

Review Article

Parallel Ecological Speciation in Plants?

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Populations that have independently evolved reproductive isolation from their ancestors while remaining reproductively cohesive have undergone parallel speciation. A specific type of parallel speciation, known as parallel ecological speciation, is one of several forms of evidence for ecology's role in speciation. In this paper we search the literature for candidate examples of parallel ecological speciation in plants. We use four explicit criteria (independence, isolation, compatibility, and selection) to judge the strength of evidence for each potential case. We find that evidence for parallel ecological speciation in plants is unexpectedly scarce, especially relative to the many well-characterized systems in animals. This does not imply that ecological speciation is uncommon in plants. It only implies that evidence from parallel ecological speciation is rare. Potential explanations for the lack of convincing examples include a lack of rigorous testing and the possibility that plants are less prone to parallel ecological speciation than animals.

1. Introduction

The past two decades have witnessed a dramatic shift in studies of speciation from an emphasis on stochastic and other nonecological processes to a focus on ecological mechanisms of speciation. Indeed, the proverbial pendulum has swung so far toward ecology that some authors have argued that essentially all plausible types of speciation involve ecological processes [1]. Despite the pervasive role of natural selection in evolution, evidence that ecologically based divergent natural selection is the primary cause of reproductive isolation (ecological speciation *sensu* Schluter, 2001 [2]) is often weak or incomplete in case studies [3].

To more critically evaluate the importance of ecological speciation in nature, several authors have suggested methods for reliably inferring ecological speciation [2–5]. These include (1) direct measurements of divergent ecological selection on parental genotypes (e.g., immigrant inviability) or hybrids (i.e., extrinsic postzygotic isolation) in the different environments; (2) natural selection studies showing that phenotypic differences underlying premating reproductive barriers are a consequence of divergent ecological selection; (3) molecular marker studies of selection against immigrants (i.e., isolation by adaptation); (4) molecular evolutionary

studies linking intrinsic genetic incompatibilities with divergent ecological selection; and (5) tests of parallel ecological speciation, which is the process in which related lineages independently evolve similar traits that confer shared reproductive isolation from their ancestral populations [6].

In plants, widespread application of the first two methods listed above points to an important role for ecology in speciation. For example, there is a long tradition of reciprocal transplant studies since early in the 20th century, and there is abundant evidence of immigrant inviability among recently diverged populations or species [7, 8]. Because habitats often are spatially segregated, divergent habitat adaptation results in ecogeographic isolation, which is considered by many botanists to be the most important reproductive barrier in plants [1, 9]. Likewise, studies that examine the relative importance of different components of reproductive isolation in plants indicate that ecologically based reproductive barriers often play a key role in the early stages of plant speciation [8]. However, evidence of extrinsic postzygotic isolation in plants is surprisingly weak, possibly because of heterosis [8, 10]. Also, few studies have explicitly tested for isolation by adaptation in plants [1] or for ecological causes of hybrid incompatibilities (reviewed in [11]). The evidence for parallel ecological speciation is perhaps least

clear because while “recurrent” formation of plant species and races is thought to be common [12], the evidence underlying these apparent examples has not been examined systematically.

On the other hand, parallel speciation is regularly cited as evidence for ecological speciation in animals (e.g., [6, 13–22]), and the evidence for many individual cases of parallel ecological speciation is strong. For example, the threespine stickleback has undergone several well-documented parallel transitions between environments. The most well-known case is likely the independent origin of “benthic” and “limnetic” ecotypes in at least five British Columbian lakes [23, 24]. Another well-studied system is the marine snail *Littorina saxatilis*, which has repeatedly evolved pairs of ecotypes on the rocky coasts of Northwestern Europe [25]. Numerous other strong candidates for parallel ecological speciation are found in animals, including but not limited to lake whitefish [26], cave fish [27], walking sticks [20], scincid lizards [21], lamprey [28], electric fish [29], horseshoe bats [30], and possibly even in the genetic model organism *Drosophila melanogaster* [31], though not all of these examples are fully validated with the criteria described below.

Here we use explicit criteria to evaluate the strength of evidence for parallel ecological speciation in plants. We evaluate plant systems using criteria that are more often used to evaluate animal systems because comparable evaluations across taxa are important for determining general patterns of speciation. We find that evidence for parallel ecological speciation in plants is surprisingly rare in comparison to animals and provide potential explanations for this finding.

2. Studying Parallel Ecological Speciation

Parallel speciation is the process in which related lineages independently evolve similar traits that confer shared reproductive isolation from their ancestral populations [6]. It is good evidence that selection drove the evolution of reproductive isolation, as it is unlikely that the same barriers would arise independently by chance [6]. Schluter and Nagel [6] listed three criteria for parallel speciation: (1) related lineages that make up the new descendent populations are phylogenetically independent; (2) descendent populations are reproductively isolated from ancestral populations; (3) independently derived descendent populations are not reproductively isolated from each other. They add that an adaptive mechanism must be identified to show that natural selection drove the evolution of reproductive isolation [6]. Together, these four conditions are the evidence necessary to demonstrate the process we refer to as parallel ecological speciation. We choose to use the term “parallel” over the alternative term “convergent” because of the initial similarity of the independent lineages [32–34] and because this vocabulary is consistent with the original description of the process [6].

If we apply these criteria to well-known examples of parallel or “recurrent” speciation in plants [12], it is clear that botanists and zoologists are mainly studying different things. For example, many auto- and allopolyploid species have

multiple independent origins (reviewed in [35]), in which independently derived polyploid lineages are reproductively isolated from their common ancestor but not from one another. Additionally, a high proportion of homoploid hybrid species studied arose in parallel [36]. Although there is evidence that natural selection is important in polyploid and hybrid speciation [10, 37, 38], the genomic changes that accompany polyploidization and hybridization reduce our ability to show that parallel ecological selection was the primary driver of reproductive isolation. This differentiates parallel polyploid and hybrid speciation from parallel ecological speciation described above and represented in the animal cases listed previously.

In cases of parallel ecological speciation, the independent descendent populations are found in a new environment where they experience new and shared ecological selection that causes speciation. However, not all cases in which multiple transitions to a new environment are associated with repeated speciation events represent true parallel ecological speciation. Several possible patterns exist and are shown in Figure 1. In parallel ecological speciation, ancestral and descendent groups each represent single compatible groups (Figure 1(a)). However, one can also envision several other patterns, in which either the ancestral or descendent groups (or both) represent multiple compatibility groups (Figures 1(b)–1(d)).

The pattern in which the descendent groups are incompatible with one another (Figure 1(b)) can be caused by mutation-order speciation in which the same selective pressure leads to different genetic changes in the multiple populations [4]. The isolation between ancestral groups could also be the result of drift. The third pattern (Figure 1(c)) has been called “replicated ecological speciation” [39] and is made up of multiple distinct speciation events. Studying similarities and differences between these replicate speciation events can help identify general patterns of speciation [39]. Finally, the last pattern (Figure 1(d)) is to our knowledge novel, and we do not know of any empirical examples.

In this survey, however, we are only interested in parallel ecological speciation (Figure 1(a)), which tells us something more specific than other patterns. In particular, parallel ecological speciation indicates that all of the new barriers present are predominantly if not entirely due to natural selection, whereas in the other cases, other forces may have been at play along with natural selection. For example, if the descendent populations are reproductively isolated from one another (Figures 1(b) and 1(c)), it is plausible that changes, driven by processes other than ecological adaptation, caused the isolation between descendent populations as well as the isolation across habitats. This means that testing the compatibility of descendent populations is essential for documenting parallel ecological speciation. However, this test is not necessary for demonstrating all forms of evidence for ecological speciation.

When studying parallel ecological speciation, it is also useful to recognize that evidence of parallelism may or may not extend across multiple levels of biological organization. Although the individuals of the descendent species must have

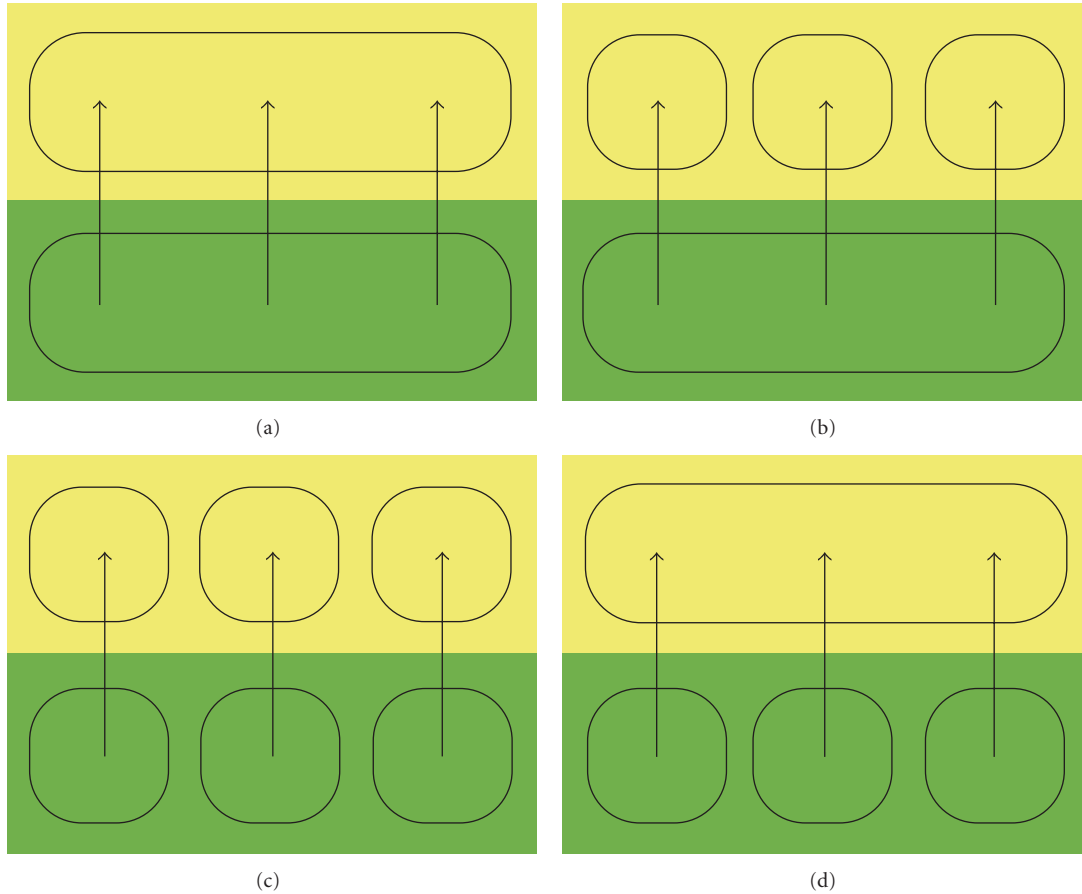


FIGURE 1: An illustration of several patterns in which multiple independent transitions to a new environment are coupled with speciation. The yellow and green boxes represent two different environments, the arrows represent multiple independent transitions between the environments, and the closed shapes represent reproductively compatible groups. Only panel (a) represents parallel ecological speciation, the process we are interested in.

the same isolating trait, this common trait is not necessarily governed by the same mutation, gene, or even pathway in the different replicates. Even when the same mutations are responsible for parallel transitions in a given isolating trait, these mutations can be either the result of recurrent *de novo* mutation or standing variation. While independent genetic changes simplify the task of reconstructing population and trait histories, parallel changes from standing genetic variation can be useful for pinpointing regions of the genome responsible for ecological selection and reproductive isolation [40].

3. Literature Survey

For this survey, we searched the scientific literature for evidence of parallel ecological speciation in plants. We used combinations of the words “parallel”, “recurrent”, “multiple”, “convergent” and “speciation”, “evolution”, “origins”, “reproductive barriers/isolation” as well as “paraphyly” as search terms in Web of Science and Google Scholar. We also examined all papers citing candidate examples and searched for additional papers about the candidate species.

Levin [12] reviewed a number of potential cases of parallel ecological speciation in plants. Although his paper was not strictly about parallel ecological speciation, we consider all of his ecological examples in our table in order to revisit their validity and discuss new evidence for each case. We used explicit criteria to determine the strength of evidence for parallel ecological speciation. Specifically, we judged the strength of evidence for each of the aforementioned four criteria: independence, isolation, compatibility, and selection. To merit inclusion, we required that each newly identified case has at minimum weak direct evidence for repeated adaptation to similar environments (independence) or multiple origins of an isolating trait (isolation) and indirect evidence for the other condition. Evidence that an example failed to meet any of the four criteria resulted in its exclusion. As a result, several promising systems were not included in our table or appendix (e.g., *Frankenia ericifolia* [41] and *Heteropappus hispidus* ssp. *Leptocladus* [42]). This was because *Frankenia ericifolia* has only indirect evidence of both independence and isolation and *Heteropappus hispidus* ssp. *Leptocladus* has no evidence of isolating traits. Lastly, we evaluated a few of the frequently cited examples of parallel ecological speciation in animals for comparison. The list of

animal examples is not exhaustive and does not necessarily include all of the best cases.

The following sections discuss each criterion and the types and strengths of evidence we considered.

3.1. Independence. Parallel speciation requires that replicate lineages be phylogenetically independent, so that the “shared traits responsible for reproductive isolation evolved separately” [6]. Estimating phylogenetic independence can be difficult for recently diverged taxa because of inadequate resolution, hybridization and introgression, and deep coalescence. These issues are exacerbated when phylogenies are based on a small number of loci or if the loci employed have little phylogenetic information content (e.g., isozymes). Additionally, it is not strictly necessary for populations to be phylogenetically independent for reproductive barriers to evolve separately, if different genes, mutations, or genetic pathways are exploited by selection in populations that remain connected by gene flow.

Therefore, in this survey, strong evidence for independent evolution includes: (1) phylogenetic analyses supporting independence with multiple, phylogenetically informative loci or (2) direct evidence that a shared isolating trait has evolved independently (e.g., the trait is a result of different mutations in different populations). Phylogenetic analyses with a single locus, or with loci having little information content, are deemed weak direct evidence. Note that we consider genetic information from completely linked markers (e.g., multiple genes sequenced from the chloroplast genome) as information from one locus. Finally, indirect evidence for independence could include the improbability of long-distance colonization or gene flow between geographically separated but ecologically similar habitats, or phenotypes that are similar but not identical suggesting different genetic bases.

3.2. Isolation. As with any test of incipient or recent speciation, reproductive isolation must have evolved between descendent and ancestral populations, though not necessarily to completion. For strong evidence of isolation, we require experimental evidence for strong reproductive barriers that are genetically based, such as substantial differences in flowering time or pollination syndrome in a common garden and/or F1 hybrid inviability or sterility. Experimentally demonstrated weak but statistically significant reproductive barriers between diverging populations (including selection against immigrants and hybrids), or genetic divergence between locally diverging populations despite the opportunity for gene flow, are considered weak evidence for isolation. We view systems with apparent immigrant or hybrid inviability (e.g., serpentine adaptation), long-term persistence of divergent populations in sympatry, or strong divergence in mating system as indirect evidence that barriers likely exist. Although we would not consider isolation that has no genetic basis as evidence for parallel ecological speciation, we acknowledge that phenotypic plasticity can facilitate or impede the evolution of reproductive barriers and is an important consideration for studies of ecological

speciation [43] (e.g., [44]). Furthermore, because explicitly testing that isolation is genetically based was rare in our candidate studies, we only required the genetic basis of isolation to be confirmed for cases to have strong direct evidence.

3.3. Compatibility. As we briefly discuss above, the lack of reproductive barriers between descendent populations is a key criterion distinguishing true parallel ecological speciation from other forms of replicated ecological speciation (Figure 1). For strong evidence of reproductive compatibility we require that descendent populations show little or no barriers to reproduction when experimentally crossed and minimal ecological divergence as demonstrated by reciprocal transplant or manipulative ecological experiments. If only one of these two components of compatibility were demonstrated, we consider the evidence to be weak. We also consider substantial genetic analysis showing little genetic differentiation at neutral markers between the descendent populations to be weak direct evidence for compatibility, although this might weaken the case for the criterion of independence. Lastly, if the evolution of environmental specificity or mating system is such that descendant populations are indistinguishable in these parallel traits and have no other phenotypic differences, we consider this indirect evidence for compatibility.

It is difficult to ascertain the strength of evidence for isolation and compatibility when multiple independent origins of self-fertilization (autogamy) have occurred. This is because replicate populations of selfers are likely to be as strongly isolated from one another as they are from the ancestral outcrossing populations. For this reason, replicated selfing lineages were excluded from consideration unless accompanied by the evolution of other reproductive barriers.

3.4. Selection. Without evidence of selection, parallel speciation cases can tell us nothing about ecology’s role in speciation. Because of this, we searched for evidence of the adaptive mechanism(s) underlying parallel isolation. For strong evidence, we include reciprocal transplants showing strong local adaptation, manipulative experiments relating adaptive traits to extrinsic fitness, and/or signatures of selective sweeps at loci underlying putatively adaptive traits. Similarly, reciprocal transplants showing weak local adaptation, manipulative experiments showing a weak relationship between traits and extrinsic fitness, or common garden experiments comparing Q_{ST} to F_{ST} are deemed weak evidence. Finally, we consider correlations between novel traits and environments or habitats to be indirect evidence for the role of selection.

4. Results of the Survey

The most striking result of this survey is that very few plant cases have strong evidence for two or more criteria of parallel ecological speciation, and most have only weak or indirect evidence for any of the criteria (Table 1; Appendix A). Only 3 of the 15 examples discussed by Levin [12] meet our

TABLE 1: Candidate examples of parallel ecological speciation in plants showing the strength of evidence for each case. The details of each example can be found in Appendix A. The strength of evidence for each case was coded as follows: ***: strong direct evidence, **: weak direct evidence, *: indirect evidence, —: no evidence, †: evidence against, and NA: no data.

Species	Min. number of origins	Independence	Isolation	Compatibility	Selection	Major parallel trait(s)	References
<i>Alopecurus myosuroides</i> ^{LX}	Many	**	NA	NA	***	Herbicide tolerance	[45–51]
<i>Agrostis capillaries</i> ^{LX}	Many	*	*	*	**	Edaphic tolerance	[52–54]
<i>Agrostis stolonifera</i> ^{LX}	NA	NA	*	*	**	Edaphic tolerance	[55–57]
<i>Agrostis tenuis</i> ^L	NA	*	**	NA	**	Edaphic tolerance	[58, 59]
<i>Armeria maritima</i> ^{LX}	NA	***	†	*	*	Edaphic tolerance	[60–63]
<i>Chaenactis</i> spp. ^{LX}	2	***	†	**	*	Flower colour	[64, 65]
<i>Cerastium alpinum</i>	2	**	*	NA	***	Edaphic tolerance	[66]
<i>Chenopodium album</i> ^{LX}	NA	*	NA	NA	*	Herbicide Tolerance	[67–70]
<i>Crepis tectorum</i> ^{LX}	2	**	NA	NA	**	Leaf morphology	[71, 72]
<i>Deschampsia caespitosa</i> ^L	2	**	*	*	*	Edaphic tolerance	[73, 74]
<i>Eucalyptus globulus</i>	3	***	**	*	*	Dwarfed morphology	[75]
<i>Geonoma macrostachys</i>	3	**	**	*	*	Habitat type; reproductive strategy	[76–78]
<i>Hemerocallis citrina</i> var. <i>vespertina</i>	3	**	*	*	NA	Nocturnal flowering	[79]
<i>Hieracium umbellatum</i> ^{LX}	NA	*	*	*	*	Habitat type (dunes)	[80]
<i>Lasthenia californica</i>	2	***	**	**	**	Edaphic tolerance	[81–87]
<i>Microseris lanceolata</i> ^L	2	***	*	**	*	Habitat type (elevation)	[88–90]
<i>Petunia axillaris</i>	6	**	***	*	—	Flower colour	[91, 92]
<i>Plantago maritima</i> ^{LX}	2	*	NA	NA	NA	Spike morphology	[93]
<i>Poa annua</i> ^{LX}	NA	*	—	*	*	Herbicide tolerance	[94, 95]
<i>Schizanthus grahamii</i>	2	**	**	NA	*	Pollination syndrome, self-compatibility	[96]
<i>Silene dioica</i> ^{LX}	NA	**	NA	NA	—	Edaphic tolerance	[97, 98]
<i>Silene vulgaris</i> ^{LX}	2	*	*	NA	***	Edaphic tolerance	[99–102]
<i>Streptanthus glandulosus</i>	Many	**	*	*	**	Edaphic tolerance	[103–107]

^L: Levin example.

^X: Example that would not have been included in this table had they not been reviewed in Levin [12].

minimum requirements for inclusion in the table. We did identify 8 new candidate systems. These were *Cerastium alpinum*, *Eucalyptus globulus*, *Geonoma macrostachys*, *Hemerocallis citrina* var. *vespertina*, *Lasthenia californica*, *Petunia axillaris*, *Schizanthus grahamii*, and *Streptanthus glandulosus*. Some of the new candidate systems are quite promising, but none have strong evidence for all criteria. These cases and a review of Levin's [12] examples are summarized in Table 1 and Appendix A. The animal cases used as a comparison are summarized in Table 2 and Appendix B. Although few of the animal cases have strong evidence for all the criteria either, these well-studied animal systems are more strongly supported than the plant examples.

Many of the putative plant cases lack evidence of compatibility among independent parallel populations. In fact, none of the examples have strong evidence for compatibility. This is unfortunate given the effectiveness of this criterion for demonstrating that ecological selection was the main cause of reproductive isolation in these systems—the primary reason for studying parallel ecological speciation in the first

place. Hopefully, future studies in these systems will test for evidence of compatibility between suspected examples of parallel species. On the other hand, the criterion with the most evidence is the independent evolution of lineages that appear to be diverging in parallel. This is unsurprising given the widespread application of molecular phylogenetic methods in plants.

One of the best candidates of parallel ecological speciation in plants to date is *Eucalyptus globulus* [75] (Appendix A). In this case, three populations of *E. globulus* that inhabit granite headlands have a dwarfed morphology. Data from several nuclear and chloroplast markers show that each of the dwarfed populations is more closely related to its nearest tall population than to other dwarfed populations. Furthermore, there are two lines of evidence for isolation. First, the dwarfed populations flower earlier than the tall populations. Second, there is no evidence of pollen flow from the tall populations to the dwarfed populations despite a thorough examination of variation at microsatellite loci. However, the genetic basis of isolation, compatibility among

TABLE 2: Examples of parallel ecological speciation in animals showing the strength of evidence for each case. This list is not exhaustive and instead is a selection of well-studied cases serving as a comparison to the plant examples. The strength of evidence for each case was coded as follows: ***: strong direct evidence, **: weak direct evidence, *: indirect evidence, —: no evidence, †: evidence against, and NA: no data.

Species	Min. number of origins	Independence	Isolation	Compatibility	Selection	Major parallel trait(s)	References
<i>Astyanax</i> cave fishes	2	***	**	**	***	Pigmentation, eye functionality	[27]
<i>Coregonus clupeaformis</i>	6	***	**	*	***	Body size and shape, foraging niche	[13, 108–115]
<i>Coregonus lavaretus</i>	3	***	*	*	***	Body size and shape, foraging niche	[14, 115–117]
<i>Gasterosteus aculeatus</i> benthic/limnetic	5	***	**	**	**	Body size and shape, foraging niche	[3, 15, 16, 23, 24, 118–122]
<i>Gasterosteus aculeatus</i> lake/stream	6	***	**	*	**	Body size and shape, foraging niche	[3, 23, 123–130]
<i>Gasterosteus aculeatus</i> anadromous/stream resident	many	***	**	**	***	Body size and shape, life history	[3, 17, 23, 131–133]
<i>Littorina saxatilis</i> -Galician Spain	3	***	***	*	***	Shell size and shape, microhabitat adaptation	[18, 19, 134–141]
<i>Timema cristinae</i>	NA	***	**	**	**	Color pattern, host plant adaptation	[20, 142–144]

dwarfed populations, and the selective advantage of being dwarfed still need to be confirmed in this example.

Other promising cases include *Lasthenia californica* [81] (Appendix A) and *Schizanthus grahamii* [96] (Appendix A). *Lasthenia californica* has strong evidence for parallel evolution of two races that have different flavonoid pigments and are found in different edaphic environments using phylogenetic analyses of ribosomal and chloroplast sequence and allozyme variation [81–84]. Race A is more tolerant of Na⁺ and Mg²⁺ and race C flowers earlier and produced more seed heads under drought conditions [85, 86]. However, isolation and compatibility between and within the races need to be confirmed. Conversely, there are clear reproductive barriers between *Schizanthus grahamii* and *Schizanthus hookeri* as they have different primary pollinators and experimental interspecific crosses produced no seeds [96]. However, it is not certain that these barriers arose multiple times independently because only chloroplast sequence data has been analyzed.

There are a few commonalities among the candidate examples. In many of the candidate systems ancestral and descendent forms have evolved particular edaphic tolerances and/or specific changes in reproductive phenotype or mating system. Under divergent ecological selection, these traits are likely to make ecological speciation relatively easier because they can cause assortative mating as a byproduct of divergent selection.

5. Why Is Parallel Ecological Speciation Seemingly Rare in Plants?

5.1. *Lack of Data.* The lack of strong examples of parallel ecological speciation in plants is probably because botanists

typically do not do the necessary tests. Perhaps this is because botanists have never doubted the importance of ecology in speciation [1, 7, 9] or because other methods of inference have been successful. However, we believe that it is useful to examine parallel ecological speciation explicitly in plants given how fruitful such studies have been in animals. In the present paper, this has allowed us to not only identify the key information that is missing in most potential case studies of parallel ecological speciation in plants, but also to recommend the experimental tests that are likely to be most profitable. For example, immigrant inviability is likely an important barrier in cases of parallel ecological speciation in plants. Therefore, reciprocal transplants between the new habitat types (as a test of isolation) and among sites in a single habitat type (as a test of compatibility) are crucial. A second essential set of tests that should be conducted is crosses between ancestral and descendent populations and crosses among populations in each habitat. It is surprising that these data are lacking given that both an explicit framework for studying parallel ecological speciation [6] and a list of possible cases [12] have been available for many years.

Furthermore, the signature of parallel speciation is easily lost. For example, if gene flow occurs between independently derived populations, the signals of phylogenetic independence may be lost. Conversely, if descendent lineages are geographically isolated (i.e., allopatric) but otherwise reproductively compatible, they will likely eventually evolve reproductive isolation from one another even if they were not originally isolated. Thus, the window of time in which parallel speciation can be detected may be relatively narrow. Interestingly, some of the strongest animal cases (*Littorina*, threespine stickleback, and whitefish) are no more than 40,000 years old (postglacial) [23, 108], and some are thought to be as young as 10,000 years [19]. However, we

see no reason why this window would be narrower in plants than animals. Thus, while the narrow window of detectability may account for the overall paucity of convincing examples of parallel ecological speciation in either the plant or animal kingdoms, it cannot explain why there are fewer examples in plants than in animals.

5.2. Plants Are Different. It is also possible that parallel ecological speciation is truly rare in plants. Considerable work would need to be done to validate this conjecture. However, should this pattern exist, there are several potential explanations. First, it is possible that the types of habitat distributions that promote parallel speciation in animals are more rare for plant populations. Many but not all of the animal examples involve adaptation to systems such as lakes or streams which are common, offer geographical isolation, and provide relatively homogeneous ecological environments. Perhaps these kinds of ecological opportunities are less frequent for plants? We think this explanation unlikely given that patchy environments (especially edaphic environments) are common in terrestrial ecosystems and parallel adaptation into those habitats occurs frequently.

It is also possible that plants have certain characteristics that make parallel ecological speciation unlikely or lack characteristics that promote parallel ecological speciation. This potential difference between plants and animals may be in part because behavior is not particularly relevant to plants. Behavior, especially behaviorally based mate preference, may be an important component of parallel ecological speciation in animal systems (though pollinator behavior in flowering plants may act analogously). Perhaps plants have no trait equivalent to body size in animals, which can act as a “magic trait” [145] to serve in both assortative mating and ecological adaptation. However, flowering time could be such a trait, and there are many examples of flowering time changing in new edaphic environments (e.g., Lord Howe Island palms [146]). On the other hand, flowering time may be quite constrained because partitioning flowering time requires narrower windows of flowering, which can have strong negative fitness consequences. Other potential traits are floral morphology and edaphic tolerances. Floral morphology may adapt to attract different pollinators and, consequently, lead to pollinator isolation. Similarly, the evolution of edaphic tolerance often leads to selection against immigrants.

The lack of evidence for parallel ecological speciation in plants is a mystery that may represent a key to understanding how species arise in plants. If parallel ecological speciation is more common than our survey suggests, then we can bolster existing evidence that ecology plays an important role in plant speciation. On the other hand, if parallel ecological speciation is determined to be rare, we can conclude that speciation may be less repeatable and more complicated than sometimes believed. We do not intend to imply that ecological speciation does not happen in plants. In fact, we believe it to be common. However, evidence of parallel ecological speciation in plants is not yet as convincing as it is for animal examples. We hope our study will spur additional investigation of the promising systems identified here, as

well as provide guidance regarding the kinds of studies that should be performed in each system.

Appendices

A. Descriptions of Potential Examples of Parallel Ecological Speciation in Plants

Note that superscript “L” (^L) indicates that the example was reviewed in Levin [12].

A.1. *Alopecurus myosuroides*^L. The black-grass *Alopecurus myosuroides* is an agricultural weed that has evolved resistance to herbicides in many locations, possibly independently [45]. Independent evolution may be occurring even on very local scales: Cavan et al. [46] used microsatellite data to show that four patches of resistant black grass in two neighbouring fields were independently derived from nonresistant plants. Herbicide resistance occurs either through plant metabolism, often polygenic, or via mutant ACCase alleles, and seven mutant resistance alleles have been identified [47–49]. A study of herbicide resistance in populations across Europe concluded that the same mutant ACCase alleles have appeared repeatedly [50]. No work has been done on reproductive barriers between resistant and nonresistant plants, although AFLP analysis shows little differentiation between resistant and nonresistant populations [51]. An important consideration in this case is that selection is human mediated and therefore unlikely to remain constant long enough to allow for speciation.

A.2. *Agrostis capillaris*^L. The corrosion of zinc-galvanized electricity pylons in South Wales has created repeated patches of zinc-contaminated soil that have been colonized by the grass *Agrostis capillaris*. Zinc tolerance levels for *A. capillaris* plants vary from low to high across multiple pylons [52]. Tolerance appears to be polygenic and dependent on standing genetic variation [53]. Jain and Bradshaw [54] determined that seed and pollen dispersal is limited beyond 5 m, suggesting that tolerance is evolving independently at each pylon, although the still relatively small distances between pylons (300 m) do not rule out occasional pylon to pylon gene flow. Further work should establish if the populations are truly independent and measure barriers to gene flow between tolerant and nontolerant neighbouring populations.

A.3. *Agrostis stolonifera*^L. Metal refining in Prescot, UK, caused considerable copper contamination to surrounding soil, and the grass *Agrostis stolonifera* has since then colonized a number of contaminated sites. Older sites were found to have more complete ground cover and a greater proportion of resistant individuals [55], suggesting that the evolution of tolerance is ongoing at younger sites. Morphological and isozyme analyses suggest, counterintuitively, that there is a reduction in clone number in uncontaminated sites compared to contaminated ones. All sites are centered on a single copper refinery, so the independence of the sites

is questionable. *Agrostis stolonifera* has also evolved salt tolerance in multiple inland and coastal sites, possibly independently [56, 57]. The strength of evidence for independent or parallel evolution in either of these cases is quite weak.

A.4. Agrostis tenuis^{L.} Copper-tolerant populations of *Agrostis tenuis*, from the UK and Germany, were shown to have different responses to copper using regression analysis [58]. This variability indicates that multiple genes or alleles are responsible for copper tolerance in different populations, although crossing experiments could further support this inference. Other work has shown asymmetric gene flow between tolerant and nontolerant populations with moderate levels of copper tolerance found in sites downwind of colonized mine tailings [59]. Although adult plants from mine sites showed high degrees of tolerance, seeds were not tested, so it is unknown if gene flow from nontolerant populations is reduced pre- or postzygotically. The adaptation to copper-contaminated soil at multiple sites may be parallel, or may be the result of the transmission of tolerant genotypes between mines. Without stronger evidence for independence, this case is very weak.

A.5. Armeria maritima^{L.} Populations of *Armeria maritima* across Europe vary in metal tolerance: those living on metalliferous soil are tolerant while those on uncontaminated soil are not [60]. Isozyme and nuclear marker data suggest that tolerance has evolved multiple times independently [61–63]. Furthermore, this tolerance is maintained even in the face of substantial gene flow between neighbouring nontolerant populations, indirect evidence for the strength of selection on the metalliferous soil. This does not appear to represent parallel speciation, however, as pollen fertility and gene flow are not reduced between populations with different levels of tolerance [61].

A.6. Cerastium alpinum. Enzyme phenotypes suggest that Northern Europe was colonized by two postglacial lineages of *Cerastium alpinum* [64]. The two lineages are found on both serpentine and nonserpentine soils but a principle components analysis of enzyme phenotype does not reveal any clustering by soil type, suggesting that serpentine tolerance evolved independently in each lineage [64]. Further experiments manipulating Ni and Mg concentrations show that serpentine populations have higher tolerance to Ni and Mg [65]. No barriers to reproduction have been documented in this system although selection against immigrants seems likely.

A.7. Chaenactis spp.^{L.} Three closely related species of pin-cushion are found in California: *Chaenactis glabriuscula*, *C. stevioides*, and *C. fremontii*. *C. glabriuscula* is found in mesic habitat, has yellow flowers, and has $n = 6$ chromosomes while both *C. stevioides* and *C. fremontii* are found in desert habitat, have white flowers, and have $n = 5$ chromosomes. Cytological analysis indicated that *C. stevioides* and *C. fremontii* arose from independent aneuploid reductions [66]. Frequent natural hybrids between the species indicate that

gene flow is possible although it may be limited by differences in edaphic preference. Future work should use molecular tools to verify the cytological data and quantify gene flow between species.

A.8. Chenopodium album^{L.} The agricultural weed *Chenopodium album* has developed resistance to triazine herbicides in multiple locations [67]. Early work showed that different resistant populations have distinct isozyme patterns in France [68] with at least two resistant genotypes in Canada [69]. Although a single amino acid mutation in the *psbA* gene has been linked to herbicide resistance [70], further molecular analysis should be performed to establish if this mutation has evolved independently. No work has been done on gene flow between populations.

A.9. Crepis tectorum^{L.} The degree of leaf dissection, a trait with fitness consequences, varies among populations of *Crepis tectorum* [71]. In the Baltic region, populations vary in leaf shape, with two island populations exhibiting more deeply lobed leaves than those from the mainland. Andersson [72] used a crossing experiment to demonstrate that while deep lobes on one island are caused by a single dominant locus, on the other island they are caused by multiple loci, which suggest an independent origin of the trait on each island. Further work is needed to confirm this independence, to elaborate the adaptive value of leaf dissection in this system and to establish if there is any reproductive isolation other than geographic between the deeply lobed and less lobed forms.

A.10. Deschampsia cespitosa^{L.} In the 1970s, this perennial grass colonized metal-contaminated soil at two locations in Southern Ontario, Canada. Isozyme analysis of the populations at both contaminated sites, as well as uncontaminated sites to the south, found reduced variability in the metal-contaminated populations [73]. Unique alleles in each contaminated site suggested that each had an independent origin. However, a more recent genetic marker analysis with the same populations has produced equivocal results, indicating that although there are two origins for the contaminated site populations, one population at one site shares its origin with all populations at the other contaminated site [74]. No work has been done on barriers to gene flow between populations or on the mechanisms of heavy metal adaptation.

A.11. Eucalyptus globulus. Three populations of *Eucalyptus globulus* that inhabit exposed granite headlands in south-eastern Australia have a dwarfed morphology and flower earlier than their tall ancestors [75]. Relatedness analyses using several nuclear and chloroplast markers show that the dwarfed populations are more closely related to the nearest population of the tall ecotype than to each other [75]. Observations of progeny allele frequency show no evidence of pollen-mediated gene flow from the much more abundant tall ecotypes to the dwarf ecotypes [75]. This suggests that there have been at least three independent transitions to

dwarfism in the novel exposed granite headland habitat (barring, of course, a long history of introgression after a single origin and dispersal). This case is quite promising, as it has strong evidence for both independence and isolation from ancestral populations. What remains is to demonstrate the compatibility of the dwarf populations with each other, and to more clearly elucidate the adaptive value of dwarfism in this system.

A.12. Geonoma macrostachys. Lowland forests in Peru are home to two subspecies of the palm *Geonoma macrostachys* that are alternately more abundant in flood plain versus tierra firme habitat [76]. The two subspecies differ in leaf shape and are reproductively isolated by phenology, flowering activity, and pollinator spectrum [77]. However, ISSR variation strongly partitions among sympatric populations of both subspecies rather than between the subspecies, and subspecific genetic classification is not possible [78]. In three different forests, Roncal [78] found consistently strong microhabitat preferences for each of the two subspecies, which, along with the genetic data, suggest an independent origin of the subspecies in each environment. Alternate hypotheses of a history of local gene flow among subspecies or phenotypic plasticity must be ruled out before this case can be considered parallel speciation, and further work on reproductive isolation and the mechanisms of microhabitat adaptation is warranted.

A.13. Hemerocallis citrina var. vespertina. On Japanese archipelagos, there appear to be three independent origins of nocturnal flowering and associated changes in floral morphology in *Hemerocallis citrina var. vespertina* from the whole-day flowering *H. flava*. Data from three chloroplast markers place *H. citrina var. vespertina* within three different geographically distinct subspecies of *H. flava* from mainland Asia, despite persistent morphological and phenological differences between the two species [79]. This could be the result of introgression leading to chloroplast capture, or incomplete lineage sorting of ancestral variation, and little is known about reproductive barrier strengths within the three clades of *H. citrina var. vespertina* or between the two species. Further study is needed to differentiate these hypotheses and elucidate reproductive isolation in the system, as well as the adaptive mechanism underlying variation in floral phenology.

A.14. Hieracium umbellatum^L. Possibly the first observed case of parallel ecotypic differentiation, Swedish *Hieracium umbellatum*, was described by Turesson in 1922 [80]. His study found that dune inhabiting plants produced more prostrate stems and thicker leaves than those in open woodlands and that these differences were heritable. Furthermore, although these ecotypes shared many morphological traits, they also retained some leaf characters more like those of neighbouring populations of a different ecotype than distant populations of the same ecotype. Ecotypes also differed in flowering time, an early-acting reproductive barrier. This case is promising, but modern population genetics should

be used to confirm the phylogenetic independence of these populations, and further work needs to characterize the adaptive mechanisms underlying the ecotypic characters and the extent of reproductive isolation between and within ecotypes.

A.15. Lasthenia californica. The common goldfield, *Lasthenia californica*, grows in a variety of habitats and has two flavonoid pigment races that strongly correlate with edaphic tolerance. Race A grows on ionically extreme habitats such as coastal bluffs, alkaline flats, vernal pools, and serpentine soil, while race C is found on ionically benign and drier locations such as pastures and oak woodlands. Phylogenetic analyses using ribosomal and chloroplast sequences along with allozyme variation indicate two cryptic clades within the species with representatives of both races in each [81–84], suggesting a parallel origin of each race. Greenhouse experiments indicate that race A plants, regardless of phylogenetic clade, have greater tolerance to Na⁺ and Mg²⁺ and in drought conditions race C plants flower earlier and produce more flower heads [85, 86]. Preliminary data shows reduced seed set between different races of the same clade and greater pollination success between populations of the same race during interclade crossing, although these data have not been formally published after being presented in Rajakaruna and Whitton [87]. This case has great potential, but further conclusions await stronger published evidence.

A.16. Microseris lanceolata^L. Australia is home to two ecotypes of *Microseris lanceolata*: a “murnong” ecotype found below 750 m elevation which produces tubers, and an “alpine” ecotype found above 1000 m elevation which reproduces vegetatively in addition to having a significantly later flowering time [88]. Phylogenetic analyses based on chloroplast markers show three geographically correlated clades within *M. lanceolata* that all include individuals of both ecotypes, suggesting parallel independent origins [89]. Nuclear AFLP markers also support this hypothesis, as genetic distance among populations correlates strongly with geographic distance rather than ecotype identity [90]. This pattern may be explained by a single origin and dispersal of each ecotype followed by significant local hybridization between ecotypes, but Vijverberg et al. [90] emphasize that these populations have managed to maintain their ecotypic characteristics even in the face of gene flow. Given this and evidence that crosses between and within ecotypes are viable, it seems likely that selection is acting in parallel to maintain or recreate fixed differences between these populations.

A.17. Petunia axillaris. *Petunia axillaris* has likely repeatedly evolved white flowers from ancestral colored flowers, as indicated by sequence data showing 6 different loss-of-function mutations of the ANTHOCYANIN2 (AN2) gene in wild *P. axillaris* populations [91, 92]. It is possible that AN2 was downregulated a single time and that the loss of function mutations occurred subsequently, but *P. axillaris* does not exhibit the low expression of AN2 that would be expected if the AN2 promoter was inactivated [92].

Furthermore, pollination experiments using introgression lines and transgenic flowers have shown that functional and nonfunctional AN2 alleles have a large effect on pollinator visitation, which is likely a strong reproductive barrier in this system [92]. However, we do not yet have evidence that these floral colour transitions have been driven by natural selection, and there is only weak evidence for directional selection at these loci [92]. It is certainly possible that this is a case of repeated adaptation to a new pollination syndrome, but this remains to be tested.

A.18. Plantago maritima^L. This widespread plant grows on inland, coastal, and salt marsh habitats across North America and Europe. In eastern North America, salt marsh plants have relatively lax spikes when compared to plants in rocky habitats. Similarly, British coastal plants also have lax spikes relative to inland populations, although in this case the spikes are less dense than North American salt march plants [93]. Although these traits appear to have evolved independently and in parallel on two different continents, little is known about the genetic basis of these traits or their effects on reproductive isolation or local adaptation.

A.19. Poa annua^L. Annual bluegrass (*Poa annua*) is an agricultural weed with populations known to be resistant to the triazine herbicides [94]. Isozyme work has found equivalent levels of variability between resistant and nonresistant populations, suggesting ongoing gene flow after the founding of resistance [95]. Although herbicide resistance is a relatively simple trait to evolve (often requiring a single amino acid change) there is no evidence to suggest independent evolution of resistance in this species beyond the geographic distance between resistant populations and no evidence that triazine resistance is involved in reproductive isolation.

A.20. Schizanthus grahamii. Two closely related Andean butterfly flowers are taxonomically differentiated by pollination syndrome, floral morphology, and mating system: *Schizanthus hookeri* is purple flowered, bee pollinated, and highly outcrossing, as are other species in the genus, while *S. grahamii* is capable of self-fertilization, primarily hummingbird pollinated, and exhibits several color morphs. The two taxa are rarely found growing sympatrically despite overlapping elevational ranges (with *S. grahamii* generally at higher elevations). Within one sympatric population, experimental interspecific crosses produced no seed set, while intraspecific seed set was 63–72% [96]. Chloroplast sequence data support two independent parallel origins of the *S. grahamii* morphotype: a southern clade characterized by red flowers that shares haplotypes with southern populations of *S. hookeri*, and a northern clade with yellow or pink flowers that shares haplotypes with the northernmost *S. hookeri* populations [96]. However, this pattern could be explained by historical hybridization followed by chloroplast capture, and further work needs to be done to rule out this possibility and characterize gene flow and reproductive barriers between the two *S. grahamii* clades.

A.21. Silene dioica^L. The red campion, *Silene dioica*, has the ability to colonize both serpentine and nonserpentine habitats. Although Westerbergh and Saura [97] demonstrated using isozymes that serpentine populations tended to group with neighbouring nonserpentine populations, indicating multiple origins of serpentine tolerance or possibly ongoing gene flow, later work showed that all populations, regardless of soil type, had serpentine soil tolerance [98]. Thus, serpentine tolerance in Swedish *S. dioica* is likely constitutive and not parallel.

A.22. Silene vulgaris^L. At mine sites across Europe, *Silene vulgaris* from two subspecies (ssp. *maritima* in coastal and ssp. *vulgaris* in continental Europe) has acquired tolerance to high levels of zinc and copper. Complementation tests between sites indicate that zinc tolerance is governed by two loci, both acting in highly tolerant populations of both subspecies [99]. In one mildly tolerant population, zinc tolerance appears to be controlled by only one of the tolerance alleles, and intolerant populations in both subspecies have neither. Similarly, copper tolerance is controlled at two loci: one common across all tolerant populations and a second found only in Imsbach, Germany where plants are extremely tolerant [100]. The presence of populations with a variable genetic basis for tolerance in two subspecies at multiple sites across Europe may represent parallel adaptation, but the phylogenetic independence of these populations has not been confirmed, and no studies of reproductive isolation in the system have been completed. At minimum, populations of both subspecies lack strong postzygotic barriers, as complementation tests are possible. Further work to understand the population genetics of metal tolerance (from ancestral variation, repeated novel mutations, or gene flow between metalliferous sites) should also be done. Additional populations of *S. vulgaris* have colonized naturally metalliferous (serpentine) soils in Switzerland and differently contaminated mine sites in Canada and Europe [101, 102], which may indicate the ease of evolving metal tolerance in this species.

A.23. Streptanthus glandulosus. The *Streptanthus glandulosus* complex contains several subspecies endemic to serpentine outcrops in California. Although a majority of populations are found on serpentine soil, nonserpentine populations are also present. Kruckeberg [103] tested serpentine and nonserpentine populations of *S. glandulosus* on serpentine soil and found that nonserpentine populations were serpentine intolerant, although this study only qualitatively examined growth rate due to technical problems. Later studies used cpDNA restriction site data and ITS sequence to show that the species is structured into several roughly geographically based subspecies [104–106]. Nonserpentine populations occur in multiple subspecies and are more closely related to nearby serpentine populations rather than further nonserpentine populations. This suggests that serpentine intolerance, as well as perhaps greater competitive ability on nonserpentine soil, has occurred multiple times in this species complex. Crossing experiments in this complex

found that hybrid fertility is inversely related to geographic distance, suggesting that nonserpentine populations would be more compatible with neighbouring serpentine populations than distant nonserpentine ones [107]. More study is needed to determine if the change in edaphic tolerance is associated with a change in compatibility, a condition necessary for parallel ecological speciation. Additionally, the serpentine intolerance of nonserpentine populations should be reevaluated in a more quantitative manner.

B. Descriptions of Frequently Cited Examples of Parallel Speciation in Animals

B.1. *Astyanax cave fishes.* In northeastern Mexico, fish of the *Astyanax* species complex have repeatedly adapted to cave environments. A recent study incorporating mitochondrial and nuclear markers supports at least two independent origins of cave-adapted *Astyanax* [27]. One genetic cluster is associated with older cave populations characterized by highly reduced eyes and pigmentation, while another is shared by many surface populations and putatively more recent cave-adapted populations with less extreme phenotypes. Nevertheless, all cave populations will interbreed in the laboratory and share many adaptations to a subterranean environment, including an increase in taste bud number, improved lateral line sense, and greater fat storage ability as well as reduced pigmentation and eyes. Although surface and cave fish will also cross in the laboratory, there is no genetic evidence of recent hybridization between the two groups in most populations. In one location, surface fish are even regularly swept into a cave by flooding—yet this cave population shows very little genetic admixture, and only two intermediate forms have ever been found despite repeated sampling [27]. In another cave with frequent introductions of surface fish, fish without a cave-adapted phenotype have been observed starving to death and being eaten by fish with cave-adapted phenotypes [27]. Yet in lighted conditions in the laboratory, surface fish outcompete cave fish for food. Taken together, the evidence is quite strong for at least two independent parallel adaptations to caves by *Astyanax*, and although reproductive isolation in the system may be primarily extrinsic it is reciprocal and appears quite effective.

B.2. *Coregonus spp.* Whitefish is potentially undergoing several parallel speciation events. The North American lake whitefish, *C. clupeaformis*, is present in at least six lakes in both a “dwarf” limnetic form and a larger-bodied, “normal” benthic form [108]. Geographical isolation during the last glaciation is reflected by three ancient mitochondrial lineages, likely without much morphological divergence [13, 109]. The data suggest that subsequent secondary contact (<15,000 years) of these lineages gave rise to parallel, independent sympatric populations of the two ecotypes [108], at least some of which exhibit strong intrinsic and extrinsic postzygotic reproductive isolation [110]. In addition to body size, these ecotypes differ in gill-raker number, age at maturation, relative fecundity, growth rate, and swimming behavior [108]. A number of quantitative trait loci for growth rate

and morphology have been identified as under divergent selection between the ecotypes [111, 112]. Further research has demonstrated parallel changes in gene expression among independent sympatric ecotype pairs [113], while changes at the genetic level between normal and dwarf populations are more weakly correlated among lakes [112, 114]. Changes in expression in at least two candidate genes are also replicated in the closely related European whitefish system ([115], see below).

In a series of Northern European lakes, European whitefish (*C. lavaretus*) has differentiated into two ecotypes: a “sparsely rakered”, larger-bodied, benthic form, and a “densely rakered” smaller limnetic form. Populations of this species form three ancient mitochondrial clades, which do not correlate with and are more ancient than gill raker divergence [116]. The divergent traits in these populations are highly bimodally distributed, and are strongly correlated with habitat use and diet [14, 117]. These morphological relationships contrast with genetic relationships—where ecotypes within a single lake cluster more closely with each other than with fish of similar morphology in other lakes [14]. These lakes are less than 15,000 years old. Although phenotypic and genetic differences in both the North American and European species complex are well characterized, evolving in parallel, and show signatures of divergent selection, comparatively little is known about the strength and nature of reproductive barriers in both systems.

B.3. *Gasterosteus aculeatus.* Threespine sticklebacks seem particularly prone to parallel evolution, with several well-documented parallel transitions between environments and foraging niches. Throughout the Northern Hemisphere (and in Japan), large-bodied anadromous threespine stickleback have repeatedly evolved into smaller stream-resident fish [17, 131]. These freshwater transitions involve the parallel fixation via natural selection of low-armor, reduced pigmentation, and pelvic loss alleles in multiple independent populations [131–133]. In the case of pelvic loss, these populations exhibit at least three different mutations at the same locus—incontrovertible evidence for the independent origin of this adaptation [133]. In addition, microsatellite data reveals that the majority of genetic variation is partitioned regionally rather than between ecotypes [17]. In the lab, stream-resident fish are more than twice as likely to mate with other stream-resident fish than with anadromous fish (and vice versa), even when from populations as distant as Iceland and Japan [17].

Stickleback have also transitioned in parallel between lake habitats and local streams at least 6 times independently in British Columbia and likely elsewhere, as demonstrated by a number of genetic analyses [123–125]. This transition involves a substantial shift in prey availability and abiotic environment, and the ecotypes differ in body size, shape, and foraging behavior [124–126]. In one British Columbian lake-stream system, common garden experiments confirmed the genetic basis of these traits, a reciprocal transplant experiment showed a weak reduction in growth rate for lake

and inlet fish enclosed in the other habitat, and release-recapture studies demonstrated a bias towards recapture of inlet fish in the inlet [126]. Taken together, this is relatively weak evidence for isolation and selection, but other lake-stream systems may have evolved stronger barriers between ecotype pairs [124].

Possibly the best-studied case of potential parallel ecological speciation is the independent origin of “benthic” and “limnetic” ecotypes in at least five British Columbian lakes [15, 24]. These ecotypes specialize in foraging niche, with a number of morphological and behavioral differences, and exhibit both prezygotic behavioral and extrinsic postzygotic barriers to gene flow [15, 16, 118]. Genetic and biogeographic data support the independent colonization of each lake [15, 119, 120]. Each ecotype is more likely to spawn with fish of the same ecotype than of the other ecotype, regardless of lake of origin [15]. Limnetic backcross hybrid fish grew twice as fast as benthic backcross fish in a limnetic environment, and vice versa for benthic backcrosses in a benthic environment [118].

In all of these threespine stickleback transitions, reproductive isolation appears to have evolved via assortative mating by body size acting concurrently with divergent selection on body size [3, 16, 23]. However, parallel cases vary widely in the strength of reproductive isolation and genetic differentiation between local ecotypes (e.g. [125, 127]). In some cases, evidence for reproductive isolation is conflicting despite evidence for genetic differentiation [128–130]. Researchers have been able to manipulate mating preferences in stickleback by rearing juveniles with individuals of the other ecotype, indicating that reproductive isolation is at least partly extrinsic [121]. Additionally, at least one independent case of “benthic” and “limnetic” ecotypes has collapsed back into a single panmictic pool, possibly due to the human-mediated introduction of an exotic crayfish [122].

B.4. *Littorina saxatilis*. The marine snail *Littorina saxatilis* has repeatedly evolved pairs of ecotypes on the rocky coasts of Northwestern Europe [19]. Although we only discuss one here, there are several regional cases of this divergence, with ecotypes adapted to different microhabitats created by tidal and substrate variation. The best-studied ecotype pair has evolved at least three times independently in Galician Spain, where the two types specialize in and prefer either the high intertidal barnacle belt or the low intertidal mussel belt and occasionally hybridize in the intermediate area between those environments [134, 135]. The main axes of morphological differentiation are in shell size and shape, which aid in resistance either to dislodging by wave action (thin, small shells with large apertures for the muscular foot) or to crab predation and desiccation stress (thick, large shells with small apertures), and there are additional differences in shell ornamentation [19]. These characters are heritable, and genetic variation partitions primarily among independent beaches rather than between ecotypes, although the ecotypes do appear genetically divergent on a local scale [136, 137]. Mitochondrial data similarly support multiple independent origins of the ecotypes [138]. In contrast, several candidate

loci discovered in an F_{ST} outlier screen appear to be under divergent selection between ecotypes in multiple populations [139]. In a reciprocal transplant experiment, each ecotype survived at much higher rates in its native microhabitat than either the other ecotype or hybrids between them [134]. A later reciprocal transplant demonstrated a strong correlation between the divergent morphological characters and survival in each environment, further evidence for the role of selection in maintaining ecotypic differences [140]. These ecotypes exhibit assortative mating by body size that, along with immigrant inviability and habitat preferences, acts to reduce but not eliminate gene flow between ecotypes [18, 141].

B.5. *Timema cristinae*. These western North American walking-stick insects specialize on two host plant species and exhibit two different color morphs that are reciprocally more cryptic on different host plants [142]. The two color morphs are found in higher proportions on the host plant species on which they are most cryptic, although this is quite variable for individual plants, and crypsis helps the insects to avoid strong predation pressure by birds and lizards [142, 143]. The color morphs also differ in average body size, host preference, and cryptic resting behavior, although again this is quite variable for individual populations [20, 143]. In one study, each color morph copulated more readily with the same color morph than the other morph, regardless of the population of origin [20]; however, there is no clear relationship between morph-specific divergent characters and reproductive isolation [143]. Phylogenetic analyses show that the color morphs are not monophyletic [20, 144], indicating possible multiple origins of at least one of the morphs, although this pattern could also be explained by a single diversification event followed by ongoing local gene flow between the morphs. One of these studies also demonstrated using an outlier approach that a small number of loci are under divergent selection between the color morphs [144]. Consequently, divergent selection appears to be acting in parallel in many independent populations. Indeed, as discussed by researchers in this system, these walking-stick insects seem to be experiencing a heterogeneous balance of gene flow and divergent selection, and it is unclear whether this process will ultimately result in speciation between the currently weakly isolated morphs.

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