

Supplementary Materials

Extended Discussion - Considerations and Opportunities

There are many aspects of coexistence theory in a speciation context that we do not have space to develop in our main article. This includes assumptions of mechanistic theory, extensions beyond competition, and applications to a community setting. Here we provide such a discussion, highlighting how our perspective should apply in a broad range of contexts, as well as pointing out knowledge gaps as opportunities for a full exposition in future work.

Substitutability of resources: For simplicity, we have drawn resource availability as a smooth curve on a single axis (Figures 1,2). Although this drawing assumes that resources are continuous and substitutable, it can easily be extended to discrete, non substitutable resources. Discrete resources can be represented simply by a bar chart, with each bar representing a discrete resource type (e.g., apples, oranges) with a height representing availability. Resources arranged on a single axis are substitutable, whereas multiple axes can each represent new groups of non-substitutable resources (e.g., axis 1 = fruit, axis 2 = nesting sites, etc. [1]). The distinction between resources that are non-substitutable is that each comes with its own requirement (Figure 1A (iv))—if requirements along any one axis are not met, the population will be inviable even if resources are replete along another axis (e.g., lots of fruit, nowhere to nest). Although this complexity of resource types is actually quite simple to conceptualize, it is much harder to draw in a simple cartoon and explain in brief, thus we refrain from expanding further in the main text, instead doing so here.

Abiotic conditions: Although our mechanistic approach focuses on resource use, this process is analogous to lineages specializing on different environments, independent of resource use (e.g., high vs. low elevations, with or without predators [2]), such that the position of the resource utilization curve in our model might be more broadly understood as a lineage's 'niche use'. Classic ecological models make a distinction between resources and conditions [3], the former being finite, depletable, and affecting density-dependent population growth (e.g., food). Conditions are not depletable and affect the density-independent component of growth (e.g., climate, germination niches [4]). However, microsites with suitable conditions (e.g., for nesting, for germination) are finite and depletable. Furthermore, abiotic conditions can affect how organisms use finite resources, for example, by reducing consumption or increasing requirements.

Multi-trophic interactions: We have not considered other forms of species interactions, such as predation or mutualism in our main article, but expect our review will provide a foundation for assessing the importance of other types of interactions in the future. Fortunately, extending MacArthur's models to multitrophic systems may not be so much of a stretch. Existing coexistence frameworks show that trophic interactions apply similarly, both in their dynamical consequences (see Box 1 in [5]) and analogs to resource consumption and requirement [6]. Note that a 'consumer' and a 'resource' could reflect any consumer species and the resources it uses regardless of trophic level: a primary consumer (i.e., a plant) consuming abiotic resources, secondary consumers (e.g., a herbivore) consuming plants, etc. In the case of a biotic resource, resource availability reflects the various growth rates of those resource species, whereas for abiotic resources, availability is net rates of supply [7]. The question then becomes to what

degree is density dependence of a focal species caused by bottom up (i.e., resources) vs. top down (i.e., predation) forces. Recently speciated lineages are unlikely to belong to different trophic levels, though this is a possibility (e.g., if body size changes and feeding interactions are size-structured). Additionally, predators may affect the risk associated with consuming a particular resource, which could be incorporated by modifying consumption curves based on predators.

Multispecies communities: Lineages do not diverge in a vacuum and are instead embedded within (often) complex community contexts [8]. As such, ecological opportunities are defined by resources that are not strongly used by any other species in the larger community, for example, if a new plant resource recently arrived. An ecological opportunity might also represent a resource currently being used by another community member, but over which a lineage might evolve to outcompete. The number of species that can be stably “packed” along a given resource axis is defined by the breadths and heights of those species’ resource consumption curves and how they align with resource requirements [9,10].

Another related issue is how meaningful pairwise competitive differences are in multi-species contexts, as the outcome of pairwise interactions can be modified by other species [11]. This problem is simplified to some degree in the context of our competitive differences among speciating lineages, which, by definition, involves a pairwise comparison. One solution might be to consider resource availability that is accessible to each lineage after accounting for use by other species, however, doing so would not deal with demographic feedbacks between those lineages and other species, especially upon arrival of a lineage that diverged elsewhere in the

landscape. We cannot offer a definitive solution here but hope that our discussion could serve as the seed for a greater exploration in future work.

Spatial scale: Spatial dynamics come into play in two interrelated ways. The first concerns the failure of speciation: whether a lineage is driven to extinction anywhere on the landscape or only in some locations (discussed in the main text). The second is the metapopulation context that determines rates of gene flow and the time course over which lineages will come into secondary contact [12]. Specifically, all else being equal, locations that are more replete with resources have higher population sizes. Because dispersal and gene flow are *per capita* rates, larger populations act as sources of individuals or gametes (e.g., pollen, if a plant) moving elsewhere, at some rate that decays with distance. As a consequence, two lineages separated by some fixed distance would be expected to come into contact sooner with increasing population sizes of one or both lineages. If lineages differ in population size, for example, as might occur in the scenario depicted in Figure 2F, gene flow and dispersal would be asymmetric, meaning that secondary contact and hybridization would be tested in the location of the lineage with smaller population size sooner than the location of the lineage with the larger population [12]. Alternatively, coexistence in any one region may simply never be tested prior to the completion of speciation, regardless of whether divergence increases or decreases lineage coexistence (e.g., if lineages are diverging on different continents)—thus, the specific form of ecological divergence would be irrelevant to persistence.

Timescale of reproductive isolation: In the main text, we have emphasized that the consequences of coexistence for speciation depend on its timing relative to the accumulation of

reproductive isolation, however, we only touch on factors that affect the rates at which reproductive isolation accumulates. Of particular interest is whether rates of ecological divergence and reproductive isolation are causally linked [13]. We consider two reasons why such a relationship might exist. The first reason would be if the same traits under selection are also involved in mating (sometimes referred to as “magic traits” [26]), for example, the switching of phytophagous insects to a new host plant [27] or when the timing of plant flowering varies with edaphic substrate [28]. Assortative mating would result, acting as a prezygotic isolating mechanism. The second reason would be if ecologically-divergent lineages come into contact and produce low-fitness hybrids, isolating barriers may evolve through the process of reinforcement [14]. Alternatively, ecological divergence and reproductive isolation may both increase over time simply due to the origination and fixation of new mutations, though not necessarily at the same rate and not through a causative relationship.

Reproductive interactions: A necessary condition of stable coexistence is that each species experiences negative frequency-dependent population growth [15]. However, ecological differences among species are not necessary to yield this condition. Several theoretical models have shown that species can coexist in the absence of any ecological differentiation if other mechanisms, such as reproductive interactions, cause negative frequency dependence [16]. For example, sexual conflict can promote stable coexistence. As intraspecific densities increase, costly male-female encounters can become more common, intensifying sexual conflict and reducing female fitness and population growth [17,18]. Coexistence can also arise through male-male competition producing spatial separation via territoriality. Even if species have identical ecological requirements, more intense competition between conspecifics than heterospecifics can

lead to the build-up of spatial separation in territories, allowing heterospecifics to occupy the area between conspecific territories [19]. As a result, competition with conspecific neighbors decreases population growth as they become common, preventing species exclusion [19]. Sexual selection through female mate choice, among otherwise ecologically equivalent species, can lead to a situation that creates priority effects and positive frequency dependence, ultimately leading to regional coexistence [20]. A number of speciose clades show little to no ecological differentiation and instead differ primarily in characters associated with reproduction: Hawaiian *Drosophila* [21], some African lake cichlids [22]), new world warblers [23], and *Enallagma* damselflies [24] are but a few examples. Although such groups may very well be ecologically equivalent, reproductive mechanisms may play a role in promoting their coexistence, but this requires empirical testing. We discuss this in Box 2, for example, in reference to polyploidy.

Supplementary References

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