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Leveraging contemporary species introductions to test phylogenetic hypotheses of trait evolution

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Plant trait evolution is a topic of interest across disciplines and scales. Phylogenetic studies are powerful for generating hypotheses about the mechanisms that have shaped plant traits and their evolution. Introduced plants are a rich source of data on contemporary trait evolution. Introductions could provide especially useful tests of a variety of evolutionary hypotheses because the environments selecting on evolving traits are still present. We review phylogenetic and contemporary studies of trait evolution and identify areas of overlap and areas for further integration. Emerging tools which can promote integration include broadly focused repositories of trait data, and comparative models of trait evolution that consider both intra and interspecific variation.

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Introduction

Multicellular life encompasses a fascinating diversity of form and function. How these forms evolve — trait evolution — is often explored using phylogenetic approaches. Phylogenies allow inference of past trait shifts, their relationship to changes in habitat and biotic interactions, and their potential impacts on lineage diversification (e.g. [1••,2]). Such phylogenetic inferences are essential, because they provide insight into the mechanisms which generate trait variation over evolutionary timescales. A persistent challenge in the field, however, is that ancient events cannot be observed directly, and so mechanistic hypotheses derived from phylogenetic patterns cannot be tested using phylogenies alone [3,4••]. Although the past can no longer be observed, cases of contemporary evolution on human timescales may offer important opportunities to test some of the same hypotheses of character evolution that are prominent in phylogenetic comparisons (Table 1). It is increasingly evident that trait evolution can and does take place on contemporary timescales, and much of this evidence comes from the burgeoning field of invasion biology [5,6]. Species have been anthropogenically introduced into new geographic ranges at unprecedented rates during the last few centuries [7], and colonizing populations have been increasingly observed to have evolved in response to a variety of changes in their abiotic and biotic environments [8•,9••].

Here we argue that, while phylogenetic studies of trait evolution and studies of contemporary evolution in introduced species largely exist as separate fields, these perspectives could be combined for powerful insights into how and why traits evolve in plants. We review the potential relevance of invasion biology to these questions, and outline examples of how species introductions could yield evidence to test key hypotheses derived from phylogenetic patterns of trait variation. We survey literature and databases for shared interests and knowledge gaps in the traits under study across fields. Finally, we detail approaches and considerations for integrating contemporary populations into phylogenetic studies of trait evolution.

Are introduced plants good models of trait evolution?

Similar to biogeographic transitions, vicariance, or other abrupt events associated with speciation across phylogenies, introductions comprise populations that are evolving independently under novel abiotic or biotic environments [10•,11•]. A special feature of species introductions versus other microevolutionary contexts is that diverging introduced populations, their sister lineage(s) in ancestral regions, as well as the environments imposing selection on these populations, are all extant. This allows for tests of specific hypotheses (Table 1) about the connections between changes in trait and environmental states (Figure 1). Phylogeographic studies have also revealed that non-native species often include introductions of the same lineage to multiple different locations [12–14], offering opportunities to study replicate evolutionary trajectories of lineages across environments on human timescales.

Table 1

Examples of trait evolution hypotheses from phylogenetic comparative perspectives, and evidence from introduced populations which could be used to test them. Example traits include those already of common interest to both phylogenetic comparative and species introduction studies (Figure 2b(ii)).

Hypothesis	Prediction for introduced populations	Examples from species introductions
Trait shifts are adaptive responses to (climatic) niche shifts)	Climatic conditions select for different trait states in introduced environment(s)	Leaf shape evolution in *Centaurea solstitialis* [61], *Centaurea stoebe* [59], *Chromolaena odorata* [60], *Phyla canescens* [62], *Rhododendron ponticum* [58]
Trait shifts are adaptive responses to changes in species interactions	Interspecific interactions generate selection for different trait states in introduced environment (s)	Flower color evolution in *Raphanus* taxa [90]; tannin content evolution in *Sapium sebiferum* [91]
Trait shifts are adaptive responses to long-distance dispersal/biogeographic transitions	Introduction events select for shifts in mating system and dispersal traits	Mating system evolution in *Eichhornia paniculata* [92]; shift to cloning in *Fallopia japonica* [93], *Oxalis pes-caprae* [94]; dispersal evolution in *Crepis sancta* [95]
Trait shifts promote (i.e., happen before) speciation	Increased divergence/reproductive isolation between populations with varying trait states	Life history evolution (perenniality) in *Centaurea stoebe* [59], *Senecio inaequidens* [96]. Additional examples of evolution in time to flowering and senescence are listed in Supp. Data 1.
Traits shift gradually via incremental mutations (vs. rapidly by mutations of large effect)	Increasing magnitude of trait differences between populations over time, due to accumulation of multiple additive/epistatic mutations	Evolution of frost tolerance in *Ambrosia artemisiifolia* [97], *Rhododendron ponticum* [58]. See also examples above.
Trait shift is more likely in some plant lineages than others (i.e., some lineages experience higher rates of trait evolution)	Increased frequency of trait state changes in populations of some taxa relative to others	Comparisons across multiple systems (e.g. Supp. Data 1 includes 70 species in 26 plant families)
Groups of traits covary and shift en suite (vs. individual traits shift independently)	Patterns of correlated trait shifts across populations	Correlated evolution of growth and reproductive traits in *Lythrum salicaria* [98])

There are several specific evolutionary mechanisms hypothesized to influence introduction success which might also underlie phylogenetic patterns of trait evolution. These include evolution of growth and defense traits in response to novel interactions with enemies [15–17], of reproductive allocation and mating systems in response to selection for colonizing ability [18,19], and of niche shifts in response to novel environments [20,21]. These same mechanisms are predicted to result in trait-environment associations and impacts on lineage diversification over long evolutionary timescales, for example, [22–27].

With diverging populations extant, it is also possible to address long-standing questions about the nature of genetic variation that gives rise to shifts in trait means [28]. Introduced populations are known to differ in their standing genetic variation [29,30], and whether this variation includes contributions from hybridization, admixture, structural variants or polyploidy (Figure 1) [28,31–33], which are also central features of interest across phylogenetic scales [34–38]. Historical collections of introduced species are also revealing the temporal pattern of genetic change in these populations [39••,40], with the potential to provide insight into the timing and order of multi-locus adaptations in response to a new selective environment.

To utilize trait states measured for introduced and native populations, it is important to recognize some caveats [41••]. The native source and introduction history of particular populations may need to be resolved to establish evolutionary relationships. Plasticity, including maternal/transgenerational effects in common environment experiments, can give a false impression of trait evolution [42], though it may be of interest to identify plastic changes that precede genetic changes [43,44]. Finally, data on patterns of selection or fitness across environments are required to distinguish between non-adaptive (stochastic/neutral) and adaptive evolution [21,39••,45–47].

Are traits of interest from a macroevolutionary perspective evolving in introduced plants?

Although evidence for trait evolution on contemporary timescales has been accumulating, it may be that such cases do not include traits whose evolution is of interest over macroevolutionary timescales, either because the nature of selection on introduced species is not representative of deeper evolutionary history, or because fundamental differences exist between traits involved in macroevolution and microevolution [48]. To what extent is there already overlap between the types of traits investigated using phylogenetic comparative approaches and those studied for contemporary evolution in introduced populations? To answer this question, we surveyed the literature for recent studies of plant trait evolution from a phylogenetic perspective (published 2007–2017; 63 studies), and collected trait information from the PROTEUS