative mating, which in turn permits further genetic differentiation. A corollary is that a loss of environmental heterogeneity will loosen reproductive isolation, inducing hybridization between divergently adapted populations and collapsing them into a single deme.

On the other hand, a growing body of empirical evidence suggests that hybrid speciation is an important generator of biodiversity in plants (Anderson 1949; Stebbins 1959; Grant 1981; Rieseberg 1997), as well as in animals (Grant & Grant 1992; Dowling & Secor 1997; Arnold 2006). Few theoretical studies have formally investigated the dependence of the evolutionary outcome of interspecific hybridization on environmental variables (Buerkle *et al.* 2000, 2003). The Buerkle *et al.* models use a population genetic approach to investigate the fate of hybridizing populations under different combinations and levels of hybrid fertility, strength of ecological selection, availability of an empty niche, and spatial structure. The model suggests that homoploid hybridization can generate a new species when (i) an empty niche is available, (ii) ecological selection is strong, (iii) hybrid fertility is high, and (iv) habitats of parental and hybrid species are spatially well separated. Apart from mechanistic models, hybridization has been hypothesized to trigger or accelerate adaptive radiation (Seehausen 2004).

Empirical examples

For this review, we only include those types of hybridization that change species numbers either locally or globally, and that happened via spontaneous movements of organisms (hence in parapatric or sympatric populations and not via anthropogenic translocations). We restrict ourselves primarily to vertebrates for two reasons. (i) They are often flagship taxa in conservation biology. (ii) The recently emerging evidence for an abundance of interspecific hybridization was perhaps least expected among vertebrates, the group that was the model for the Biological Species Concept (Mayr 1963). We classify empirical examples into five groups based on the type of influence of hybridization on species diversity. In the first two categories hybridization negatively impacts on overall species diversity, whereas it positively impacts on species diversity in the other three categories. As it turns out, these dual roles of hybridization on biodiversity dynamics are clearly context-dependent, and a function of environmental heterogeneity.

Collapse of multispecies assemblages into hybrid swarms

Collapse of a species assemblage to a hybrid swarm is normally associated with a loss of environmental heterogeneity, and/or with reduced population densities. Both the rapid erosion of cichlid diversity in Lake Victoria and the complete collapse of the cisco (*Coregonus* spp.) radiation in the Laurentian Great Lakes were likely the result of increased levels of introgressive hybridization. In both cases multiple episodes of speciation had taken place in rapid succession during the Holocene in response to the emergence of ecological opportunity.

Replacement of a diverse natural predation regime by a strongly size-selective predation (due to invasive sea lamprey and fishery practices) caused large shifts in the abundances in Great Lake ciscoes, with the six larger growing of the eight species becoming very rare in the first half of the 20th century (Smith 1964). The lakes experienced strong eutrophication at the same time. By the 1960s, hybrid phenotypes dominated the catches in Lake Michigan, and several species had disappeared altogether (Smith 1964). Morphological data for the last two abundant species in Lake Huron, *Coregonus artedii* and *Coregonus hoyi*, suggest that even these collapsed into a hybrid swarm (Todd & Stedman 1989).

In Lake Victoria, reduction in cichlid abundances due to an introduced predator (Barel *et al.* 1985) coincided with loss of heterogeneity of the visual environment due to eutrophication (Seehausen *et al.* 1997a). Intermediate cichlid phenotypes came to dominate turbid waters with a complete collapse of some species complexes into single species (Seehausen *et al.* 1997a). Some populations that recovered after predator density decreased in the 1990s

consisted of new phenotypes (Seehausen *et al.* 1997b). It is likely that reduced visibility and population density made mate choice more costly (reduced mate encounter rates) and less effective, increasing the fitness of random, relative to selectively, mating individuals (Seehausen *et al.* 2003; Candolin *et al.* 2006). The heterogeneity of the selective environment (*sensu* Brandon 1990) collapsed with changes in the predation regime and light environment, significantly homogenizing the differences between optimal phenotypes and relaxing selection for assortative mating.

Pre-diversity-collapse molecular genetic data are lacking both in the ciscoes and the cichlids. Such data are available, however, for a speciation reversal in the postglacial radiation of the three-spined stickleback (Gow *et al.* 2006; Taylor *et al.* 2006). Enos and Paxton Lake on the British Columbian coast held independently evolved endemic stickleback pairs, with a benthic and a limnetic type differing markedly in size, shape, habitat, feeding, colour vision and male breeding colours (Boughman 2001; McKinnon & Rundle 2002). Some gene flow between the species has probably always existed (McPhail 1994), but was constrained by nesting site segregation, size assortative mate choice, sexual selection and ecological selection favouring extreme over intermediate morphologies (McPhail 1994).

Morphological and genetic analysis (Kraak *et al.* 2001; Taylor *et al.* 2006) for samples in Enos from 1977 to 2002, showed the progressive collapse of the initially genetically and morphologically very distinct species. By 1997 the species pair was replaced by a single morphologically intermediate hybrid population. The establishment of a crayfish in Enos over the course of the study likely changed the system from relatively clear waters with abundant littoral vegetation, to very turbid waters devoid of macrophytes (cf. Candolin *et al.* 2006). Taylor *et al.* (2006) suggest that these changes made mate choice and nesting habitat partitioning of the sticklebacks less effective. Food resources and their distribution might also have changed, impacting upon the fitness of different phenotypes and perhaps removing the disadvantage of intermediate phenotypes relative to the parental types. Crayfish establishment and substantial modification to this system may have been facilitated by increased nutrient loads from urban run-off (Taylor *et al.* 2006).

Gow *et al.* (2006) found similar patterns in Paxton Lake where molecular evidence suggested a period of historical introgression, which correlates with a known history of human-induced environmental change from the 1950s to the 1970s, followed by re-differentiation. Fluctuating water levels in Paxton due to quarry-mining between the 1950s and 1970s and the simultaneous introduction of Coho salmon (a predator of sticklebacks) likely impacted the suitability and distinctiveness of alternative spawning habitats. With return of the lake to more or less pristine conditions, the Paxton stickleback pair is genetically distinct again.

Geographical mosaics of species coexistence in some environments but collapse into hybrid swarms in others

Multispecies communities may collapse to hybrid swarms in some environments, but continue coexistence in other environments. An example of such a geographical mosaic comes from North American wild dog relatives. Grey wolf (*Canis lupus*) and coyote (*Canis latrans*) historically coexisted in North America except in the northeast. Coyotes occupy open country and the edge of forests while grey wolves are in larger forested areas, taiga and tundra (Leonard *et al.* 2005). Molecular population genetic investigations demonstrated that the two species have merged into hybrid swarms in areas where previously forested landscapes have been converted into agricultural land. Similar local species merging may have happened in the wake of habitat change during glacial cycles (Lehman *et al.* 1991). Highly human-modified landscapes east and southeast of the Great Lakes are currently occupied by a coyote–wolf hybrid swarm that may be better adapted to the prey size spectrum in converted landscapes than either of the parent species (Lehman *et al.* 1991; Wayne *et al.* 1998). In those areas of sympatry where conversion to agriculture is slow, hybridization has not been observed (Lehman *et al.* 1991).

Interestingly, the red wolf (*Canis rufus*), purportedly endemic to the US southeast, appears to have originated from hybridization between coyote and grey wolf long ago (Roy *et al.* 1996). It may have come into existence during landscape transformation following settling by Europeans (Roy *et al.* 1996; Wayne *et al.* 1998). Reintroduction of this hybrid species, extirpated from the wild, is heavily constrained by introgression from coyotes. Similar introgressive hybridization with coyotes was observed in the wake of the near extinction of the Mexican wolf (*C. lupus baileyi*, Roy *et al.* 1996).

The two African elephant species, savannah (*Loxodonta africana*) and forest elephant (*Loxodonta cyclotis*), share ecological relationships similar to coyotes and grey wolves; a 2.5-million-year evolutionary history of ecologically maintained parapatry with little evidence for introgressive hybridization over much of their ranges. Molecular genetic evidence, however, suggests that in areas that lost forest cover during the Holocene, displacement of *L. cyclotis* by *L. africana* occurred through introgressive hybridization. Additionally, there is evidence for current and recent introgressive hybridization in forest/savannah ecotones, and the ongoing deforestation and landscape conversion may foster genetic replacement of forest elephants (Roca *et al.* 2005).

Loss of ecological differentiation may come from surprising directions as the recent example by Hendry *et al.* (2006) demonstrates. They show that during the past 40 years a near-town population of the Galapagos ground finch, *Geospiza fortis*, has lost bimodality in the beak size, but a comparable population in an unpopulated area retains strong bimodality. The suspected reason is bird

feeding, which has effectively smoothed a previously rugged adaptive landscape for beak sizes. Naturally occurring changes in the resource base can have similar consequences (Grant & Grant 2002).

These vertebrate cases are just the more visible among a most likely very large number of cases of speciation reversal in human-altered environments. For instance, lowland and pre-alpine lakes of Europe have been greatly influenced by eutrophication from agricultural land use. Keller *et al.* (2002) hatched daphnid species from the egg bank stored in the sediments of such lakes dating back almost 50 years. Time series analyses showed that as eutrophication progressed, the once abundant *Daphnia hyalina* and *Daphnia galeata* were being replaced by viable and more productive F₁ hybrids. As oligotrophication efforts continue, data from Lake Greifensee suggests some resurgence of *D. galeata*-like genotypes, but *D. hyalina* seems lost and the majority of the current *Daphnia* present are *hyalina*–*galeata* hybrids (Keller & Spaak 2004).

The evolution of invasiveness through hybridization

If founders are few, colonizing populations may contain little genetic variation and lack opportunity for mate choice. The starting conditions for a new population of colonists are similar to the late stage of the extinction vortex (see fur seals below). Hybridization between different populations of colonists or with already established species may promote the establishment of the colonists while simultaneously allowing new genetic combinations to exploit underused or open niches. Such a hypothesis is consistent with the colonization of North America by the Cuban brown anole (*Anolis sagrei*; Kolbe *et al.* 2004, 2007).

Hybridization rescuing local biota from looming extinction

Hybridization may also rescue local biota from looming extinction. This can be very similar to evolutionary ecology and genetics of invasions. Three species of fur seal occupy the Antarctic and sub-Antarctic waters. Fur seal harvesting in the 19th century caused extinction of the populations on the isolated sub-Antarctic island of Macquarie. Slow recolonization, beginning from 1948, has involved male New Zealand fur seals (*Arctocephalus forsteri*), male subantarctic fur seals (*Arctocephalus tropicalis*) and female Antarctic fur seals (*Arctocephalus gazella*). Complete hybridization between the three species resulted in establishment of a hybrid population with steadily increasing pup production from 1963. Later, subantarctic females arrived in the 1980s followed by Antarctic males in the 1990s. The current Macquarie Island population is a composite of a hybrid swarm and nonhybrid individuals derived from more recent immigration (Lancaster *et al.* 2006). Hence, interspecific

hybridization was important for the recolonization of Macquarie Island, rescuing the initial colonists from immediate extinction through lack of breeding opportunity. The case of fur seals on Macquarie is similar to hybrid speciation, except that the hybrid population may not become genetically stabilized, and may experience further gene flow from, and into, the parental species.

Hybrid speciation leading to an increase in species numbers

Hybrid taxa can become genetically stabilized and coexist with the parental taxa as distinct species (Mallet 2007). This is in many cases associated with colonization of novel or extreme habitats. These include extreme novel water flow regimes colonized by a hybrid sculpin species (Nolte *et al.* 2005), extreme feeding niches colonized by a hybrid cichlid fish species (Schliewen & Klee 2004). Less often it is associated with colonization of intermediate habitats, e.g. intermediate-sized tributaries inhabited by a river chub species of hybrid origin (DeMarais *et al.* 1992). Even though we confine this review to vertebrates, we wish to note that a large number of cases of hybrid speciation have in recent years been documented in invertebrates and plants, and almost all are associated with colonization of novel or extreme habitats as well, i.e. new host plants colonized by hybrid tephritid fruitfly species (Feder *et al.* 2003; Schwarz *et al.* 2005), extreme soils colonized by hybrid sunflower species (Rieseberg *et al.* 2003), extreme climates colonized by hybrid butterfly species (Gompert *et al.* 2006). Association between hybridization and colonization of new niches suggests strongly that species diversity can be importantly supplemented by hybrid speciation. There is also increasing evidence for hybrid speciation within large adaptive radiations, as in cichlid fish of Lake Tanganyika (Salzburger *et al.* 2002) and Lake Malawi (Kidd *et al.* 2006). Finally, there is evidence from at least three cases that adaptive radiations were seeded by interspecific hybridization (Barrier *et al.* 1999; Joyce *et al.* 2005; Herder *et al.* 2006).

The dynamic model of biodiversity with hybridization

The review of empirical examples suggests that the context-dependent dual roles of hybridization can strongly influence the biodiversity dynamics of a given biota. Currently, there have been few attempts to formulate biodiversity dynamics with hybridization taken into account. Here we develop a mathematical model to study how hybridization may influence biodiversity dynamics. Although it is fairly simple and should be viewed as an initial step toward a fuller theoretical framework, the model provides insightful theoretical expectations on how biota-specific speciation and extinction rates determine the effects of hybridization on biodiversity dynamics in the context of environmental change.

The model assumes a closed system (no immigration) with average rates of speciation, extinction and hybridization. The model is thus species neutral, likewise to the MacArthur–Wilson model of island biogeography (MacArthur & Wilson 1963; MacArthur & Wilson 1967; Hubbell 2001). Traditionally, biodiversity dynamics have been modelled using a dynamical equation in which speciation and extinction counteract (Rosenzweig 1995). Here we add new terms to such an equation in order to study the consequences of introgressive hybridization. Hybridization can have net positive or negative effects on biodiversity via hybrid speciation or merging of species (speciation reversal):

$$\frac{dR}{dt} = s(1-\Omega)R - eR + h\frac{R(R-1)}{2}(1-2\Omega) \quad (\text{eqn 1})$$

where R is the number of species; s is the intrinsic speciation rate of a given species; e is the intrinsic extinction rate of a given species; h is the rate at which the average pair of species produces a population of viable and fertile hybrids; Ω is the probability that a new species fails to establish itself, and also gives the probability that a hybrid population fails to establish as a new hybrid species.

The intrinsic speciation rate, s , is the average rate, across all species in the system, at which a species splits into two. A speciation event can be annulled with the probability Ω , meaning that the new species is merged to one of the existing species. We assume that the degree of ecological overlap determines the degree of genetic admixture, such that reproductive isolation is a by-product of niche differentiation as observed in instances of ecological speciation (Bush & Butlin 2001; Rundle & Nosil 2005), including ecological hybrid speciation (Rieseberg *et al.* 2003; Nolte *et al.* 2006; Schwarz *et al.* 2006). The probability Ω depends on the degree of environmental heterogeneity of the system and the extent to which other species utilize this heterogeneity. Formally

$$\Omega = \frac{R}{H+R}, \quad (\text{eqn 2})$$

where H is an index of environmental heterogeneity. This formulation means that the probability becomes minimum (zero) when there is no species in the system, and asymptotically increases to 1 as the number of species increases. The environmental heterogeneity index, H , represents the number of species at which the probability Ω becomes 0.5. As H increases, Ω approaches to 1 in response to an increase in R . In other words, $\Omega < 0.5$ if $R < H$, and $\Omega \geq 0.5$ if $R \geq H$.

Environmental heterogeneity can affect both the rate at which hybridization occurs and the fate of hybrid populations (Schluter 2000; Hendry *et al.* 2006). Both types of influences may be important, and they can potentially interact (e.g. high hybrid survival and reproductive success may elevate the rates of hybrid formation). To keep our model tractable, we focus on the effect of environmental heterogeneity on the fate of hybrid populations, and assume

that heterogeneity does not influence the rate of hybrid formation. Because h is the average rate at which any pair of species in the system forms a hybrid population, the overall rate at which a hybrid population is produced is $hR(R-1)/2$ [because the total number of species pairs in the system is $R(R-1)/2$]. Upon formation of a hybrid population, three outcomes are possible: (i) both hybridizing species may be replaced by the hybrid population, which can be interpreted as genetic merging or speciation reversal, (ii) two species may remain, or (iii) a hybrid population may get established as a third species in addition to the two parental species (hybrid speciation). By the same mechanisms operating on speciation (where the extent of ecological niche differentiation determines the extent of reproductive isolation), a hybrid population may merge to one of the existing species with the probability Ω depending on environmental heterogeneity and the number of extant species. If a hybrid population mediates a merger between parental species (which occurs with probability Ω^2), hybridization results in a net loss of one species. This corresponds to the above outcome (i). If a hybrid population merges with only one of the parental species [with probability $2\Omega(1-\Omega)$], hybridization causes no apparent change in species number, corresponding to the outcome (ii). Finally, if a hybrid population does not merge with any of its parental species [with probability $(1-\Omega)^2$], hybridization produces a net increase of one species. Thus, adding up all of these outcomes multiplied with respective probabilities, the expected change in species number caused by hybridization is

$$\left[(-1) \times \Omega^2\right] + \left[0 \times 2\Omega(1-\Omega)\right] + \left[1 \times (1-\Omega)^2\right] = 1 - 2\Omega. \quad (\text{eqn 3})$$

Multiplying this with the gross hybridization rate [$hR(R-1)/2$] gives the last term of eqn 1.

This mathematical formulation gives a simple representation of hypothetical mechanisms underlying speciation reversal and hybrid speciation in real examples (e.g. Seehausen *et al.* 1997a; Schwarz *et al.* 2005). For example, we may consider two sympatric cichlid fishes continuously producing hybrids at low frequency. While high heterogeneity in visual environment (i.e. a wide range of ambient wavelengths available for sexual signalling) allows the discrimination of two alternative male nuptial colours, there may be disruptive selection against hybrids bearing intermediate colours and preferences, maintaining the two parental species (i.e. there are two adaptive peaks). If environmental heterogeneity declines, such that the wavelengths range of ambient light becomes considerably narrower, the disruptive selection against hybrids is lost (i.e. the two adaptive peaks are flattened) and speciation reversal will occur. In case of hybrid speciation, imagine two tephritid fruitflies continuously producing hybrid populations. When a new host plant species is introduced by humans, a hybrid population may be able

to establish itself as a new hybrid species on the introduced host plant (in this case, human activities actually increase environmental heterogeneity, adding the third adaptive peak).

Model analysis

The model is most appropriate when R is sufficiently large. When R is close to 1, stochasticity inherent in the processes of speciation, extinction, and hybridization may dominate the dynamics of biodiversity. The current model that assumes the average rates of these processes may be unsuitable for capturing strongly stochastic dynamics, and is likely to under-represent the random events that cause species loss when number of species is small. To fully address the outcome of hybridization for a system with a small number of species, stochastic simulation models would be more appropriate. However, we leave this issue for future development, and analyse the model (eqn 1) by assuming $R \gg 1$. The results from this simple model will help construct and analyse a fuller stochastic model. With the assumption $R-1 \approx R$, the model (eqn 1) incorporating eqn 2 becomes

$$\frac{dR}{dt} = \frac{R[s-e+(h/2)R]}{H+R} \left[H - \frac{e+(h/2)R}{s-e+(h/2)R} R \right]. \quad (\text{eqn 4})$$

We analyse the dynamics of this model at equilibrium (Rosenzweig 2001). The equilibrium number of species, \bar{R} , is then given as an implicit function of H :

$$H = \frac{e+(h/2)\bar{R}}{s-e+(h/2)\bar{R}} \bar{R}. \quad (\text{eqn 5})$$

The geometry of this function (e.g. intercepts, slope, and asymptotic behaviour) can be gained analytically with straightforward algebra (summarized in the Appendix).

Model results

The model predicts several different scenarios. In all, the loss of environmental heterogeneity (i.e. a decrease in H) reduces the equilibrium number of species. Depending on the relative magnitude of speciation and extinction rates, impacts of hybridization on the relationship between environmental heterogeneity and species number are different.

We begin with the benchmark scenario where $h=0$ (i.e. no hybridization). The equilibrium species number is then given from eqn 5 as

$$\bar{R} = \left(\frac{s}{e} - 1 \right) H. \quad (\text{eqn 6})$$

This means that s must be greater than e for \bar{R} to be positive. When $s > e$ and $h=0$, \bar{R} will increase proportionally with an increase in H .

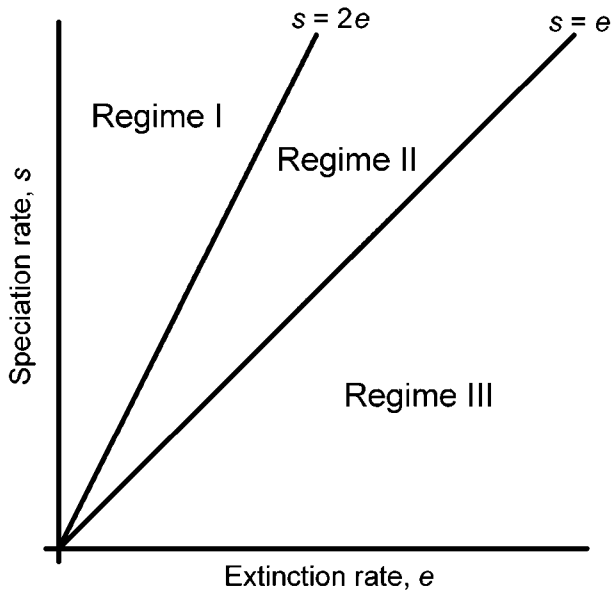


Fig. 1 Parameter regions for regimes I, II and III. These regions are entirely determined by the speciation rate, s , and the extinction rate, e , and do not depend on h .

In more general scenarios where $h > 0$, we find three regimes with qualitatively different relationships between \bar{R} and H . The relative magnitude of s and e determines these alternative regimes (Fig. 1): $s \geq 2e$ (regime I), $2e > s > e$ (regime II), and $e \geq s$ (regime III). One important result is directly derived from eqn 3. That is, hybridization results in a net increase of species number if Ω is smaller than 0.5 (and vice versa). This further means that hybridization causes a net increase of species if $R < H$ (recall $\Omega < 0.5$ if $R < H$).

In regime I, \bar{R} is uniquely determined as a monotonically increasing convex function of H (Fig. 2a). The steepness of an increase in \bar{R} with an increase in H is noticeably greater than 1 when H is small, and decreases asymptotically to 1 as H increases (Fig. 2a, S1A). \bar{R} is always greater than H , meaning that hybridization causes a net loss of species at equilibrium. Thus, hybridization is playing the negative role of reducing species number. Because of this, increasing hybridization rate h lowers \bar{R} across all H , reducing the range of H with high steepness (Fig. 2d). As a result, a loss of environmental heterogeneity causes a smaller reduction in species number where the hybridization rate is high than where it is low.

In regime II, \bar{R} is uniquely determined as a monotonically increasing concave function of H (Fig. 2b). The steepness of the relationship between \bar{R} and H is shallow (i.e. smaller than 1) where H is small, and increases asymptotically to 1 as H becomes larger. In contrast to regime I, \bar{R} is always smaller than H , meaning that hybridization plays the positive role of increasing species number at equilibrium. Hybridization always increases the equilibrium spe-

cies number given a certain amount of environmental heterogeneity (Fig. 2e). The loss of species to a given decrease of environmental heterogeneity is greater if the hybridization rate is higher (Fig. 2e).

Regime III predicts an interesting distinct relationship between \bar{R} and H (Fig. 2c). In this regime, the equilibrium species number cannot be positive without hybridization because e is greater than s . \bar{R} is smaller than H , meaning that hybridization is playing the positive role of increasing species number at equilibrium (Fig. 2F, S1C). Notably, there is a threshold of environmental heterogeneity, $H_{\text{threshold}}$, below which no positive species number is predicted. This threshold is given by

$$H_{\text{threshold}} = \frac{4(3e - 2s)}{h}, \quad (\text{eqn 7})$$

indicating that the threshold decreases as hybridization becomes more frequent. Above this threshold, the model predicts two equilibrium species numbers: one at the upper equilibrium that is locally stable, and the other at the lower unstable equilibrium. As H increases beyond $H_{\text{threshold}}$, the species number at the higher equilibrium approaches to H , and that at the smaller equilibrium approaches to $2(e - s)/h$. If a community starts off from an initial species number below the lower equilibrium, the species number never reaches the larger equilibrium and collapses to zero. This is because in a community with few species there is little opportunity for hybridization between two species to occur. This is critical because a positive species number is impossible without hybrid speciation in this regime. Only if the species number in the community is initially greater than the smaller equilibrium, can the species number converge to a positive value (at the larger equilibrium). Importantly for scenarios where environmental heterogeneity degrades, a degradation across $H_{\text{threshold}}$ predicts a sudden collapse of species number to zero. Once this has happened, a recovery of environmental heterogeneity beyond $H_{\text{threshold}}$ cannot by itself restore a positive species number, unless a community is seeded with a number of species exceeding the lower equilibrium.

Model discussion

The major predictions of the model are twofold: (i) hybridization can have profound influences on biodiversity dynamics, and (ii) the relative magnitude of biota-specific speciation and extinction rates determines how hybridization mediates the impacts of environmental homogenization on biodiversity. In this subsection, we discuss these predictions and potential future directions for a more comprehensive theoretical framework for biodiversity dynamics with hybridization.

Our simple model offers several important expectations for the effects of hybridization on diversity dynamics in changing environments. First, in species-rich biota that

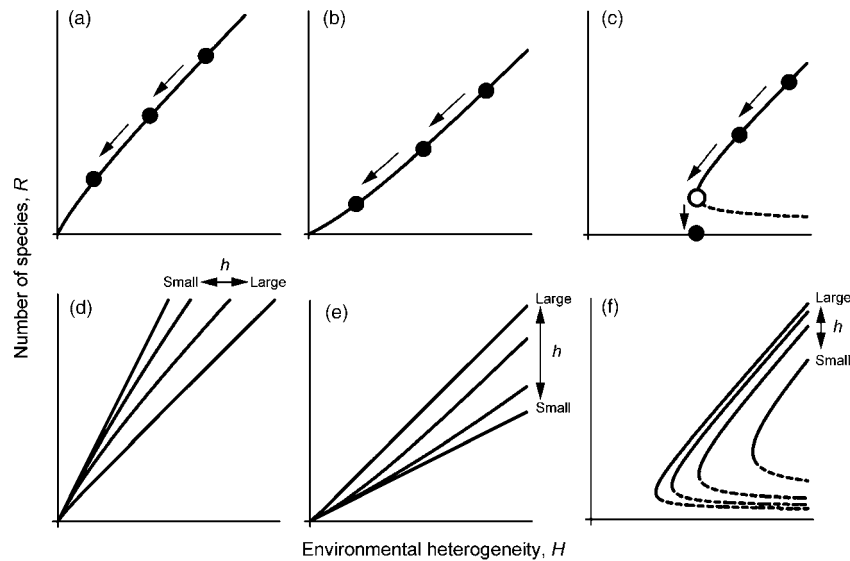


Fig. 2 Number of species along a gradient of environmental heterogeneity predicted by the model in regime I (a, d), regime II (b, e), and regime III (c, f). The solid lines and filled circles represent stable equilibria, and the dashed lines and open circle unstable equilibria. The arrows between the circles indicate the shifts of equilibrium points in response to declining environmental heterogeneity. (a, b) A gradual habitat degradation causes a gradual decrease in species number. (c) A gradual habitat degradation turns a stable equilibrium into an unstable equilibrium, causing a sudden decline in species number. (d–f) Responses of equilibria to changes in the hybridization rate. In (d), increasing the hybridization rate reduces the number of species. In (e) and (f), increasing the hybridization rate increases the number of species at a given environmental heterogeneity. However, in (e) the diversity response to heterogeneity loss is much steeper when there is more hybridization.

have sustained high intrinsic speciation rates and low extinction rates (regime I), hybridization plays the negative role of reducing equilibrium biodiversity. An increase of the intrinsic rate of hybridization will thus lead to a major reduction in species richness even without a reduction of environmental heterogeneity, and to a dramatic reduction in species richness when coupled with reduction of environmental heterogeneity.

Second, when intrinsic speciation rates do not, or only narrowly exceed the background extinction rates (regimes II and III), hybridization becomes an important potential generator of species diversity and helps to sustain species richness at the level that is supported by niche heterogeneity. Regime II (i.e. speciation rate slightly exceeds extinction rate) might apply to any biota that are not currently in an ‘expansive’ phase. When such a biota contains species that are young enough to hybridize (as in most postexpansive phase adaptive radiations of Pliocene/Pleistocene origin), reduction in environmental heterogeneity leads to a rapid erosion of species diversity, the rate of which is even higher if hybridization is more frequent.

Third, when background extinction rates exceed intrinsic speciation rates, but environmental heterogeneity remains large, hybridization can buffer diversity to some degree against net extinction (regime III). Such a situation might correspond to taxa suffering from reductions in population size and genetic variation due to exploitation or fragmenta-

tion. However, the buffering effect of hybridization is lost when species richness falls below a minimum threshold. The slope of the decline in species richness as a function of reduction in niche heterogeneity in such a regime is not strongly affected by the rate of hybridization until the threshold species richness is reached. At that stage diversity is suddenly lost entirely.

A future theoretical framework for biodiversity dynamics with hybridization should relax some assumptions made for our simple model. At least, five issues are particularly important. First, our model omits the mechanistic details of speciation and speciation reversal. Specifically, we assume that (i) occupation of different niches dictates genetic differentiation, (ii) invasion of a new habitat niche equates to speciation, and (iii) sharing the same niche in the face of gene flow forces collapse of two species into one. We can interpret this as a strict ecological by-product speciation scenario, where cessation of gene flow is a pleiotropic consequence of divergent adaptation. While speciation that resembles this scenario may indeed occur in nature (Rieseberg *et al.* 2003; Rundle & Nosil 2005; Schwarz *et al.* 2005; Nolte *et al.* 2006), other cases of ecological speciation may require genetic linkage disequilibria to evolve between ecological and mating traits before cessation of gene flow is possible (Rundle & Nosil 2005). We think that the population genetic constraints on building and maintaining linkage disequilibria between ecological and mating traits

(Felsenstein 1981; Kirkpatrick & Ravigné 2002) may narrow the opportunity for hybrid speciation and increase the opportunity for speciation reversal. While it is likely that this affects species dynamics quantitatively, we think that the dynamics in our model are unlikely to change qualitatively.

Second, our model considers a closed system. In reality, most systems receive immigrants from the outside. Indeed, as reviewed in the empirical evidence section, recurrent immigration to spatially open systems can provide individuals in a dwindling population with mating partners and help sustain the local population (Lancaster *et al.* 2006), or provide invading populations with novel genetic materials with which to swiftly adapt to new environments (Kolbe *et al.* 2004). Along this line, taking into account hybridization within the framework of MacArthur–Wilson’s island-biogeography theory (MacArthur & Wilson 1967) or Hubbell’s unified neutral theory (Hubbell 2001) seems promising.

Third, we assumed time-invariant speciation, extinction, and hybridization rates that on average apply to all species in the biota. However, these rates likely change through time. In addition, the rich complexity of biodiversity behaviour (Boucot 1975; Miller & Foote 1996; Alroy 1998) may not be fully captured at equilibrium, but potentially occur at nonequilibrium attractors and transient dynamics (Hastings *et al.* 1993; Hastings 2004). Adaptive radiation, whether seeded by hybridization or not, may in particular be a likely candidate for such nonequilibrium biodiversity dynamics.

Fourth, from the viewpoint of adaptive landscapes, our model considers a loss of heterogeneity as a loss of the valley between two adaptive peaks occupied by extant species (which increases the probability of hybridizing species collapsing into one species), or a loss of an unused adaptive peak (which prevents an incipient species from establishing). Our model does not directly consider that the loss of an adaptive peak occupied by an extant species could cause the extinction of this species also in the absence of hybridization with species occupying neighbour peaks. Such an effect could be modelled by assuming the extinction rate as a decreasing function of heterogeneity.

Fifth, we assumed that the probability that an incipient species establish itself is the same ($1 - \Omega$), whether it is of hybrid origin or not. However, as several empirical examples indicate, an incipient species of hybrid origin may have higher genetic diversity than one originating from normal speciation, and thus have a higher probability of successfully establishing when a new ecological niche is available. This might have led our results to underestimating the effect of hybrid speciation.

Conclusions

In the introduction, we made a general prediction that, where genetic differentiation between species is the result

of adaptive evolution in heterogeneous environments, a loss of environmental heterogeneity will bring the system to a new steady state with much reduced biodiversity. Our empirical review and mathematical model find that interspecific hybridization is an important mechanism underlying this general prediction. A likely outcome is that hybridization collapses sympatric, ecologically divergent pairs of related species upon loss of environmental heterogeneity.

In order to judge the significance of hybridization-driven biodiversity dynamics that we describe in this paper, it is helpful to derive estimates of the proportion of the global vertebrate species diversity that is sensitive to hybridization (Table 1). A critical time window could be the first 2–5 million years after speciation during which intrinsic postzygotic isolation is absent or incomplete (Coyne & Orr 2004). Because this is several orders of magnitude longer than the time required for ecological speciation (Schluter 2000; Seehausen 2002; Coyne & Orr 2004; Hendry *et al.* 2007), we predict that a large proportion of global species diversity is susceptible to hybridization-driven diversity change. This is true regardless of the geographical setting of ecological speciation and applies equally to species arising from allopatric by-product speciation, ecologically driven reinforcement and parapatric or sympatric speciation. To estimate the fraction of biodiversity sensitive to hybridization, the clade-specific ratio of young species to older ones no longer able to exchange genes may be a useful first approximation (Seehausen 2006). Even a conservative, nonexhaustive, cursory survey of the literature on taxa from very different environments (mammals, fish) shown in Table 1 demonstrates the rather ubiquitous susceptibility of many species to hybridization. Such estimates indicate that a very large proportion of global species richness may be vulnerable to hybridization-driven biodiversity dynamics.

Many influences of human activities on biodiversity, such as the extinction of species and biological invasions, and effects of climate change on both, are rather direct and obvious. Less obvious, but potentially equally or more important, are the anthropogenic influences on evolutionary processes generating and maintaining biodiversity (Myers & Knoll 2001; Rosenzweig 2001). Interspecific hybridization is such an evolutionary process that is (i) highly susceptible to human influences, and (ii) very fast. Decreasing landscape heterogeneity at all spatial scales from microhabitats to biomes most likely elevates the general likelihood of hybridization by relaxing ecological divergent selection among species and/or by elevating the costs of mate choice in declining populations. The most probable proximate outcome of such hybridization will be a collapse of hybridizing species and subsequent loss of biodiversity.

Collapsing the diversity of young ‘ecological’ species into fewer species may not immediately cause loss of diversity of genes, but is a tremendous loss of standing biodiversity with likely major repercussions to ecosystem function

Table 1 Teleost fish and mammal taxa and their estimated susceptibility to speciation reversal by hybridization using estimated times to most recent common ancestor (MRCA). Susceptibility calculated as the proportion of taxa pairs, out of those listed, characterized by divergence times less than or equal to 2 and to 5 million years (Myr), and is based on predictions of half establishment (i.e. only homogametic sex is inviable or infertile after 2 Myr), and full establishment of postzygotic isolation (both sexes are inviable or infertile after 5 Myr) (i.e. Haldane's rule as expressed by Coyne & Orr, 2004). Divergence based on genetic distances calculated between sequences listed on GenBank or expressed in cited studies. Sequence divergence calculated using Kimura 2-parameter distances with $\gamma = 1.0$ substitution rate. Sequence divergence was converted to time to MRCA by assuming a constant rate of divergence set at 2%/Myr. Average divergence susceptibilities calculated over taxa groups used in analysis

Taxa groups	Number of taxa used	Average genetic distance between taxa (± 2 SD)	Average time to MRCA in Myr (± 2 SD)	Proportion with high susceptibility (≤ 2 Myr)	Proportion with moderate susceptibility (≤ 5 Myr)	Reference	Marker	Hybridization already observed
Teleost fishes								
Salmonids	14	0.09 (0.02–0.16)	4.41 (1.07–7.76)	0.07	0.62	2–8	Complete mtDNA	✓
Pacific salmonids	11	0.07 (0.02–0.12)	3.38 (0.82–5.94)	0.13	1.00	2–7	Complete mtDNA	✓
Coregonids	24	0.02 (0.00–0.04)	0.99 (0.0–2.21)	0.92	1.0	9–11	mtDNA	✓
Lake Tanganyika cichlids	42	0.09 (0.02–0.16)	4.71 (1.21–8.21)	0.06	0.55	12–13	mtDNA	✓
Lake Malawi cichlids	66	0.04 (0.01–0.08)	2.18 (0.05–3.91)	0.41*	1*	13–16	mtDNA	✓
Lake Victoria cichlids	79	< 0.01 (0.00–0.02)	0.41 (0.0–1.13)	0.97*	1*	13, 16–19	mtDNA	✓
Lake Matano silver sides	3	0.03 (0.01–0.05)	1.55 (0.49–2.61)	0.33	1	20	mtDNA	✓
Average	7	0.06 (0.00–0.12)	2.52 (0.00–5.88)	0.41	0.88			
Mammals								
Canids	24	0.13 (0.05–0.21)	6.61 (2.61–10.61)	0.04	0.17	21	mtDNA	✓
North American wolf-like canids	14	3.29 (0–7.36)	1.64 (0–3.68)	0.58	1.0	22	mtDNA	✓
Ursus (bears)	5	0.08 (0.02–0.15)	4.13 (0.9–7.38)	0.2	0.60	23–25	mtDNA	✓
	8	0.04 (0.00–0.16)	2.08 (0.0–5.21)	0.75	0.75	23	Nuclear DNA	
Pinipeds (seals and sea lions)	30	0.18 (0.04–0.31)	9.02 (2.45–15.58)	0.06	0.14	24–29	Complete mtDNA	✓
Elephants	2	0.04 (0.00–0.10)	2.02 (0.00–4.79)	1.0	1.0	30	mtDNA	
	2	< 0.01 (0.00–0.01)	0.07 (0.0–0.24)	1.0	1.0	30, 31	Nuclear DNA	✓
Primates	56	0.07 (0.00–0.36)	3.26 (0.10–17.88)	0.21	0.66	32	NA	
<i>Strepsirhines</i>	8	0.17 (0.05–0.24)	8.66 (2.70–12.0)	0	0.13	32	NA	
<i>Platyrrhines</i>	29	0.07 (0.03–0.43)	3.27 (1.33–21.36)	0.17	0.66	32	NA	
<i>Catarrhines</i>	19	0.05 (0.00–0.10)	2.70 (0.10–5.0)	0.37	0.89	32	NA	✓
<i>Hominoids</i>	5	0.14 (0.03–0.24)	6.93 (1.67–12.20)	0.1	0.2	33–34	Complete mtDNA	
Average	10	0.42 (0.00–2.44)	4.82 (0.00–10.3)	0.23	0.55	Based on mtDNA only		

Means and ± 2 SD range (in brackets), negative ranges reported as 0.0. *Estimated time to most recent common ancestry among taxa with incomplete mitochondrial DNA (mtDNA) lineage sorting likely underestimates actual amount of hybrid susceptibility. NA, molecular data not provided in cited study.

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(Chapin *et al.* 2000). Of course eventually, the loss of gene diversity will ensue too if diversifying selection is weakened. As conservation and evolutionary biologists we should therefore be as much concerned about the maintenance of the ecological processes that provide the basis for evolutionary mechanisms generating and maintaining species diversity, as we already are about the maintenance of genetic and species diversity. Furthermore, human-induced hybridization might ultimately provide important sources of genetic novelty for organisms to adapt in changing environments, but the outcome may not always be desirable from the viewpoint of human society. It is an urgent task to develop conceptual grounds on which we can discuss the future of evolution, and we hope that this paper may make a little contribution towards that goal.

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- Ole Seehausen is interested in biodiversity dynamics, including speciation, adaptive radiation and evolutionary mechanisms that drive loss of diversity. Gaku Takimoto is interested in how biodiversity evolves and is maintained at different levels of biological organization from genes to ecosystems. Denis Roy is interested in quantitative evolutionary ecology, specifically in underlying mechanisms of speciation and adaptation. Jukka Jokela's research is focused on evolutionary ecology of host parasite interactions.
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Appendix

In regime I, the curve $H = R + F(R)$ intersects the origin and asymptotes to $R = H + 2 (s - 2e)/h$ as H goes to infinity. Because $s \geq 2 e$, the line $R = H + 2 (s - 2e)/h$ lies above the line $R = H$. Where $R \geq 0$, $R + F(R)$ is always positive because

$$\left. \frac{\partial [R + F(R)]}{\partial R} \right|_{R=0} = \frac{e}{s - e} > 0$$

dR/dt is negative on the upper side of the curve, and positive on the lower side, ensuring that \bar{R} is stable.

In regime II, the curve intersects the origin and asymptotes to $R + 2 (2e - s)/h$ as R goes to infinity. Unlike regime I, the line $R = H + 2 (s - 2e)/h$ lies below the line $R = H$, because $s < 2e$. \bar{R} is found stable as in regime I.

In regime III, the curve $H = R + F(R)$ shows a parabola. The upper segment of the parabola asymptotes to $R = H + 2 (s - 2e)/h$ as H goes to infinity, while the lower segment approaches $R = 2 (e - s)/h$. The upper and lower segments meet where $R = 2 (3e - 2s)/h$ and $H = 4 (3e - 2s) / h$. dR/dt is positive on the right area of the parabola, and negative in the remaining area, meaning that \bar{R} on the lower segment is unstable, and that on the upper segment is stable.

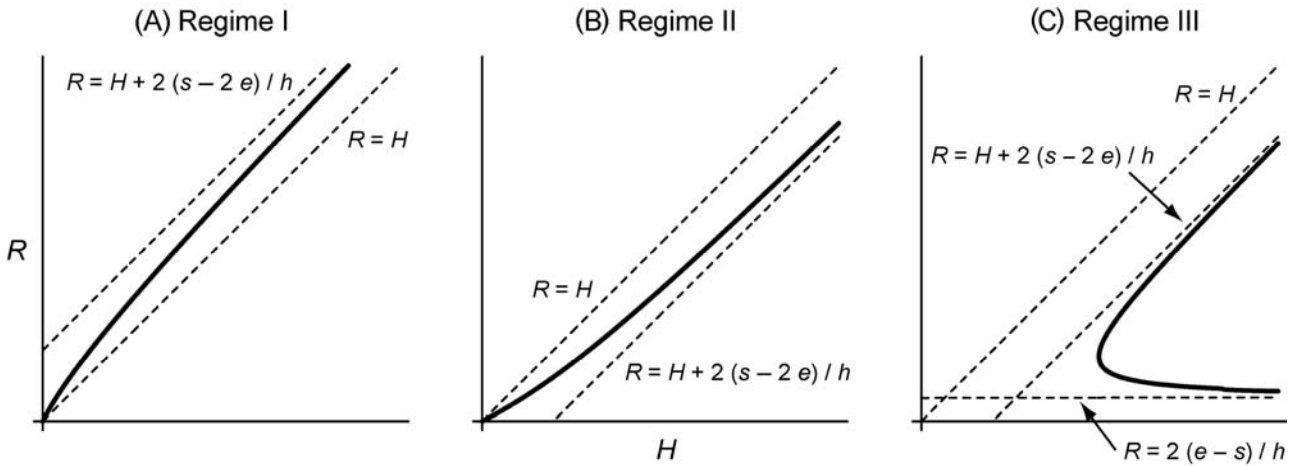


Fig. A1 The shape of the relationship between equilibrium species number and environmental heterogeneity for regime I (A), regime II (B), and regime III (C). The thick curves represent $H = R + F(R)$.