

An evolutionary framework for understanding habitat partitioning in plants

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Abstract

Many plant species with overlapping geographic ranges segregate at smaller spatial scales. This spatial segregation—zonation when it follows an abiotic gradient and habitat partitioning when it does not—has been experimentally investigated for over a century often using distantly related taxa, such as different genera of algae or barnacles. In those foundational studies, trade-offs between stress tolerance and competitive ability were found to be the major driving factors of habitat partitioning for both animals and plants. Yet, the evolutionary relationships among segregating species are usually not taken into account. Since close relatives are hypothesized to compete more intensely and are more likely to interact during mating compared to distant relatives, the mechanisms underlying habitat partitioning may differ depending on the relatedness of the species in question. Here, I propose an integration of ecological and evolutionary factors contributing to habitat partitioning in plants, specifically how the relative contributions of factors predictably change with relatedness of taxa. Interspecific reproductive interactions in particular are understudied, yet important drivers of habitat partitioning. In spatially segregated species, interspecific mating can reduce the fitness of rare immigrants, preventing their establishment and maintaining patterns of spatial segregation. In this synthesis, I review the literature on mechanisms of habitat partitioning in plants within an evolutionary framework, identifying knowledge gaps and detailing future directions for this rapidly growing field of study.

KEYWORDS

competition, habitat partitioning, herbivory, reproductive interference, zonation

The abundances of co-occurring species often vary predictably along environmental gradients at local scales, a pattern termed zonation (Southward, 1958). This pattern, long observed by naturalists (Connell, 1972), occurs worldwide in plants and animals (Watson, 1915; Colman, 1933) and terrestrial and aquatic systems (Sharitz and McCormick, 1973; Hay, 1981) and has been studied experimentally for over a century (Baker, 1909). Classic ecological investigations on zonation have resulted in fundamental insights into the relative and interactive roles of abiotic and biotic factors in determining the distribution and abundance of species. Because of its experimental tractability, small scale physical gradients have been a model system for investigating

mechanisms of habitat partitioning among co-occurring species. However, species may spatially segregate at local sites along discrete physical boundaries (e.g., between adjacent soil types), without an obvious gradient, or without an obvious abiotic correlate (Christie and Strauss, 2020) (Figure 1A–C). Rarely do ecological studies of habitat partitioning (zonation or otherwise) consider evolutionary relationships among species, which may influence the type and relative importance of factors driving these local patterns of spatial segregation.

Early experimental studies of sessile marine organisms in the rocky intertidal zone identified two major factors contributing to zonation: physiological tolerance to the

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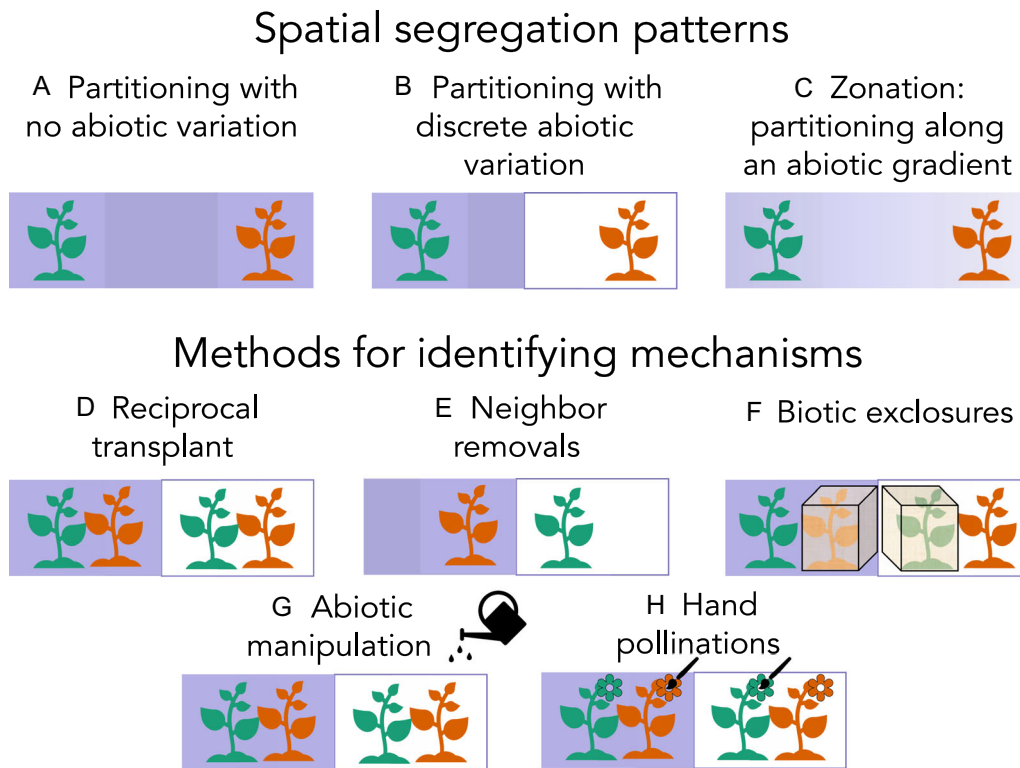


FIGURE 1 (A–C) Patterns of habitat partitioning in plants and (D–G) methods for identifying contributing factors. Habitat partitioning can occur when (A) species abundances are not correlated with abiotic factors, (B) species abundances vary between discrete abiotic factors, and (C) species abundances vary along an abiotic gradient. Methods for identifying factors contributing to habitat partitioning include (D) reciprocal transplant experiments, (E) neighbor removals, (F) biotic exclusions, (G) abiotic manipulations, and (H) hand pollinations.

physical environment and species interactions (Baker, 1909; Connell, 1961a). These interactions included competition (Connell, 1961a), predation (Connell, 1961b; Menge, 1976), and herbivory (Lubchenco, 1980). Mirroring studies in the intertidal zone, early work in plants largely focused on the role of the abiotic environment in driving species turnover along physical gradients (Whittaker, 1967). Likewise, subsequent experimental work in plants highlighted the importance of competition (Grace and Wetzel, 1981; Silander and Antonovics, 1982; Gurevitch, 1986), seed predation (Smith, 1987), and herbivory (Ellison, 1987). In this synthesis, I make the case that the factors that govern habitat partitioning in closely related species differ predictably from those of distant relatives.

HOW EVOLUTION INFLUENCES LOCAL SPECIES DISTRIBUTIONS

The ultimate source of local species diversity is through the origin and persistence of new species, which arise through the evolution of reproductive isolating barriers. Most speciation occurs in allopatry (Coyne and Orr, 2004); thus, range expansion is necessary for geographic overlap and co-occurrence within the same local species pool. When species that are incompletely reproductively isolated meet in secondary

sympatry, mating between them may result in fusion, demographic displacement of one species in sympatry, or may generate selection for increased reproductive isolation (Servedio and Noor, 2003).

Macroevolutionary studies suggest that secondary sympatry is limited by incomplete reproductive isolation and strong competition (Weir and Price, 2011; Price et al., 2014). Thus, species persistence in secondary sympatry also depends on evolution of niche differences. Species can evolve niche differences before secondary contact via adaptation to different environmental conditions in allopatry. If species meet in secondary sympatry with little niche divergence, then competition may lead to competitive exclusion and a lack of co-occurrence within the same community. However, evolution in secondary sympatry can promote species coexistence through the process of character displacement.

Intense resource competition and frequent interspecific reproductive interactions can generate selection for, and may result in the evolution of, traits that minimize these interactions, allowing for coexistence (Brown and Wilson, 1956). Across multiple plant genera, sympatric sister pairs have greater reproductive trait divergence than allopatric sister pairs, consistent with character displacement in close relatives (Muchhala and Potts, 2007; Grossenbacher and Whittall, 2011; Koski and Ashman, 2016;

Weber et al., 2018; Newman and Anderson, 2020). However, the evolution of character displacement is more likely when selection against interactions with heterospecifics is sufficiently strong, and populations have sufficient genetic variation for traits that minimize resource use or reproductive interactions (Pfennig and Pfennig, 2009). In the absence of character displacement, competitive or reproductive exclusion can result in a lack of fine-scale coexistence but may still result in habitat partitioning (fine-scale segregation but co-occurrence within the same habitat).

Other modes of speciation may result in more rapid rates of secondary contact (e.g., via budding speciation, when a small population nested within the range of a widespread species becomes reproductively isolated; Anacker and Strauss, 2014; Grossenbacher et al., 2014). When speciation occurs in sympatry (commonly in plants through polyploidy; Wood et al., 2009), the newly formed species already co-occur within the same local community. However, arising in sympatry does not guarantee long term co-occurrence; whether these newly formed species persist in sympatry also depends on the evolution of niche differences. In the classic example, when a polyploid species arises within a diploid population, they are initially at a mating disadvantage due to their local rarity and ecological similarity to their diploid progenitor (Levin, 1975). The rarer polyploid has fewer potential mates for successful reproduction, and consequently fewer effectual pollinations resulting in the production of fewer conspecific seeds per capita than the more common diploid. These newly formed polyploid species can overcome their minority disadvantage and coexist with their diploid progenitor through the evolution of traits that increase assortative mating and reduce interspecific competition (Levin, 1975; Fowler and Levin, 1984). Closely related species that meet in secondary sympatry face similar hurdles to local coexistence and often segregate locally within the zone of range overlap.

HOW EVOLUTIONARY RELATIONSHIPS AMONG SPECIES INFLUENCE MECHANISMS OF HABITAT PARTITIONING

Niche overlap in close relatives

Closely related species may be more similar ecologically than distant relatives (Burns and Strauss, 2011; Anacker and Strauss, 2016; Strauss et al., 2021), because of similar abiotic tolerances (potential competition for space, Figure 2E), greater overlap in resource use (potential resource competition, Figure 2A), and more similar floral morphology and phenology (potential competition for shared mutualists, including pollinators and microbes, Figure 2B, D) compared to distant relatives. Consequently, close relatives are predicted to compete more intensely and interact more frequently through pollination than distant relatives (Darwin, 1859; Elton, 1946; Harper et al., 1961; Figure 2A, B).

The outcome of competitive interactions depends on the degree of niche overlap (i.e., the extent to which species share limited resources) and the degree to which species affect other species through shared resources (e.g., by being more efficient at using up shared limited resources) (Chesson, 2000). When average fitness differences (species differences in their intrinsic rate of increase [or fecundity] and sensitivity to competition in annual plants; Adler et al., 2007; Godoy and Levine, 2014) are large, even a small overlap in resource use can lead to competitive displacement. When average fitness differences (sensu Chesson, 2000) are small, larger overlap in resource use is necessary for displacement. Even if close relatives overlap more in resource use, the outcome of competition may be less deterministic if average fitness (sensu Chesson, 2000) is also more similar in close relatives than distant relatives (Figure 2F). For example, Godoy et al. (2014) found that more-distant relatives had greater sensitivities to competition, resulting in larger average fitness differences that increase the likelihood of competitive displacement in distant relatives compared to close relatives.

When species have high niche overlap and similar fitness (as we predict for close relatives), the outcome of competition may depend on the order of arrival of species, with early-arriving species displacing later-arriving species, a phenomenon termed priority effects (Grace, 1987; Kardol et al., 2013; Fukami, 2015; Stuble and Souza, 2016; Christie and Strauss, 2020). In plants, the order of arrival in a community may depend on the timing of dispersal or germination. Species differences in germination timing can reduce niche overlap and promote coexistence or can increase competitive asymmetries between species and reduce the probability of coexistence (e.g., if an earlier-germinating species reduces resources for a later-germinating species) (Rudolf, 2019; Blackford et al., 2020). In cases where species abundances and abiotic factors are not correlated and neither species is competitively dominant, habitat partitioning may arise entirely through priority effects.

Reproductive interactions between close relatives

In plants, reproductive barriers that reduce the probability of interspecific mating (pre-mating barriers) are generally stronger than barriers that reduce hybrid survival or fertility (post-mating barriers) (Lowry et al., 2008; Baack et al., 2015; Christie et al., 2022). Despite their relative strength, pre-mating barriers are rarely complete, individually reducing the probability of interspecific mating on average by up to 61% (Christie et al., 2022). Pre- and post-mating barriers tend to increase over evolutionary time, completing the process of speciation (reviewed by Matute and Cooper, 2021). As a result, the frequency of interspecific mating increases with increasing relatedness between species.

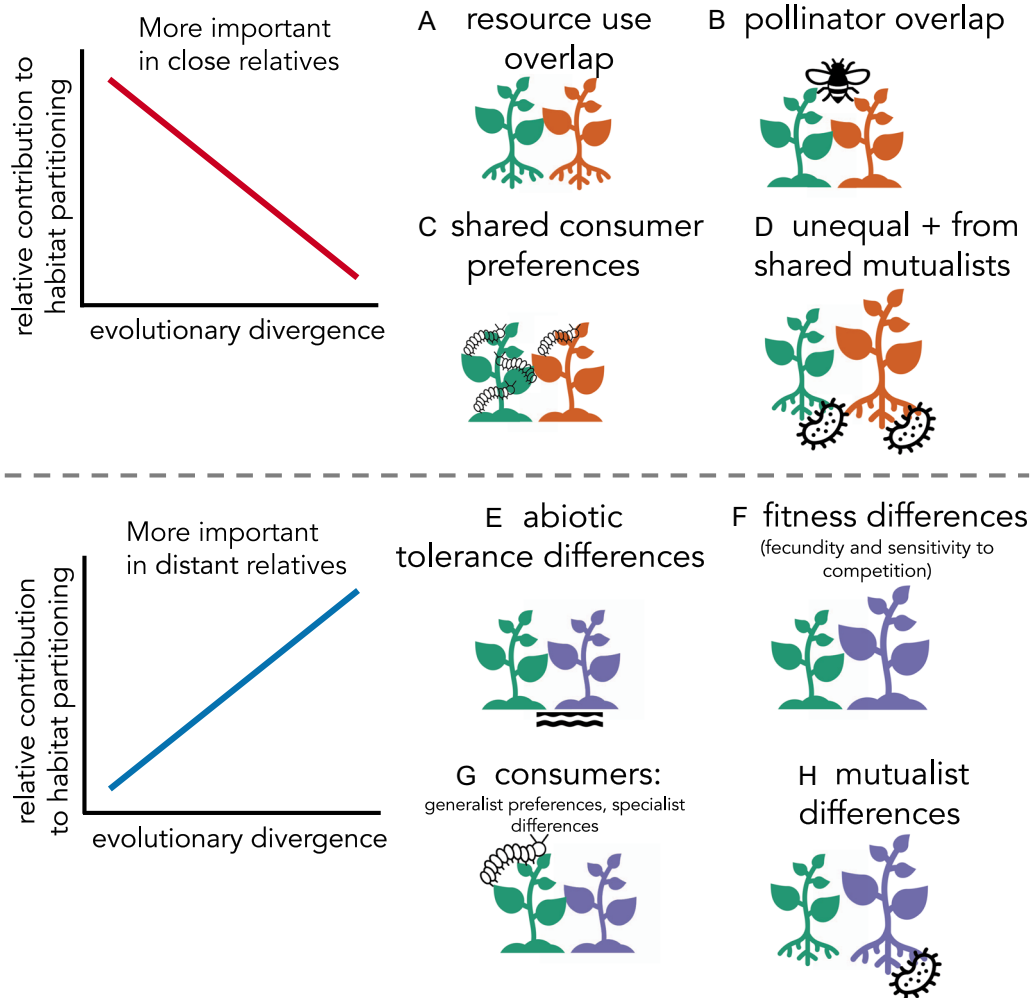


FIGURE 2 Factors contributing to habitat partitioning may vary in importance depending on evolutionary relationships among taxa. Factors predicted to be more important in close relatives (i.e., decrease in importance with divergence) include (A) niche similarity like resource-use overlap, (B) competition for pollination (including interspecific pollen transfer), (C) shared consumer preferences, and (D) unequal benefit from shared mutualists. Factors predicted to be more important in distant relatives (i.e., increase in importance with divergence) include (E) differences in abiotic tolerance, (F) fitness differences (sensu Chesson, 2000; species differences in their intrinsic rate of increase [or fecundity] and sensitivity to competition in annual plants; Adler et al., 2007; Godoy and Levine, 2014), (G) generalist consumer preferences and specialist consumer differences, and (H) mutualist differences.

Interspecific mating often reduces fitness (Groning and Hochkirch, 2008; Kyogoku, 2020), a phenomenon termed reproductive interference. The effect of reproductive interference depends on the relative abundance of the interacting species—fitness decreases with decreasing abundance (Levin and Anderson, 1970; Levin, 1975; Kuno, 1992). The cost of reproductive interference is often asymmetric (Takakura et al., 2009; Briscoe Runquist and Stanton, 2013), likely due to the widespread asymmetry of reproductive barriers (Christie et al., 2022). This asymmetry is expected to result in the exclusion of the species most negatively affected by interspecific mating, possibly contributing to habitat partitioning. Even when reproductive interference affects both species equally, because of its density dependence, it could still result in habitat partitioning via priority effects, whereby the species that arrives first at a site excludes heterospecifics chiefly through mating (Christie and Strauss, 2020).

A SYNTHESIS OF FACTORS CONTRIBUTING TO HABITAT PARTITIONING

The key insights of classic ecological studies remain relatively unchanged; abiotic stressors and interspecific competition continue to be important drivers of habitat partitioning in both close and distant relatives (Emery et al., 2009; DeMarche et al., 2013). The most frequently invoked species interaction in studies of habitat partitioning in plants is resource competition (Qi et al., 2018; Campbell and Keddy, 2022). However, rarely do single factors explain habitat partitioning; multiple interacting factors collectively contribute, and others are rarely examined. Further, few studies explicitly consider evolutionary relationships when experimentally investigating mechanisms of habitat partitioning.

Recent studies have highlighted the important contributions of consumers and indirect interactions through pollinators and in doing so, give a fuller picture of factors that may be especially important in closely related species. To fill this major gap in our knowledge, below I discuss several key factors and highlight some future directions for investigations of habitat partitioning in plants.

Herbivores

Consumers, including herbivores and predators, have long been known as important drivers of zonation in the intertidal zone (Menge, 1976; Lubchenco, 1980), but their importance has been relatively understudied in plants. The distribution and abundance of herbivores and seed predators can vary with abiotic factors at small scales, influencing plant distribution and abundance (Cantor and Whitham, 1989; Manson and Stiles, 1998; Rand, 2002; Elder, 2006). Proximity to plant species with shared herbivores can increase herbivore attack rates, decrease plant fitness, and contribute to habitat partitioning (Parker and Root, 1981; Thomas, 1986; Rand, 1999). Since most herbivores specialize on single plant clades, closely related plant species are more likely to share herbivores than distant relatives (Forister et al., 2015; Cirtwill et al., 2020), influencing how herbivores may contribute to habitat partitioning. Herbivores could contribute to habitat partitioning in different ways, depending on whether herbivores have a host plant preference, whether herbivore abundances vary spatially (Fine et al., 2006), whether plant species differ in tolerance to herbivory (Whittaker, 1982), and whether plant species differ in susceptibility to herbivory (e.g., due to phenological differences between plant species; Futuyma and Wasserman, 1980). Shared herbivore preferences may be more likely to contribute to habitat partitioning in close relatives, while spatial variation in specialist herbivore abundance and widespread generalist herbivore preferences may be more likely to contribute to habitat partitioning between distant relatives (Costa et al., 2003; He et al., 2015; Figure 2C, G).

However, very few studies have quantified the extent of herbivore overlap in the context of habitat partitioning (Nakadai et al., 2014; Katz and Ibáñez, 2016), yet we know herbivore densities can be patchy at small scales (Cantor and Whitham, 1989; Louda and Rodman, 1996; Manson and Stiles, 1998; Rand, 2002). Plant pathogens and parasites are even more understudied in the context of habitat partitioning but may contribute in similar ways as herbivores (e.g., by reducing the fitness of a dominant competitor, causing apparent competition, Holt, 1977; Callaway and Pennings, 1998; Power and Mitchell, 2004; Cobb et al., 2010). Future studies on both closely related and distantly related plant species should quantify herbivore, pathogen, and parasite damage across microsites and

among species. If herbivory, disease, or parasitism is occurring, studies should quantify its effect on plant performance (i.e., tolerance) with experimental removals of herbivores, pathogens, or parasites (e.g., with exclosures (Figure 1F), manual removals, or pesticide applications) or clipping experiments. In addition, future studies should determine the identity of herbivores, pathogens, and parasites and quantify the local distribution of focal herbivores, pathogens, and parasites at sites where habitat partitioning is occurring among their host plants.

Positive interactions

While most studies of habitat partitioning largely focus on antagonistic species interactions, the role of positive interactions remains understudied. The relative importance of negative or positive species interactions often varies with environmental stress, whereby the frequency of positive interactions such as facilitation and mutualisms increase in physically harsh environments (Bertness and Callaway, 1994). Spatial variation in the abundance of mutualists, such as pollinators, mycorrhizal fungi, or rhizobia, could also influence the distribution of co-occurring plant species. For example, variation in the abundance of pollinators influences the distributional limits of subspecies with contrasting mating systems (Fausto et al., 2001; Moeller, 2006). Mutualists could also contribute to habitat partitioning by altering the outcome of competition in different abiotic contexts (Daleo et al., 2008). Mutualists are unlikely to contribute to habitat partitioning if their presence benefits plant species equally, reduces competition between them, or if one plant species changes the composition of mutualists that then provide a greater benefit to a different plant species (Bever, 1999, 2002; Siefert et al., 2018). On the other hand, mutualisms may influence habitat partitioning when plant species increase the abundance or change the composition of mutualists that in turn increase their (plant species') performance or competitive ability (Bever et al., 1997; Bever, 1999, 2002; Keller, 2014). Since mutualists are often shared between closely related species (e.g., pollinators, Cirtwill et al., 2020; seed dispersers, Rezende et al., 2007; mycorrhizal fungi, Jacquemyn et al., 2011), plant species differences in the benefit derived from shared mutualists are more likely to contribute to habitat partitioning in close relatives, while spatial variation in mutualist abundance is more likely to contribute to habitat partitioning in distant relatives (Figure 2D, H). Future studies should consider how the distribution and abundance of mutualists may shape habitat partitioning, either by directly influencing species performance or indirectly by changing the outcome of other species interactions in close and distant relatives. Investigators can manipulate the presence or absence of hypothesized mutualists with experimental removals and additions in natural and controlled settings, in the presence and absence of heterospecifics, to test whether mutualists directly or indirectly contribute to habitat partitioning (Daleo et al., 2008; Siefert et al., 2018; Figure 1F).

Indirect interactions through shared pollinators

Since closely related plant species are more likely to share pollinators and indirectly influence other plant species through pollinators than distant relatives (Carvalho et al., 2014; Cirtwill et al., 2020), plant–pollinator interactions are likely important but understudied drivers of habitat partitioning in close relatives (Figure 2B). Indirect interactions among plant species through shared pollinators can be competitive when sharing decreases visitation rates or increases heterospecific pollen transfer (Levin and Anderson, 1970; Waser, 1978; Morales and Traveset, 2008); alternatively, they can be facilitative when plant species jointly increase the attraction or maintenance of pollinators (Laverty, 1992; Johnson et al., 2003; Moeller, 2004). While facilitative and competitive interactions can operate simultaneously (Rathcke, 1983), the negative consequences of competitive interactions through pollinators on plant fitness may be greater between close relatives than distant relatives (demonstrated in Arceo-Gomez and Ashman, 2016).

Co-occurrence patterns of species with divergent mating or sexual systems patterns suggest that costly interspecific mating limits coexistence in close relatives (Whitton et al., 2017; Christie et al., 2021). As one of the earliest-acting reproductive isolating barriers, microhabitat isolation often contributes disproportionately to reproductive isolation (Kay, 2006; Yost et al., 2012; Paudel et al., 2018; Arida et al., 2021). Habitat partitioning can reduce the probability of interspecific mating through the physical or temporal separation of mating (e.g., through flowering time plasticity; Levin, 2009; Strauss et al., 2021). Yet because of local dispersal, habitat partitioning must be continuously maintained, sometimes through reproductive interactions (DeMarche et al., 2013; Toll and Willis, 2018; Toll et al., 2021). Quantifying reproductive isolating barriers can help predict the outcome of interspecific mating on plant performance and its contribution to habitat partitioning in the field. For example, if reproductive barriers between a species pair are asymmetric, the species that suffers more by receiving more heterospecific pollen is more likely to be excluded from zones occupied by heterospecifics (Briscoe Runquist, 2012; Christie and Strauss, 2019).

We currently lack the ability to assess the relative contribution of reproductive interactions in driving habitat partitioning across evolutionary divergence. To address this gap, future studies investigating both close and distant relatives should first determine whether co-occurring, spatially segregated species interact during mating (e.g., by observing pollinator behavior or by examining pollen loads on stigmas). If species are observed to interact during mating, the outcome of interspecific mating interactions should be ascertained by hand-pollinating co-occurring species reciprocally and quantifying the effect of cross pollination on conspecific seed set. Ideally, these observations and crosses should be performed in concert with reciprocal translocations across microhabitats (Figure 1D, H), allowing for the quantification of the extent to which habitat partitioning influences interspecific mating and fitness.

Interspecific mating is costlier for rare species, a situation common during immigration. To study frequency-dependent interactions, studies could make use of natural variation in plant abundance across the landscape and correlate fitness costs of interspecific mating with plant frequencies (Takemori et al., 2019; Toll and Lowry, 2022). Experimental approaches could include reciprocal transplants manipulating plant frequencies (Briscoe Runquist and Stanton, 2013; Toll and Lowry, 2022) or laboratory crosses with mixed pollen loads at different frequencies, then quantifying conspecific seed set.

Longer-term processes

Many studies investigating mechanisms of habitat partitioning are on relatively short time scales of no more than a few years. The assumption of these studies is that the short-term effects of manipulations (e.g., reciprocal transplants, neighbor removals, exclosures, abiotic manipulations, hand pollinations; Figure 1D–H) on fitness will translate into long-term effects on demography that result in the observed spatial patterns (Toll et al., 2021). In many studies, the fitness of key life stages is difficult to estimate or not measured (e.g., seed survival). These life stages may contribute disproportionately to population growth rates (Elder and Doak, 2006), and their omission may obscure the actual relative importance of factors contributing to long-term habitat partitioning. In addition, these factors may vary by year (Emery et al., 2009), and thus short-term studies may poorly capture long-term dynamics (Toll et al., 2021). Furthermore, factors contributing to habitat partitioning may also act as selective agents and populations may evolve shifts in their spatial niches over time.

To capture these longer-term dynamics, studies should be started and maintained over several years or multiple generations may be planted out simultaneously in shorter-term studies to examine demographic change (e.g., Toll et al., 2021). Treatments would need to be implemented yearly in annual plants or established and monitored for several years in long-lived perennials. Long-term monitoring of manipulations in natural communities can be coupled with the establishment of experimental communities, where the initial abundances of species are varied, and the dynamics can be followed (Lewis, 1961). With longer-term studies in close and distant relatives, we can begin to compare the relative importance and variability of different factors contributing to habitat partitioning.

CONCLUSIONS

Despite over a century of research into habitat partitioning, we lack an understanding of how its underlying mechanisms vary with evolutionary relationships among taxa. Multiple, interacting context dependent factors contribute,

in both close and distant relatives, and their relative importance varies with evolutionary relationships among taxa. Habitat partitioning is more likely to be driven by niche similarity in close relatives that results in reproductive interference, resource and pollinator competition, apparent competition via preferences of shared consumers, and differences in the benefits derived from shared mutualists. In distant relatives, habitat partitioning is more likely to be caused by species differences in abiotic tolerance, fitness differences (species differences in intrinsic rates of increase and sensitivities to competition), and the distribution and abundance of consumers and mutualists. Thus, incorporating evolutionary relationships can lead to a better understanding of how different processes contribute to habitat partitioning in close and distant relatives.

AUTHOR CONTRIBUTIONS

K.T. Conceptualization; Writing – original draft; Writing – review & editing.

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