



## Abstract

The neutral theory of biodiversity purports that patterns in the distribution and abundance of species do not depend on adaptive differences between species (i.e. niche differentiation), but solely on random fluctuations in population size (“ecological drift”), along with dispersal and speciation. In this framework, the ultimate driver of biodiversity is speciation. However, the original neutral theory made strongly simplifying assumptions about the mechanisms of speciation, which has led to some clearly unrealistic predictions. In response, several recent studies have combined neutral community models with more elaborate speciation models. These efforts have alleviated some of the problems of the earlier approaches, while confirming the general ability of neutral theory to predict empirical patterns of biodiversity. However, the models also show that the mode of speciation can have a strong impact on relative species abundances. Future work should compare these results to diversity patterns arising from non-neutral modes of speciation, such as adaptive radiations.

## The neutral theory of biodiversity

Over the course of the last half-century, several major controversies in biology have been fought over the scopes and limits of natural selection. These include the neutralist-selectionist debate [1, 2], and the controversies over levels of selection [3], sociobiology [4], and adaptationism [5]. In several instances, the conflict revolved around “chance and necessity” [6], that is the relative importance of deterministic versus stochastic forces. For example, Kimura claimed that much of DNA or protein sequence variation can be explained by genetic drift alone [1], and Gould stressed the importance of mass extinctions and contingency for the history of life on earth [7]. The latest incarnation of this debate is currently taking place in the field of ecology. Here, the question is whether adaptive differences between species are important for explaining large-scale patterns of biodiversity.

Why is it that some communities are species-rich and others species-poor? Why are some species common and others rare? How does the composition of communities change over space and time? – Traditionally, answers to these questions have been sought within niche theory [8–11], which posits that, in order to coexist, species need to be sufficiently different and use resources in sufficiently different ways [12]. The twin principles of competitive exclusion

1 [13] and limiting similarity [14, 15] have long been among the corner stones of ecological  
2 thinking. However, many feel that niche theory has problems in explaining highly species-  
3 rich communities in relatively homogeneous environments [16, 17], such as marine plankton,  
4 tropical forests or coral reefs (but see [18]). Furthermore, competitive exclusion can be  
5 effectively infinitely delayed by dispersal-limitation [19].

6 In his 2001 monograph [20], Hubbell – building on MacArthur’s and Wilson’s theory of is-  
7 land biogeography [21] and Kimura’s neutral theory of population genetics [1] – proposed a  
8 radically different theory of biodiversity, which focuses on the effects of demographic stochas-  
9 ticity and dispersal-limitation (for reviews, see [22–27], and for a nice summary, [28, 29]). He  
10 starts out from the premise that all individuals from all species within a given trophic level  
11 are “ecologically equivalent”, that is, they have the same probabilities of dying, reproducing,  
12 dispersing and even of giving birth to a new species. Species abundances fluctuate randomly  
13 due to stochastic birth and death events, leading to a process of “ecological drift”, which  
14 is analogous to genetic drift of neutral alleles and inevitably leads to random extinctions.  
15 Hubbell’s main model has two levels: In local communities, extinctions are balanced by  
16 immigration of new species from a regional pool called the metacommunity. In the metacom-  
17 munity itself, drift is slow, and biodiversity is maintained in a balance between extinction and  
18 speciation. Hubbell used his theory to derive the species-abundance distribution (SAD) at  
19 both levels (see Box 1). Furthermore, he developed a spatially explicit version of the theory,  
20 which allows to deduce the species-area curve (SAC). It is because of these two predictions  
21 that he called his theory the “unified neutral theory of biodiversity and biogeography”. Here,  
22 I will use the simpler term neutral biodiversity theory (NBT).

23 The rise of NBT is generally seen as one of the most important developments in ecology during  
24 the past decade [30]. Predictably, by radically pushing aside ecological complexity, it has  
25 aroused abundant controversy. For example, NBT has been criticized for having insufficient  
26 empirical support [31], focusing solely on pattern while neglecting process [26, 32], having a  
27 limited scope of predictions [18, 26], and not being helpful for conservation [32]. In return,  
28 its proponents have put forward that NBT has reinvigorated ecology [28], that it gives due  
29 importance to sampling issues, demographic stochasticity and dispersal limitation [24], that  
30 it can be viewed as a first approximation or a null model [33, 34], and that it is intended as a  
31 stepping stone towards a more inclusive theory, which will combine neutral and niche-based

1 processes [20]. Nobody denies that niche differences do exist [20], but it has been argued  
2 that they might be less important than commonly accepted [20, 33, 35] and that ecological  
3 equivalence may arise as an emergent property of evolving communities [33, 35–37].

4 While most debates over NBT have focused on the central assumption of neutrality (or the  
5 “niche versus neutrality” dichotomy), other aspects of the theory may be equally important  
6 for its predictions. In the following, I will focus on one such aspect: the role of speciation.

## 7 **Speciation models in neutral biodiversity theory**

### 8 **Point-mutation speciation**

9 Speciation plays a key role in NBT, because it is the ultimate driver of biodiversity. In  
10 Hubbell’s original model (as well as in the vast majority of subsequent studies), speciation  
11 is analogous to point mutation: Each individual has a small probability of producing an  
12 offspring that is the first member of a new species. Obviously, this assumption is a caricature  
13 of biological reality. The only compatible speciation mechanism is polyploid speciation, which  
14 has been estimated to account for 2 – 7% of speciation events in plants [38]. However, this  
15 does not by itself mean that point-mutation speciation cannot be a useful simplification  
16 in the context of NBT. Indeed, the point-mutation analogy has made it possible to directly  
17 import results from neutral population genetics [17, 23, 26, 39]. For example, metacommunity  
18 diversity is described by the Ewens sampling formula [40] and is uniquely determined by a  
19 “fundamental biodiversity number”  $\theta = 2J_m\nu$ , which is not only completely analogous to the  
20 respective parameter in population genetics but also asymptotically identical to Fisher’s  $\alpha$ ,  
21 a common measure of biodiversity [20, 41]. (Here,  $J_m$  is the size of the metacommunity and  
22  $\nu$  the per-capita speciation rate; the exact equation for  $\theta$  may vary slightly, depending on  
23 model details [25].)

24 What is problematic, however, is that point-mutation speciation, though only an auxiliary  
25 assumption of NBT, has a strong impact on many of its predictions. Because new species  
26 appear as single individuals, most of them will go extinct almost immediately. In consequence,  
27 the mean lifetime of species is extremely short, and most of the ephemeral species are unlikely  
28 to ever be recognized by taxonomists. On the other hand, the time for a surviving species to

1 reach high abundance is extremely long and the speciation rate needed to explain a given total  
2 diversity is unrealistically high. For example, the best-fitting model for a 50 ha plot of tropical  
3 forest predicts the appearance of 25 new species every 100 years, with the mean lifetime of  
4 all species being about 1100 years [42], whereas the time required by a species to reach a  
5 relative abundance of 1% would equal the age of the angiosperms [17]. The latter problem  
6 is part of a more general issue, namely that ecological drift is too slow to explain realistic  
7 turn-over rates [43]. The high influx of singleton species due to point-mutation speciation  
8 also explains why the metacommunity SAD follows the highly asymmetric logseries (Box 1).  
9 Indeed, under these conditions, the logseries also arises in non-neutral models [44]. Thus, it  
10 appears to be a direct consequence of the speciation mode, not of neutrality per se.

11 For these reasons, the point-mutation assumption has recently been identified as a key weak-  
12 ness of NBT [45]. Clearly, alternative speciation models need to be explored before the  
13 neutrality assumption itself can be properly evaluated. In the following, I outline two main  
14 ways in which neutral theorists have tried to deal with this challenge.

## 15 **Other phenomenological models**

16 The first class of alternative approaches sticks with phenomenological models, which neglect  
17 the population-genetics details of speciation. Several variants have been explored, which  
18 differ in the statistical properties of new species.

19 **The random-fission model** The earliest alternative to the point-mutation model was  
20 the random-fission model, originally proposed in Hubbell's book. Mathematical details have  
21 recently been worked out by Etienne and Haegeman [46, 47]. In the random-fission model,  
22 each species has a probability (proportional to its abundance) of randomly splitting into two  
23 daughter species (as in allopatric speciation). The resulting SAD for the metacommunity is  
24 very different from the logseries predicted under point-mutation speciation. It is unimodal  
25 and predicts fewer rare, but also fewer very common species [20, 46]. In contrast to Hubbell's  
26 original conjecture, however, it is also different from the zero-sum multinomial distribution.  
27 Instead, it turns out to be identical to MacArthur's classical broken-stick model [46, 48]!  
28 Furthermore, the distribution depends on a modified version of the fundamental biodiversity

1 number,  $\theta_{\text{rf}} = J_m \sqrt{\nu}$  [46]. When applied to SAD data, the random-fission model generally  
2 fares worse (sometimes much worse) than the point-mutation model [20, 46], but it makes  
3 more realistic predictions for speciation rates and species lifetimes [46]. Etienne and Haeghe-  
4 man therefore conclude that both models have to be rejected in their current form, but they  
5 caution against premature conclusions regarding the mode of speciation in nature [46].

6 **The peripheral-isolate model** In response to the early critique by Ricklefs [42], Hubbell  
7 argued that point-mutation and random-fission speciation should be seen as the end points of  
8 a continuum. He therefore suggested a third model, called peripheral-isolate model [28, 29],  
9 in which the population size of newly formed species is small but greater than one (as in  
10 founder effect speciation [49]). A similar approach has later been used by Allen and Savage  
11 [43]. As expected, the peripheral-isolate model produces predictions intermediate between  
12 those of the previous two models. However, it has not yet been tested against empirical data.

13 **The Etienne *et al.* model** Etienne *et al.* analyzed a variant of the point-mutation model,  
14 in which the speciation rate is independent of the abundance of the parent species [50, 51]  
15 (i.e. the per capita speciation rate is inversely proportional to population size; see also [52]).  
16 This is the usual assumption in phylogenetic studies, and it has some limited empirical  
17 support [53]. However, the new model produces a much poorer fit to SAD data than the  
18 original point-mutation model, mostly because it fails to produce a sufficient total number  
19 of species. The only exception concerns the frequency of highly abundant species, which  
20 is poorly predicted by the point-mutation model. The authors tentatively suggest that the  
21 best of both worlds is contained in a third model, in which speciation rate is a saturating  
22 function of species abundance. A high frequency of abundant species is also predicted by  
23 a variant of the random-fission model with constant speciation rate per species [46]. Tests  
24 of the latter two models are difficult, however, (and have not been attempted), because no  
25 analytical sampling formulas exist.

26 **The protracted-speciation model** In contrast to the previous models, speciation events  
27 in nature are not instantaneous. To capture this aspect, Rosindell *et al.* recently developed a  
28 model of “protracted speciation” [45], which is identical to the point-mutation model, except  
29 that new species are recognized as such only after a given number of generations. Therefore,

1 many short-lived lineages are never counted as good species, but instead are interpreted  
2 as natural variation within the parent species. The resulting metacommunity SAD is a  
3 “difference logseries”, which contains fewer rare species than the ordinary logseries (predicted  
4 under point-mutation speciation), but otherwise is nearly identical to the latter. While the  
5 two models cannot be distinguished using SAD data (because the rare species for which they  
6 differ are impossible to sample), the protracted speciation model predicts speciation rates  
7 and species lifetimes that are much more realistic. Basically, the model provides a formal  
8 justification for reinterpreting the fundamental biodiversity number  $\theta$  in terms of the rate  
9 of speciation initiation rather than successful speciation. More rigorous tests will require  
10 independent estimates for the duration of speciation.

11 The above studies have shown that the mode of speciation leaves a signature in the SAD,  
12 especially at the metacommunity level [20, 44–46, 50]. (Local communities are more strongly  
13 influenced by the immigration rate.) This is remarkable, since SADs have often been claimed  
14 to have low discriminatory power [54]. So far, however, none of the alternative models has  
15 produced a significantly better fit to empirical SAD data than the point-mutation model. This  
16 has been interpreted as supporting the position that most incipient species have small pop-  
17 ulation sizes [20, 26, 28, 45], which might indeed be the case in tropical trees [55]. However,  
18 the point-mutation model makes clearly wrong predictions about speciation rates, species  
19 lifetimes and the abundance of rare species. Some of these problems can be alleviated by  
20 assuming protracted speciation. An alternative explanation is that an apparent signature  
21 of point-mutation speciation is created by immigration of species via long-distance dispersal  
22 [56]. Finally, it should be noted that the mode of speciation may also leave signatures in the  
23 structure of phylogenetic trees. So far, however, these signatures have only been investigated  
24 for the point-mutation model [20], and will not be discussed further here.

## 25 **Population-genetics models of reproductive isolation**

26 None of the phenomenological approaches to speciation is satisfactory from a population-  
27 genetic point of view. At least for sexual taxa, new species do not simply appear, but  
28 their formation is the outcome of a population-level process that results in the evolution  
29 of reproductive isolation. Research into this process has made considerable progress in the

1 last decade [57–60]. Much less attention has been paid to the community-level consequences  
2 of different speciation modes, and a recent volume on this topic is largely focused on niche  
3 differentiation [61] (for a notable exception see [62]). The work by de Aguiar *et al.* [63] is the  
4 first explicit attempt to relate a population-genetics speciation model to NBT.

5 **The de Aguiar *et al.* model** A speciation model for NBT must itself be neutral, that  
6 is, compatible with the assumption of ecological equivalence [26, 64]. It should also reflect  
7 the importance of dispersal limitation. The model by de Aguiar *et al.* [63] fulfills both  
8 requirements (Box 2). Using a spatially explicit version of NBT, the authors performed  
9 individual-based simulations of a community living on either a linear array or a rectangular  
10 grid of habitat sites. Each individual has a genome consisting of a large number of loci. When  
11 an individual dies, it is replaced by a new-born, which results from sexual reproduction of  
12 two parents. The first parent (the one being replaced) chooses a partner from its spatial  
13 neighborhood. The key point of the model is that potential partners must be genetically  
14 similar (i.e. their genotypes cannot differ at more than  $G$  positions, where  $G$  is a parameter).  
15 The offspring genotype is created from the parent genotypes by recombination and mutation,  
16 and the new-born may disperse to a neighboring site.

17 Under suitable conditions (high genetic similarity and spatial proximity between partners),  
18 this model results in speciation, that is, the formation of well-defined genotypic clusters, which  
19 occupy coherent areas of space and are reproductively isolated from each other. Speciation is  
20 rapid (the first split occurs within several hundred generations) and occurs at a higher rate  
21 in one-dimensional habitats (such as rivers or shore lines) than in two-dimensional habitats.  
22 Notably, it does not require any geographic barriers (i.e. it is parapatric), nor an involvement  
23 of natural selection. It is worth noting, though, that sexual selection plays an important  
24 role: It facilitates cluster formation, because locally rare genotypes have a low probability  
25 of being chosen as mating partners. All these results are in line with previous models of  
26 parapatric speciation [59, 62, 65–67]. What is new about the analysis by de Aguiar *et al.* is  
27 that the authors proceed to analyze the patterns of biodiversity resulting from this speciation  
28 process. While they do not directly compare their results to those obtained by standard NBT,  
29 they obtain the same kinds of patterns: in particular, a SAD that is lognormal-like with an  
30 excess of rare species, and a tri-phasic SAC, which follows a power law at intermediate  
31 spatial scales (see Box 1). After “scaling up” their results to larger community sizes (which

1 are computationally unfeasible in their simulations), the model also provides good fits to  
2 empirical data from, among others, British birds and Panamanian trees.

3 **The Melián *et al.* model** An approach similar to that by de Aguiar *et al.* has recently  
4 been developed by Melián *et al.* [68] Their model, which is based on earlier work by Higgs and  
5 Derrida [69, 70], assumes no spatial structure, that is, it is a model of sympatric speciation. (It  
6 should be noted, though, that speciation in the Higgs-Derrida model requires high mutation  
7 rates [59, 71] and that the current intense debate about sympatric speciation [58, 72–75] has  
8 mostly been concerned with niche-based models.) The authors investigate how the speciation  
9 rate and the resulting biodiversity depend on the genomic mutation rate and the minimal  
10 genetic distance required for reproductive isolation. They also compare the sexual model with  
11 an asexual alternative (in which species are defined by an arbitrary cut-off value for genotypic  
12 distance) and a point-mutation model. The three models yield distinctly different SADs,  
13 with the sexual model producing lower levels of diversity than the asexual one (apparently  
14 because many new species have low abundance). The asexual model yielded a better fit than  
15 the sexual model for 33 out of 180 data sets from coral communities. These 33 communities  
16 are characterized by high overall diversity and a large number of species with intermediate  
17 abundance. In a second study [76], Melián *et al.* investigated the effects of negative frequency-  
18 dependent selection (i.e. increased reproductive success for rare genotypes), as might occur,  
19 for example, due to reduced selection pressure from pathogens [77]. They find a decrease in  
20 speciation rate over time, a common pattern of radiations that is usually attributed to niche  
21 filling [78].

22 The study of NBT with sexual selection and reproductive isolation is just beginning. The  
23 de Aguiar *et al.* model can be seen a proof of principle, demonstrating that such models  
24 can produce diversity patterns similar to those seen in nature. Melián *et al.* started the  
25 important task of comparing the predictions of population-genetic and phenomenological  
26 speciation models. Their analysis has already confirmed the conclusion from the previous  
27 section, namely that the mode of speciation can leave a signature in the SAD. By their nature,  
28 the population-genetics models avoid some of the difficulties of the point-mutation model  
29 concerning speciation rates and species lifetimes. They resemble the protracted-speciation  
30 model in that the speciation rate and the abundance of incipient species are model outputs,

1 not parameters. An important challenge for future work will be to derive analytical results  
2 comparable to those obtained for the simpler phenomenological models. Where simulations  
3 are necessary, it is worth noting that deme-based models [62] might be a computationally  
4 efficient alternative to individual-based approaches.

## 5 **Outlook: Neutral versus non-neutral mechanisms of speci-** 6 **ation**

7 The population-genetics models reviewed above have focused on a specific model of repro-  
8 ductive isolation. However, there are many mechanisms of isolation and many modes of  
9 speciation [57]. With respect to NBT, the most pertinent classification contrasts ecological  
10 and non-ecological speciation [79]. Ecological speciation occurs in response to divergent selec-  
11 tion [79–82] and, thus, produces species adapted to different niches. Non-ecological speciation  
12 occurs in response to drift, habitat-independent sexual selection, sexual conflict, or spatially  
13 uniform natural selection, and produces species that are ecologically equivalent. Thus, only  
14 non-ecological speciation is directly compatible with NBT (Box 2).

15 The relative importance of ecological versus non-ecological speciation is unknown. However,  
16 there is currently more evidence favoring the former than the latter [79, 82] (but see [83]).  
17 Furthermore, it is by no means clear how common mutation-driven mechanisms like those  
18 studied by de Aguiar *et al.* are in nature [66]. How should NBT deal with this situation?  
19 Some have argued that only non-ecological speciation leads to neutrally behaving commu-  
20 nities [64]. However, it seems unlikely that ecological speciation did not play a role in the  
21 evolution of communities such as tropical forests or coral reefs. This then leads to the more  
22 general question of why NBT works so well despite the fact that species and niche differ-  
23 ences undoubtedly exist [20, 33, 35]. Yet, if ecological speciation plays a role, there are good  
24 reasons to believe that it has a profound impact on community structure [84]. First, it pro-  
25 duces species that can coexist through niche-based mechanisms in addition to neutral ones.  
26 Second, a large number of models have shown that divergent selection greatly increases the  
27 rate of speciation [59], and it appears likely that it also influences the abundance of incipient  
28 species. Thus, ecological speciation has the potential to affect key determinants of biodiver-  
29 sity dynamics. These effects need to be understood before one can make robust inferences

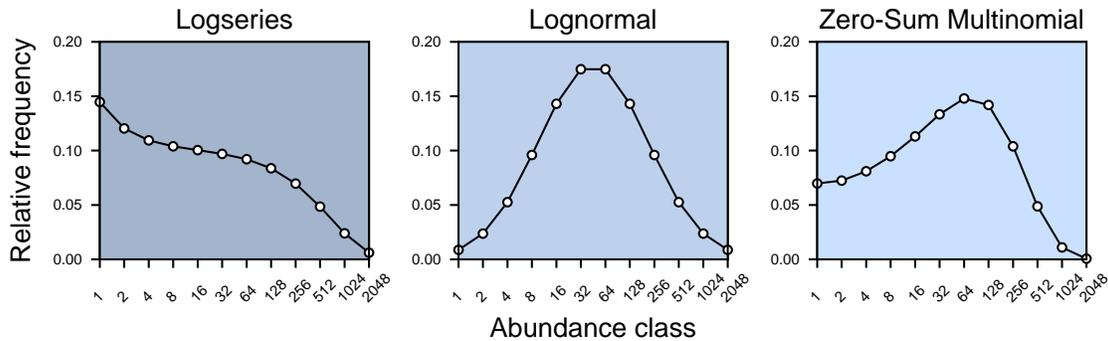


Figure 1: Different theoretical shapes of the species-abundance distribution (SAD): Fisher’s logseries, Preston’s lognormal, and Hubbell’s zero-sum multinomial (ZSM). The ZSM is for a local community of size  $J = 20000$  experiencing immigration at rate  $m = 0.01$  from a metacommunity with fundamental biodiversity number  $\theta = 50$  (data points calculated according to [90]). All plots show the relative frequency of species with 1, 2-3, 4-7, etc. individuals.

1 about speciation modes from SAD data.

2 One possible way forward might be to compare the patterns of diversity predicted by NBT

3 with those produced by adaptive radiations. Adaptive radiations imply repeated ecological

4 speciation and, therefore, may be seen as a niche-based alternative to neutral community

5 dynamics. Indeed, adaptive radiations have been modelled in a spatially explicit way [78, 85,

6 86], and variants of these models might be used to predict SADs and SACs in a way similar

7 to the one used by de Aguiar *et al.* It seems also possible to combine models of adaptive and

8 non-adaptive radiations [87], where speciation may occur due to either niche differentiation

9 or genetic drift and sexual selection. Such models would constitute a step towards a general

10 theory of biodiversity that combines neutral and non-neutral processes [18, 88, 89].

## 11 **Box 1: Predictions of neutral biodiversity theory**

12 Two key predictions of NBT are the species-abundance distribution and the species-area

13 curve. The **species-abundance distribution (SAD)** describes the number of species with

14 a given number of individuals [91]. Classical models include Fisher’s logseries [92], Preston’s

15 lognormal [93] and MacArthur’s broken-stick model [48]. With point-mutation speciation

1 (see main text), Hubbell’s model predicts the logseries for the metacommunity, and a new  
2 distribution, called “zero-sum multinomial” for local communities. In the logseries, most  
3 species are rare. In the zero-sum multinomial, most species have intermediate abundance  
4 (but the number of rare species is higher than in the lognormal, Fig. 1). The reason meta-  
5 community and local SADs differ is that rare species from the metacommunity are unlikely to  
6 immigrate into any given local community (i.e. most immigrants are from common species).  
7 This difference increases with decreasing immigration rate.

8 The **species-area curve (SAC)** shows how the number of species increases with geographic  
9 area. In agreement with empirical data, spatially explicit versions of NBT predict that SACs  
10 are triphasic [20, 56]. At very small scales, species richness increases quickly due to an  
11 increase in sample size. At intermediate spatial scales, the species-area curve follows a power  
12 law ( $S = cA^z$ ). At very large scales, finally, biota are completely uncorrelated, and the SAC  
13 increases linearly.

14 **Empirical tests of NBT** have yielded mixed results [31]. Most studies have focused on  
15 the SAD. The zero-sum multinomial often provides good fits to data from local communities.  
16 However, this may simply reflect its flexibility [31], and it is unclear whether the fit is better  
17 than that of a standard lognormal [31, 94, 95]. Furthermore, similarly good fits can be  
18 achieved by many alternative models, including niche-based ones [54, 91]. Therefore, fitting  
19 a model to local SAD data is generally considered a weak test of the underlying theory,  
20 whereas failure to fit the data is a strong argument for rejection. Metacommunity data  
21 are consistent with the logseries [20, 96]. However, the frequency of extremely rare species is  
22 virtually impossible to estimate from even the largest datasets – how would one find a species  
23 that consists of only one or two trees in the whole Amazon? – and in practice, nobody really  
24 believes that there are as many rare species as predicted by the logseries.

## 25 **Box 2: Neutral speciation models**

26 In the population-genetics models reviewed here, reproductive isolation emerges as a by-  
27 product of genetic divergence: Two individuals are reproductively isolated if they differ at  
28 more than  $G$  loci. This assumption may seem overly simplistic, but it is backed up by a rather  
29 sophisticated body of theory. In particular, it can be derived from a multilocus extension of  
30 the standard Dobzhansky-Muller model [59, 97]. While the step function used by de Aguiar

1 *et al.* and Melián *et al.* is a limiting case [59], the exact shape of the function does not seem  
2 to be overly important, as other forms (including a linear decrease of compatibility with  
3 genetic distance) yield similar results [67]. Speciation in these models is relatively insensitive  
4 to genetic details such as linkage and diploidy, but it strongly depends on the mutation rate  
5 [63, 66].

6 In the Dobzhansky-Muller model, evolution in each of the diverging lineages is unopposed by  
7 selection (i.e. substitutions are either neutral or beneficial). Therefore, it is a prime example  
8 for evolution and speciation on “holey adaptive landscapes” [59, 71, 98]. This metaphor has  
9 been created to describe evolution in high-dimensional genotype spaces. Such spaces nec-  
10 essarily contain “nearly neutral networks” of mutationally connected high-fitness genotypes,  
11 on which populations can evolve by genetic drift, sexual selection, or weak natural selection,  
12 and which are punctuated by holes representing genotypes with low fitness. If two diverging  
13 populations arrive at opposite sides of a hole, they are reproductively isolated – either be-  
14 cause they do not recognize each other as potential mates (prezygotic isolation) or because  
15 their offspring have low fitness (postzygotic isolation). The theory of nearly neutral networks  
16 and holey adaptive landscapes thus provides a natural framework for speciation in neutral  
17 communities.

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