Opinion

On the Origin of Coexisting Species

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Speciation is frequently initiated but rarely completed, a phenomenon hypothesized to arise due to the failure of nascent lineages to persist. Although a failure to persist often has ecological causes, key gaps exist between ecological and evolutionary theories that, if filled, would clarify when and why speciation succeeds or fails. Here, we apply ecological coexistence theory to show how the alignment between different forms of niche opportunity and niche use shape the initiation, progression, and completion of speciation. Niche evolution may drive coexistence or competitive exclusion, and an ability to coexist ecologically may help or hinder speciation. Our perspective allows progress towards unifying the origin and maintenance of species diversity across the tree of life.

The Origin and Persistence of Species: Ecological Insights into the Speciation Process

Why is life on Earth so diverse? Historically, ecological and evolutionary explanations of species diversity were intertwined—key papers by G. Evelyn Hutchinson [1] and Robert H. MacArthur [2], famous for formalizing modern-day niche theory [3], drew on species' evolutionary histories to provide evidence that diversity is constrained by **ecological opportunity** (see Glossary). In the *Origin of Species*, Darwin [4] identified competition as a unifying driver in the origin of species diversity, that competing in the 'struggle for existence' underlies natural selection, initiating speciation [5]. Beyond simply initiating speciation, competition affects the likelihood that newly formed lineages persist, completing speciation [6,7]. Thus, fully understanding the origin and maintenance of biodiversity requires understanding the evolution of ecological differences that permit **coexistence** [8].

In this article, we reframe speciation in the context of coexistence theory, asking how ecological differences among lineages evolve during the speciation process and, in turn, how their evolution helps or hinders the coexistence of diverging lineages. We address: (i) how ecological opportunities shape patterns of selection, determining whether speciation is initiated and at what frequency, (ii) how those patterns of selection drive population divergence, and (iii) the consequences of different forms of divergence for the completion of speciation, if and when lineages come back into contact. We posit that **speciation modes** (e.g., sympatric, mutation-order, etc., Box 1) reflect how selection is shaped by ecological opportunity (i.e., the **resource** environment) and how this selection interacts with gene flow, genetic drift, and mutation. Our central thesis is that the coexistence of different lineages depends on the alignment between ecological opportunities present when speciation is first initiated and ecological opportunities in the **region** of secondary contact. Overall, we aim to make explicit the demographic controls on lineage persistence and coexistence (i.e., persistence of both lineages [6,7]), allowing new, testable predictions about the role of ecology throughout the speciation process.

Highlights

Speciation is the process by which new species are formed, shaped by ecological conditions within which lineages live and evolve.

We argue that the distribution of available resources within and among regions dictates if and how speciation will be initiated, as well as whether newly formed lineages will persist ecologically.

Lineages may diverge to use different resource types, but whether divergence confers niche differentiation or a competitive asymmetry depends on resource availability in the location of secondary contact.

Coexistence may sometimes help and sometimes halt speciation, depending on its timing relative to reproductive isolation, and may frequently fail due to stochastic extinction.

Speciation modes emerge as a consequence of how different forms of ecological opportunity shape microevolutionary processes, giving rise to new persistent species at different rates.

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Box 1. Redefining Speciation Modes by Microevolutionary Processes

Speciation requires the accumulation of reproductive isolation among diverging lineages, reducing gene flow. In early models of speciation, geographic separation, or 'allopatry', was considered a prerequisite for the evolution of reproductive isolation [47], preventing gene flow from overwhelming lineage divergence. However, examples exist of speciation occurring with complete (sympatric speciation) or partial (parapatric speciation) overlap in geographic ranges [44]. More recently, speciation has been recategorized as ecological (i.e., driven by selection) versus nonecological (i.e., purely genetic), regardless of geographical context [25]. We argue that neither geography nor ecology alone are sufficient to capture the full range of ways in which speciation processes play out, for example, how it is initiated, time to completion, and as we critically discuss in the main text, consequences for lineage persistence.

To reconcile different definitions of speciation modes, we differentiate each by the relative importance of four microevolutionary processes: selection, gene flow, genetic drift, and mutation (Figure I). For example, sympatric speciation is characterized by strong divergent selection and high gene flow (Figure I, cube 1), whereas 'mutation-order speciation' is the result of low gene flow and stochastic mutation (Figure I, cube 5). This process-based definition encompasses ecology, genetics, and geography, as well as speciation modes that were hard to place under any one definition. Note that, although we identify seven discrete points in this 4D process space that correspond to named speciation modes from the literature, it is most appropriate to think of each as a point in continuous parameter space with a characteristic dynamic. For example, any point between cubes 1 and 3 in Figure I could be viewed as occurring at a continuum of spatial scales, with parapatry (i.e., speciation with partial geographic overlap; cube 2, Figure I) falling in between. A process-based (rather than mode-based) perspective of different forms of speciation eases links between ecology and evolution, given that the resource environment affects all four microevolutionary processes (see 'Stage 1' in the main text). Speciation modes are not expected to give rise to new species at the same rate (if at all), nor are they likely to give rise to new species with similar coexistence probabilities (see Box 2).
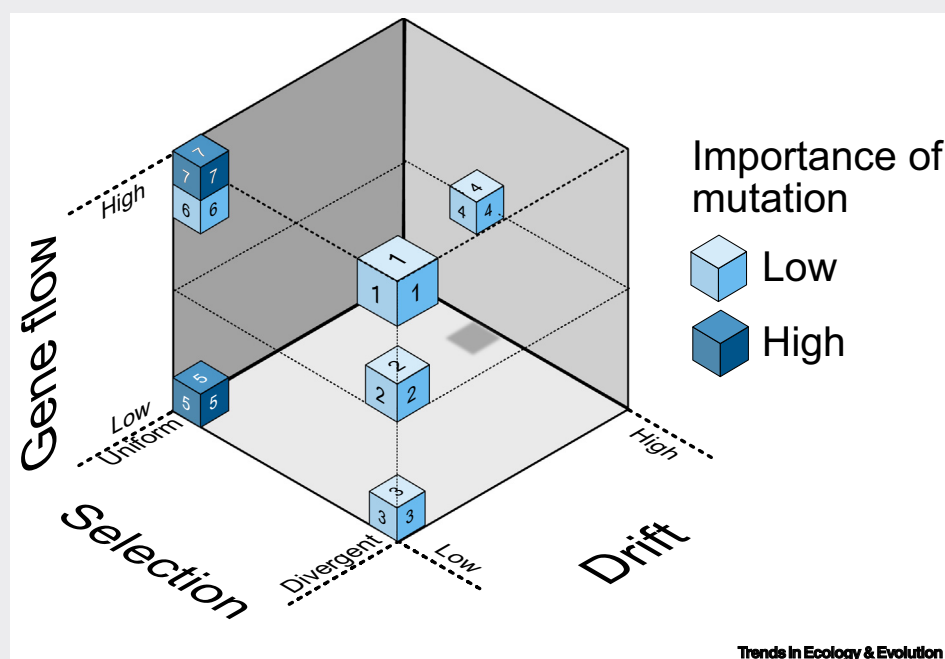

Trends in Ecology & Evolution

Figure I. A Process-Based Delineation of Speciation Modes. We delineate seven speciation modes commonly described in the literature by their differences in the four microevolutionary processes they involve: (1) sympatric; (2) parapatric; (3) allopatric (ecological); (4) peripatric; (5) allopatric (mutation-order); (6) hybrid; and (7) polyploid. Although there are variants of each mode, we base our delineations around their most widely adopted definitions. The size of the cubes shows the depth in the 3D volume.

Linkages among Processes in Ecology and Evolution

Before being able to delve into the specifics of the ecology of speciation, we first need a common framework within which general requirements for speciation and coexistence can be understood. The dominant paradigm for predicting species coexistence is to take a **phenomenological**

approach (e.g., the translation of demographic parameters into competitive outcomes), while studies of speciation often rely on more **mechanistic** definitions of the niche, underpinned by evolutionary change in specific traits, such as **resource use** traits [9]. Uniting these disparate approaches should be a priority to better understand when and why trait evolution translates into coexistence or exclusion of speciating lineages. To make progress, we first take a graphical, mechanistic approach based on MacArthur [10] for describing competition for resources between different lineages (Figure 1). While we use this graphical approach as an heuristic tool, we emphasize that the model is grounded in biologically informed quantitative theory [11–13], with strong, historical links to studies of both speciation and coexistence [9,14].

Important to the ecological persistence of nascent lineages is the translation of mechanistic resource use into competitive differences that dictate coexistence or exclusion (Figure 1) [15,16]. Contemporary ecological studies emphasize two types of differences between species that determine their ability to coexist: **niche differences** that promote coexistence and **competitive asymmetries** that can cause exclusion in any one region. In general, niche differences arise when lineages use different, available resources [Figure 1B (ii),(iv)]. By contrast, competitive asymmetries arise when species differ in: (i) per capita consumption of a given set of resources, (ii) the availability of resources each consumes most, (iii) the breadth of resources used, or (iv) the amount of resources individuals require to produce offspring (Figure 1A). This understanding of the determinants of coexistence implies that niche differences increase if lineages evolve to specialize on different resources, while competitive differences increase if one of
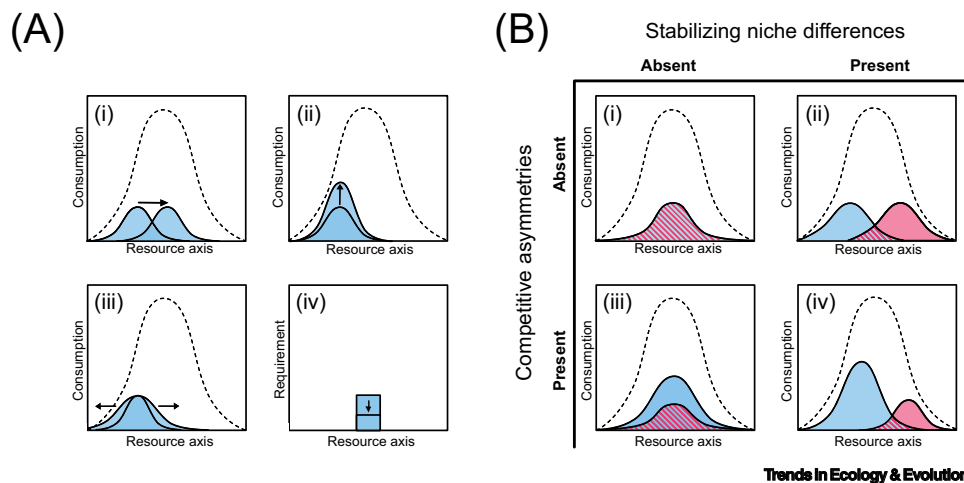

Figure 1. Illustration of (A) Components of Resource Use and (B) Their Translation into Competitive Differences among Lineages. In both panels, the resource axis represents a limited substitutable resource with subtypes (e.g., seeds of various sizes) that vary in availability (broken lines). Per capita resource consumption (i.e., ability to consume a given resource type) is represented by solid curves for two lineages (blue and pink). Individual consumption and competition for resources, along with the resource supply rate (i.e., 'resource availability'), jointly determine population growth and equilibrium size (not shown [15]). In (A), the directions of the arrows show a potential evolutionary change in the curve [i.e., position (i), height (ii), and breadth (iii)] that leads to an increase in an average individual's total resource consumption (i.e., per capita resource consumption × resource availability) for a given distribution of available resources. Resource requirement (iv) is the sum total amount of resources that must be consumed across a given resource axis before an individual can reproduce; the arrow pointing to a smaller requirement indicates that fewer resources need to be consumed before reproduction is possible. (B) With competition, lineages may overlap (hashed fill) partially or completely in resource consumption; complete overlap means that lineages are ecologically equivalent, and one will randomly drift to extinction when competing in sympatry (i). With less overlap in resource consumption curves, niches differ more, promoting coexistence so long as similar amounts of resources are available to each lineage (ii). By contrast, competitive asymmetries arise when species differ in their ability to consume the same resources (iii) or if species specialize on resources that differ in availability (iv). See supplemental information online for a discussion of nonsubstitutable resources.

Glossary

Coexistence: the ability of lineages to stably persist at any spatial scale when faced with competition by another lineage. To coexist in any one region, each competitor must be able to invade (i.e., have positive population growth rates) when rare, against the other competitor at its equilibrium [57]. If this criterion is not met, it is still possible to coexist at a scale that encompasses multiple regions, so long as each competitor can invade in at least one region. Lineages that persist only because they have yet to compete do not count as 'coexisting' [58].

Competitive asymmetries: capture differences in competitive ability due to number of offspring produced and/or sensitivity to competition, such that greater differences in competitive ability hinder the coexistence of competitors [59].

Ecological opportunity: spectrum of evolutionarily accessible resources [60] that if accessed, would reduce competition. Resources may become evolutionarily accessible, following colonization, evolution of a key innovation, extinction of competitors, or the arrival of new resources, as examples.

Genetic incompatibilities: occurrence of noncompatible genes in hybrids that reduce their viability or fertility, promoting reproductive isolation.

Mechanistic (coexistence theory): a mathematical theory of species coexistence formalized by R. MacArthur [2], based on individual-level resource use in different resource environments, which can be scaled to estimate population parameters (i.e., interaction strengths).

Niche differences: capture the strength of intra- to interspecific competition, such that greater intraspecific relative to interspecific competition stabilizes the coexistence of competitors due to negative frequency dependence.

Phenomenological (coexistence theory): a mathematical theory of species coexistence formalized by P. Chesson [61], based on population-level demographic responses to intraspecific and interspecific densities in fluctuating and nonfluctuating environments.

Region: by 'region', we simply mean a location with a given spatial extent that encompasses a population, at far

the lineages evolves to consume more resources in excess of requirement (Figure 1). Ultimately, coexistence occurs when there is sufficient niche differentiation to overcome any competitive asymmetries between species [17]; smaller niche differences are needed if competitive asymmetries are small, and large niche differences are required if competitive asymmetries are large. This coexistence criterion, as we will make clear, becomes useful when considering the likelihood that recently diverged lineages will coexist at any spatial scale; we consider scale explicitly later, particularly when discussing how speciation is completed. Although we focus here on differentiation in resource use, we discuss implications for coexistence under alternative sources of differentiation (e.g., abiotic conditions, predators, and mating preferences) in the supplemental information online.

The Importance of Ecology throughout the Speciation Process

Our graphical depiction of coexistence theory (Figure 2) serves as the scaffold around which we examine how ecology and evolution interact at different stages of the speciation process: the initiation of speciation (stage 1), trajectories of lineage divergence (stage 2), and outcomes when lineages come into secondary contact (stage 3), as well as lineage diversification on macroevolutionary timescales.

Stage 1: Initiation of Speciation

Speciation is the process by which one species splits into two **reproductively isolated** species. We argue that the distribution of available resources across a landscape is key to the initiation of

Figure 2. Selection Imposed by Resource Availability within and among Regions of a Landscape. Availability curves (broken lines) may differ among regions in several ways: location of peak, modality, height (i.e., total availability of each resource type), breadth (i.e., range of resource types), and skewness. Different regions on a landscape may have identical resource distributions (B,C) or differ in some respect (D–F). Blue curves are resource consumption rates of ancestral lineages in region 1, which enters region 2 (faded-blue curve) and adapts to the resource environment of the new region (solid-pink curve). Consumption curves are Gaussian distributed with a fixed upper limit on breadth to reflect biological constraints on consumption (discussed in the 'Stage 2' section in the main text). Note that, here, we do not consider all possible ways in which regions may differ ecologically, or scenarios where conditions change over time. Rather, we aim to illustrate different ways in which resource availability may change the evolution of resource use, providing a basis for application to other scenarios.

enough distances from other populations that gene flow is reduced. For a population of lizards, a region may be an island, but for a population of plants, regions may be resource patches within islands.

Reproductive isolation: cumulative effect of all intrinsic or extrinsic barriers that reduce gene flow between populations or species, typically caused by mechanisms that prevent fertilization (prezygotic) or that reduce hybrid viability or fertility (postzygotic) [62].

Resource: a finite depletable energetic or material source that allows for growth, maintenance, and reproduction of an organism. Resources may be substitutable or nonsubstitutable, biotic or abiotic, and, if interpreted broadly, can encompass microsites (e.g., availability of suitable space; see supplemental information online).

Resource availability: in a given landscape, 'availability' is the range and total amount (set by rate of supply) of resource types (corresponding to the breadth and height of resource curves, respectively).
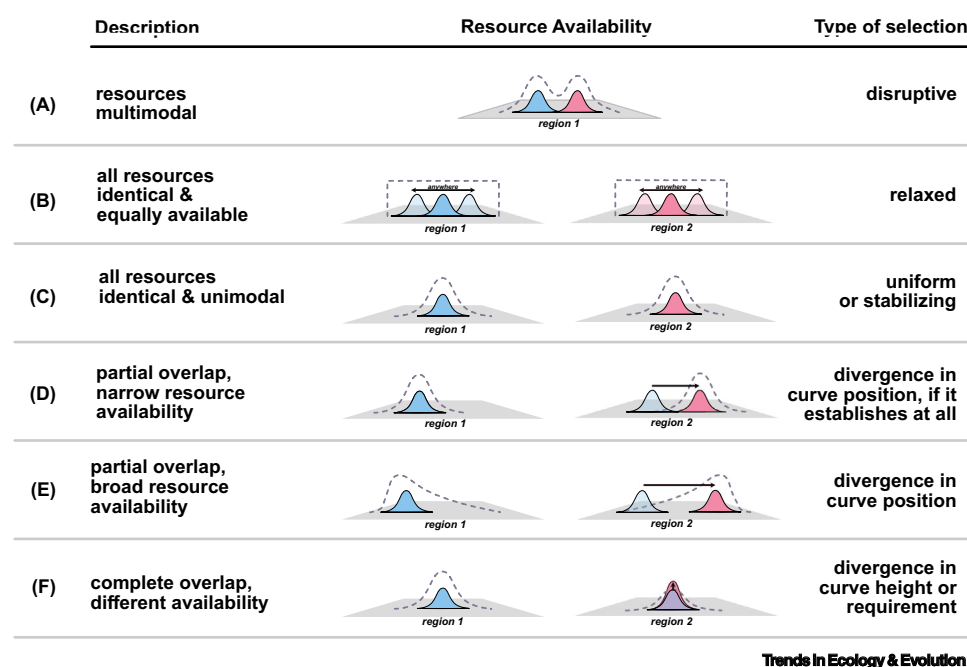
Resource consumption: average, per capita consumption of resources for a given population or species, defined by both the range and amount of resources consumed (corresponding to the breadth and height of resource consumption curves, respectively).

Resource requirement: the minimum amount of resources an individual must consume to sustain its metabolic function, which, when consumed in excess of requirement, can be allocated to reproduction.

Resource use: an umbrella term used to encompass how individuals use resources that they require and consume.

Speciation modes: range of pathways by which speciation can occur. In our process-based definition (see Box 1), speciation modes exist along a continuum of parameter space defined by the relative importance of microevolutionary forces (selection, gene flow, genetic drift, and mutation) in driving speciation.

Sympatry: locations in a landscape in which two diverging lineages co-occur and, thus, potentially or actually interact.

this process through two distinct mechanisms. The first mechanism is selection. Consider two populations formed from one lineage, now separated geographically (i.e., vicariance). If the resource environment differs among locations, populations would experience divergent selection to better consume resources available in their respective environments (Figure 2D). For speciation to even be possible, the two environments cannot be so different that viable populations cannot persist at both locations. This means that **resource consumption** curves must overlap with resource availability curves at least enough to meet the **resource requirements** of a few individuals, a threshold that is met more easily in environments with broader resource spectrums (Figure 2E). In the absence of geographical barriers (i.e., in **sympatry**), the key ecological question is whether an alternative resource is abundant enough to allow persistence and is relatively free of competition to allow coexistence [11,18]. The key evolutionary question is then if assortative mating can arise alongside resource specialization to avoid collapsing the incipient species [19,20].

The second mechanism by which **resource availability** could influence the initiation of speciation is via its effects on mutation and genetic drift, because these two processes can create **genetic incompatibilities** among lineages even in the absence of divergent selection, so long as gene flow is sufficiently restricted [21] (see Figure I in Box 1). Although one might assume that resource availability is unimportant given a purely genetic mode of speciation, some modes (e.g., mutation-order speciation) assume that lineages experience identical selective pressures even if selection is not a driver of genetic divergence. Implicit in this assumption is that each lineage is evolving in a similar resource environment (Figure 2C), rather than the resource environment simply being irrelevant [22,23]. Under this scenario, speciation may be achieved via mutations unrelated to ecological traits (e.g., mating interactions [24] or intragenomic conflict [25]), or alternatively, and most relevant to our discussion here, via the fixation of mutations that confer alternative, incompatible phenotypes (e.g., via negative epistasis) of similar fitness value in a given environment [23]. Additionally, all else being equal, increased resource availability translates into increased population size. The exact relationship between population size and rates of evolutionary processes can sometimes be counterintuitive [26], but one might expect larger populations to not only acquire mutations at a faster rate, but also to be less subject to genetic drift. Although these opposing forces might suggest that large or small populations are both likely to speciate for different reasons, purely drift-based speciation is thought to be rare [27]. As we will discuss, the initiation of speciation, shaped by resource availability encountered by nascent lineages, becomes critical to determining whether speciation ultimately succeeds or fails (stage 3).

Stage 2: Trajectories and Timescales of Lineage Divergence

Ecological divergence among lineages arises as a byproduct of selection to maximize resource gain in different environments, balancing ecological opportunity and biological constraint. In the implausible scenario of an absence of constraints (i.e., a 'Darwinian demon'), lineages would evolve to consume all available resources in an environment because this strategy would maximize energy capture by individuals [9,11]. However, constraints on resource utilization, such as trade-offs in resource capture of different food items [28] (i.e., upper limits on niche breadths), frequently result in resource consumption that underfills resource availability [9]. As such, the resource consumption curve that evolves would reflect an optimal cost–benefit strategy: the maximum total resource capture possible given costs imposed by the constraint [9].

An optimal consumption curve is one that improves efficiency at capturing common, essential resources, while reducing effort spent capturing uncommon or nonessential resources [9,29]. If multiple strategies are equally optimal [i.e., resource availability is multimodal or if selection on

resource utilization is relaxed (i.e., availability is uniform; Figure 2B)], the consumption curve that evolves might simply reflect which strategy happens to evolve first by chance or that evolves more easily (i.e., associated with a higher mutation rate or a lower amount of pleiotropic counter-selection). If instead two regions contain an identical range of resources, but differ in how available those resources are (Figure 2F), then lineages in low-availability environments should evolve more conservative resource use strategies, such as lower overall resource requirements (if possible, given metabolic constraints) or increased efficiency of search and attack [30]. Note, however, that environments with fewer resources support smaller populations, limiting the efficacy of selection relative to genetic drift, reducing levels of standing genetic variation even of alleles that are otherwise beneficial, slowing the speed of adaptive ecological divergence [31]. This balance of selection and drift, mediated by population size, might be one reason why unproductive environments tend to contain fewer species than more productive ones [32].

Stage 3: Lineage Persistence and the Completion of Speciation Upon Contact

Whether speciation, once initiated, is successfully completed depends on whether diverging lineages persist on a landscape long enough for sufficient reproductive isolation to accumulate [33]. Critically for persistence, geographic context determines whether incipient species compete in sympatry throughout the speciation process or only upon secondary contact following dispersal and range expansion, if they come into contact at all [7]. If there is contact, a failure to persist may occur for two reasons: (i) one lineage is reabsorbed by the other via hybridization [6,34] or (ii) lineages are unable to coexist ecologically [35]. Here, we delve more deeply into coexistence theory to predict when newly formed species are likely to persist or fail, why, and the role that scales of space and time play (see Box 2 for an expanded discussion of specific speciation modes).

How ecological divergence before contact (stage 2) translates into niche differences and competitive asymmetries and, thus, coexistence or exclusion (stage 3), cannot be understood without knowledge of resource availability in the location of initial contact. To coexist in sympatry, lineages must have diverged sufficiently to specialize on different resources (Figure 1B). However, even with specialization, competitive asymmetries can arise if the resources each lineage has specialized on are unequally available [or, even more extremely, the resources uniquely used by one lineage are entirely absent, as in Figure 1B (iii)], causing either deterministic exclusion (see Figure 2 in [2]) or stochastic extinction due to small population size. In other words, not only is it true that ecological divergence sometimes helps or hurts coexistence depending on the type of divergence, but additionally, which type of divergence it is also depends on the resource environment as much as it depends on the lineages themselves. Note also that, viewed through this lens, the evolution of competitive differences is a by-product of evolution to maximize resource use rather than the direct action of selection on the strength of competitive interactions.

At first glance, it might appear as though a failure of lineages to coexist ecologically would cause speciation to fail, however, this is not always the case depending on the timescale and spatial scale of coexistence. A failure to coexist in any one region might in fact reinforce speciation in two scenarios. The first scenario is if coexistence increases the risk of collapse of the species before the accumulation of sufficient reproductive isolation (i.e., timescale matters). If reproductively compatible lineages were able to coexist ecologically, lineages would be more likely to hybridize, increasing the likelihood of lineage reabsorption [35]. By contrast, the failure of lineages to coexist in sympatry would act to reinforce speciation, preventing hybridization or imposing selection against hybrids [21,36].

The second scenario arises when coexistence is not possible in any one location on a landscape but is possible on larger scales (i.e., spatial scale matters [37]). For example, if

lineages of a hypothetical fruit fly evolve to specialize on apples in one environment and oranges in another (e.g., scenario in Figure 2D), but apples and oranges do not overlap geographically, the two lineages would coexist only at a scale that encompasses both resource types but not on smaller scales, reducing opportunities to mate, reinforcing speciation. Given that speciation concerns the persistence of lineages anywhere on Earth, for speciation to fail, one lineage must be driven to extinction everywhere it occurs, an outcome that is more likely under some speciation modes than others (e.g., one lineage has a competitive advantage everywhere; Box 2) and is increasingly improbable as lineages spread out geographically.
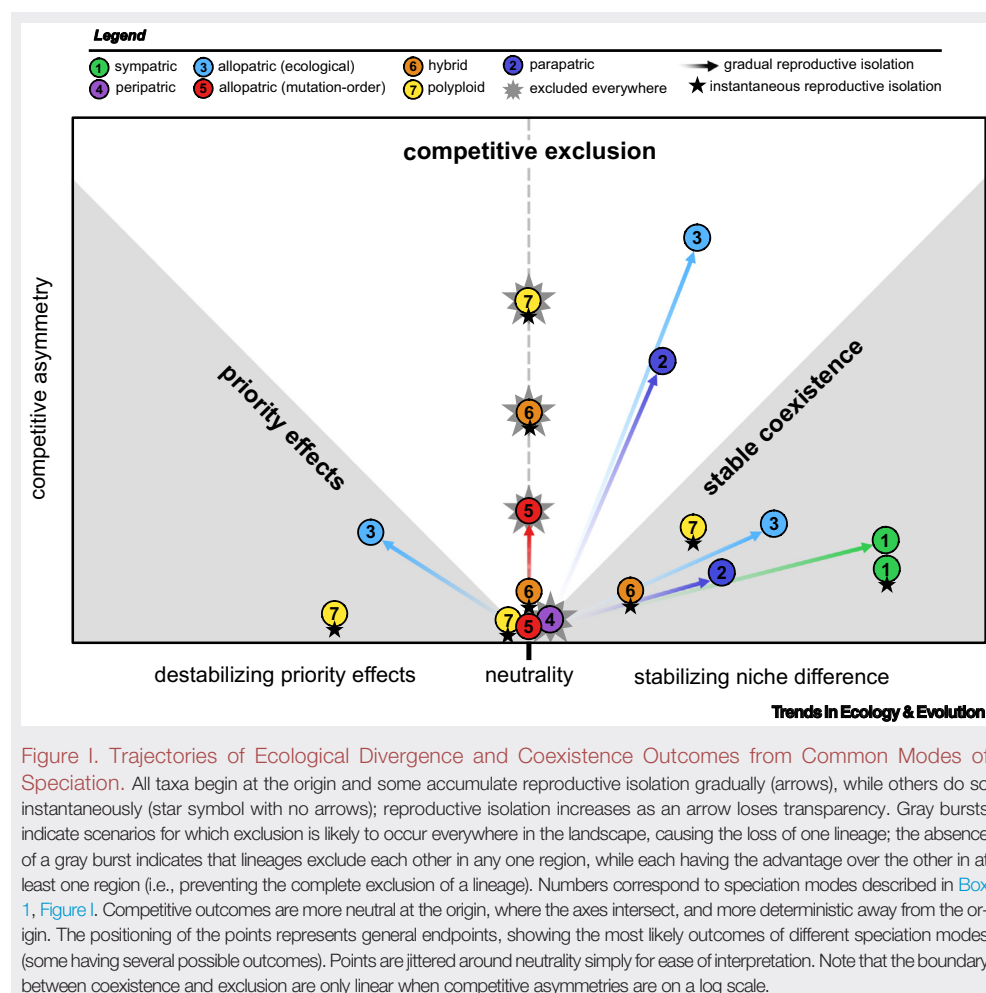

Box 2. Speciation Modes and the Outcome of Competition upon Secondary Contact

Speciation modes likely differ in trajectories and timescales of ecological divergence and, as a consequence, likelihoods that the new species will coexist at any scale. Immediately before the initiation of speciation, all individuals belong to the same population: they use resources in a similar way and, thus, compete equivalently. As speciation progresses, four competitive outcomes are possible depending on the balance of evolved niche differences and competitive asymmetries (Figure I): (i) equivalence ('neutrality'), (ii) exclusion, (iii) coexistence, and (iv) first to arrive wins ('priority effects'). Coexistence may be possible in any one region or only at scales that encompass multiple regions.

Modes for which divergent or disruptive selection drives speciation (see Box 1) might result in the evolution of niche differences or, equally, might evolve competitive asymmetries; neutrality is not an expected outcome. Under sympatric speciation, because of complete geographic overlap, coexistence of lineages is tested immediately, throughout divergence. Speciation would be successful only if niche differences evolve at faster rates than competitive asymmetries, and reproductive isolation either occurs instantaneously or hybrids are strongly selected against (preventing reabsorption). For lineages formed via allopatric ecological speciation, one of three outcomes are possible. First, if lineages have diverged in the type of resources used (i.e., niche differentiation occurs), and both types of resources are similarly available in the region of secondary contact, coexistence is possible (see the 'Stage 3' section in the main text for consequences for speciation). Second, if lineages evolved to specialize on resources that are not similarly available, then deterministic exclusion is likely when each lineage tries to invade the region of the other lineage, allowing lineages to coexist at scales that encompass multiple regions. Third, if lineages occur at high densities in allopatry, priority effects might evolve if selection favors a decrease in sensitivity to intraspecific competition (reducing its per capita strength). Note, however, that other outcomes are also possible in response to selection imposed by conspecifics.

Speciation modes driven by genetic incompatibilities differ from speciation driven by selection (see Box 1) in an important way: because of a lack of divergent selective pressures, any phenotypic changes are unlikely to promote niche differences. Allopatric mutation-order speciation occurs through the fixation of alternative advantageous mutations in allopatry under similar selection pressures. Two outcomes seem most possible: (i) prolonged neutrality, eventually leading to stochastic exclusion upon secondary contact, or (ii) one lineage evolves a competitive advantage. Speciation would fail, because the more competitive lineage would exclude or reabsorb the other upon secondary contact, even in the region that the less competitive lineage evolved in [23]. Under polyploid speciation, reproductive isolation can occur instantaneously in sympatry, meaning that the ability of lineages to coexist is tested immediately. Without associated phenotypic changes, polyploid speciation would result in neutrality. Given their low initial population size, neopolyploids are more likely to go extinct either stochastically due to small populations or deterministically due to a mating disadvantage (called 'minority cytotype exclusion', a type of priority effect) [48,49]. However, growing evidence shows that neopolyploids may often differ in ecologically important traits, such as body size, which may permit coexistence [50] or result in the exclusion of the progenitor [51,52].

Finally, some speciation modes are differentiated by gene flow and genetic drift. During peripatric speciation, a new lineage forms via the establishment of a small peripheral population. Although stable coexistence may be possible if strong niche differences evolve, extinction of the peripheral lineage is more likely due to reabsorption, via asymmetrical gene flow [21] or through stochastic loss of small populations (possible even without competition). During parapatric speciation, lineages diverge along a continuous geographic range of variable ecological conditions. In contrast to peripatric speciation, parapatric lineages are likely to coexist at scales that encompass the full geographic range. In the mid-geographic range, where lineages come into contact, lineages would compete similarly (i.e., neutrality) and, if not entirely reproductively isolated, form hybrids [21]. Over time, persistent competition in the contact zone could allow the evolution of reinforcement (i.e., enhanced reproductive isolation [53]) and niche differentiation (via character displacement [53]), promoting coexistence. When speciation occurs through hybridization, hybrids tend to overlap geographically with one or both parent species. If hybrids have ecological traits similar to one or both parents, competitive outcomes are strongly influenced by ecological drift (i.e., neutrality). If hybrids have more extreme traits than parents, several outcomes are possible [54], including the exclusion of hybrids (i.e., hybrids are inferior [55,56]), hybrids exclude their non-hybrid parents (i.e., 'hybrid vigor' [54]), and parents and hybrids use different resources and coexist.

Figure I. Trajectories of Ecological Divergence and Coexistence Outcomes from Common Modes of Speciation. All taxa begin at the origin and some accumulate reproductive isolation gradually (arrows), while others do so instantaneously (star symbol with no arrows); reproductive isolation increases as an arrow loses transparency. Gray bursts indicate scenarios for which exclusion is likely to occur everywhere in the landscape, causing the loss of one lineage; the absence of a gray burst indicates that lineages exclude each other in any one region, while each having the advantage over the other in at least one region (i.e., preventing the complete exclusion of a lineage). Numbers correspond to speciation modes described in Box 1, Figure I. Competitive outcomes are more neutral at the origin, where the axes intersect, and more deterministic away from the origin. The positioning of the points represents general endpoints, showing the most likely outcomes of different speciation modes (some having several possible outcomes). Points are jittered around neutrality simply for ease of interpretation. Note that the boundary between coexistence and exclusion are only linear when competitive asymmetries are on a log scale.

Paths Forward towards Understanding the Origin and Persistence of Species

We began this article by articulating how coexistence theory can be applied to achieve insights into the speciation process, with clear relevance to lineage persistence. In this section, we highlight three overarching and interrelated priority questions that deserve further research. We also discuss extensions to our synthesis that go beyond resource competition in the supplemental information online.

Priority Question 1: How Does the Resource Environment Shape the Initiation, Progression, and Completion of Speciation?

Although the resource environment as a driver of speciation (i.e., through ecological opportunity) is well acknowledged (e.g., sticklebacks specializing on benthic or limnetic resources [38]), studies rarely examine the resource environment in observational studies [39] or manipulate its complexity and availability (e.g., [40–42]). Doing so would allow tests of the hypothesis that resource divergence in allopatry does not guarantee coexistence upon secondary contact; quite the contrary, divergence may frequently generate competitive asymmetries, causing competitive exclusion upon contact. The consequences of competitive exclusion for the success or failure of speciation should depend on the spatial scale of exclusion and the timescale over which coexistence is tested relative to the accumulation of reproductive isolation (discussed in 'Stage 3').

Priority Question 2: Which Components of Resource Use Evolve, and in What Ways, in Different Environments?

Our discussion highlights that the average position of a lineage's resource consumption curve is just one of several components of resource use (Figure 1A). Yet, few empirical studies have examined the evolution of resource requirements (but see [30] for an excellent example), and theoretical work often makes the simplifying assumption that resource requirements do not evolve (e.g., [29]). To our knowledge, no study has examined the evolution of resource position, resource breadth, and resource requirement in tandem in different resource environments in any system. We highlight this area as an exciting priority for speciation research, most amenable to experimental evolution in microcosms (e.g., [30,41]), to elucidate fundamental mechanisms of lineage persistence.

Priority Question 3: How Have the Ecological Drivers of Lineage Persistence Shaped the Tree of Life?

The species we observe today are those that have persisted long enough to cross the species boundary, the rare successes out of many unobserved failures [6,7]. We hypothesize that different speciation modes do not give rise to new species at the same rate (stage 1), nor do they give rise to new species with similar coexistence probabilities (stage 3). For some speciation modes (e.g., polyploid speciation), speciation is frequently initiated but rarely completed [43], whereas for others (e.g., sympatric speciation), speciation is rarely initiated, but once it is, the likelihood of yielding persistent species is higher [44,45] (Box 2). However, a direct comparison of the numerical dominance of speciation by different speciation modes does not, to our knowledge, exist. Although such a comparison with empirical data may be impractical, theory would likely yield valuable insights.

Concluding Remarks

Every species on Earth is a product of speciation. Although the role of species' ecologies in the speciation process is well recognized [46], we have identified key gaps between ecological and evolutionary knowledge, offering coexistence theory as the bridge. Across this bridge, we have highlighted how the rich complexity of interactions between species and their environments provides equally rich opportunities for discovery in speciation research (see Outstanding Questions). We hope that our perspective will stimulate new experiments and theory, guided by the three priority questions above, ultimately providing resolution to the question of what role ecological persistence might play in the origin of species [7].

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Outstanding Questions

How often does speciation fail via lineage reabsorption versus a failure to coexist ecologically, and for the latter, is resource competition a common driver?

What effects do different resource environments have on the speciation process, directly through selection and indirectly through other evolutionary processes (e.g., via population size)?

How constrained is the evolution of resource use (i.e., breadth of resources used or rates of consumption) versus resource requirement, and what are the consequences of these constraints for speciation?

How ecologically similar are recently formed sister species, does the answer vary by speciation mode, and how does similarity change on deeper timescales, once lineages cross the species boundary?

Do different speciation modes have different coexistence probabilities, affecting rates of diversification and numerical dominance of species formed by each mode on macroevolutionary timescales?

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