

1 **Leveraging contemporary species introductions to test phylogenetic hypotheses of trait**
2 **evolution**

3
4
5 **Authors and affiliations**

6 Patricia Lu-Irving^{a,1}, Hannah E. Marx^a, Katrina M. Dlugosch^a

7 ^aDepartment of Ecology and Evolutionary Biology, University of Arizona, PO Box 210088,
8 Tucson, Arizona, 85721, USA.

9
10 **Corresponding author**

11 Patricia Lu-Irving, patricia.lu-irving@bgcp.nsw.gov.au

12 ¹Present address: Evolutionary Ecology, Science and Conservation, Royal Botanic Gardens
13 Sydney, Mrs. Macquaries Rd, Sydney, NSW 2000, Australia.

14
15 **Short title**

16 Using species introductions to study trait evolution

17
18 **Keywords**

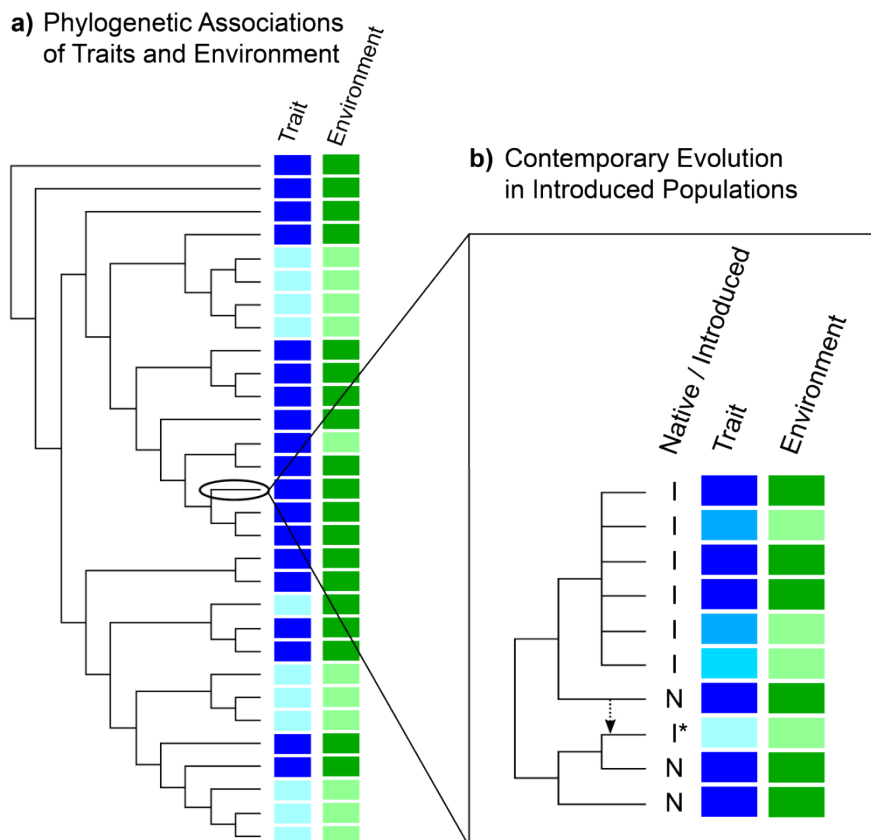
19 trait evolution; macroevolution; niche shifts; introduced species; macroecology; microevolution;
20 contemporary evolution; trait databases; phylogenetic comparative methods

21
22 **Highlights**

- 23 • There is a need to test character evolution hypotheses over human timescales
24 • Introduced species could provide good models of some evolutionary transitions in traits
25 • Phylogenetic and contemporary studies investigate some of the same traits
26 • Many traits show promising evidence of rapid evolution
27 • Trait databases can help link disciplines, particularly if expanded toward this goal
28

Abstract

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.



Graphical Abstract a) Phylogenetic studies are powerful for generating hypotheses (see Table 1) about macroevolutionary associations between phenotypic or genetic trait states (shown in blue) and potential abiotic or biotic selective environments (shown in green). Tips on the cladogram represent species. b) Contemporary evolution in introduced and invading (I) populations can be leveraged to test these hypotheses. Introduced populations of a lineage are often replicated across multiple environments and vary in both traits and the genetic diversity available for adaptation (including through admixture among native (N) subpopulations, shown here by asterisk *).

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^{**}]. While 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 invasions 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.

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, e.g. [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?

While 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 macro- and micro-evolution [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 database, a collaborative resource holding 153,789 records of plant species-level character data, with a focus on floral structure [49*,50]. We categorized the traits under study using the Plant Trait Ontology (TO), a resource which aims to provide interdisciplinary frameworks for defining plant traits [51**,52]. We compared these traits from phylogenetic studies to traits of introduced plants grown in common garden/environment experiments (87 studies).

Our survey of this literature reveals both commonalities and differences in traits of interest to these fields (Figure 2a). Phylogenetic studies are strongly focused on morphology, while studies of introductions include more even emphasis on morphology, growth, and yield traits, as well as substantial attention to fertility. Interest in growth/yield/fertility traits in the contemporary evolution literature reflects a general interest in traits that measure fitness and potential contributions to spread of introduced populations [53]. Nevertheless, morphological traits are the

largest single category represented in both studies of introductions and the phylogenetic literature.

The TO system employs broad definitions of traits; eg., “morphology” includes anatomical traits as well as traits related to plant size and the number of modular parts (such as branches, leaves, nodes). We further explored the representation of individual traits in this category using a graphical word cloud approach for traits in each field, as well as for traits that are shared between fields (Figure 2b). These again highlight the differences in the objectives of these studies, with a focus on major niche-related traits (eg. habit and life history) and taxonomically important traits (eg. pollen, embryo and floral morphology; Figure 2b (i)) in phylogenetic studies compared with focus on plant performance in the invasion literature (eg. biomass and time to flowering; Figure 2b (iii)). Importantly, however, a number of focal traits are already shared (2b (ii)), including characteristics of leaf and flower size, number, and shape, as well as seed and whole plant size.

To what extent have these traits demonstrated contemporary evolution? In our dataset, more than 50% of traits reported across studies were found to have evolved (Figure 3), with evolution identified particularly frequently in biochemical traits (e.g. phenolic content) and traits related to growth and development (e.g. flowering phenology). While there is likely to be publication bias in favor of reporting significant divergence of traits, these studies support the value of exploring introduced populations for tests of hypotheses about trait evolution. For example, variation in leaf shape has been studied from both phylogenetic comparative and contemporary evolutionary perspectives (Fig. 2). On long evolutionary timescales, leaf teeth and dissection are positively correlated with cooler climates [54,55]; i.e., it is hypothesized that climatic niches generate selective pressures which shape evolution of these traits (Table 1). Introduced species demonstrating contemporary shifts in leaf shape [56–62] can be used to test this hypothesis. As a specific case, some introduced populations of *Centaurea solstitialis* have larger, less lobed leaves than natives [61]. Invading populations of this species occupy a variety of different climatic niches [63], where selection on leaf shape and adaptive responses across environments could be quantified.

Potential to integrate perspectives on trait evolution

Macroevolutionary ecologists may find it fruitful and relatively straightforward to seek out introduced populations in clades of interest and integrate these into existing studies on an individual basis. Accessions of introduced populations could be added directly to phylogenetic analyses of their traits or genotypes. Genetic variation in invading and native populations could also be included in phylogenetic models that explicitly incorporate intraspecific variance, e.g. [64*]. At a more involved level, experimental common garden and selection studies with invading populations could be used to identify the mechanisms driving phenotypic divergence (including plastic, adaptive genetic, and stochastic genetic change).

Important opportunities also exist for integration across fields at the level of genes. For loci that have already been identified as potentially important to evolutionary history, such as key developmental genes or divergent paralogous loci [2,65,66], evolution and selection on these

loci can be studied in introduced populations. For traits that do not yet have loci of interest, divergent extant populations could be used to identify loci or pathways for further analyses across phylogenetic scales, e.g. through genetic mapping or gene expression comparisons [67,68**].

More broadly, ecological trait databases offer opportunities to bring together data across fields and taxa to identify promising traits for contemporary analyses. A survey of two of the largest databases, TRY v. 3 (6.9 million records of individual-level traits; [69*]) and BIEN v. 3.4 (81.7 million records of individual-level traits; [70*]), reveal shared areas of focus with both the species introduction literature, and the phylogenetic comparative literature and PROTEUS (Figure 2). There are biases in these overlaps, however, most notably a strong focus on functional traits in the TRY and BIEN databases. Recent developments in plant macroevolution leverage large trait data sets together with the availability of large scale phylogenies to explore trait evolution across thousands of species, often representative of the entire land plant tree of life [50,71–78]. Unless authors of such large-scale phylogenetic studies invest major effort in data gathering (eg. [50,74,76*,79]), the types of traits examined in these studies will be heavily influenced by the availability of existing trait data [71,72,77,78]. As databases expand, it will be important to strive for a broader representation of traits, as well as consistent identification of the native or introduced status of the individual plants from which trait data are collected.

Notably included in traits databases and phylogeny papers, but missing from species introduction papers, are “sterility/fertility” and “miscellaneous” traits: respectively comprising traits to do with breeding system, and features of plant taxa that have no equivalent TO category, eg. geographic distribution, environmental niche, and pollination syndrome. Contemporary evolution in these traits is rarely tested in the common-environment experiments we surveyed. Mating system shift is predicted to often follow invasion and self-compatibility appears to enhance invasiveness in some cases [18,53,80], suggesting that these traits would in fact be fruitful to examine in contemporary invasions. Similarly, post-introduction climatic niche shift is an active area of interest in plant invasions [81,82]. Thus the ecological trait databases are a potential “common ground” which might be utilized to further develop links across different perspectives on trait evolution.

While it is relatively recently that we have recognized that adaptive evolution can be studied on contemporary timescales [5], it is worth considering why this has not been immediately incorporated into phylogenetic trait comparisons. Indeed, there is a long debate about whether evolutionary processes are equivalent across micro- and macro-evolutionary timescales (e.g., [48,83,84]), and statistical methods for directly combining these data in phylogenies are only now being developed [64*]. In general, many traits studied over phylogenetic timescales are not expected to vary at or below species level (e.g., basic floral architecture). Particularly if novel large-effect mutations have been required for trait evolution to occur, we might not see such mutations arise and respond to selection in contemporary time, though the first investigations of this question in introduced populations have revealed surprising evidence of adaptation via new mutations [85,86]. Aggressively invading introduced populations might also share particular traits that might bias evolutionary patterns in these populations, including unusually large

population sizes, high rates of gene flow, and repeated founding events that might facilitate shifts in allele frequencies, making these fast evolving and perhaps adapted to colonization *per se* (e.g. via dispersal-related traits, plasticity, fast development time, [87–89]), rather than other aspects of environmental differences. Nevertheless, it has also been notoriously difficult to identify consistent traits shared by invasive species, indicating that populations might typically represent individual responses of a lineage to new environments [53].

Conclusions

Contemporary trait evolution in introduced plants is frequent, however the potential for plant introductions to provide tests of phylogenetic comparative hypotheses of trait evolution is largely untapped. We identify several features of contemporary species introductions that could make them particularly well suited to advancing general questions in trait evolution questions, and outline how non-native populations could be fruitfully integrated into existing individual research programs. Approaches include incorporating accessions and trait states from known introduced populations into phylogenetic analyses, quantifying contemporary patterns of selection on traits and candidate genes identified in phylogenetic comparisons, and testing for predicted evolutionary trait-environmental associations in introduced populations.

Trait databases offer perhaps the most immediate opportunities to obtain traits from a common resource for both phylogenetic and contemporary evolution studies. It is timely now to invest in adopting standards and practices that promote database use and cross-compatibility, including universal trait ontology, integration of individual-level data (eg. field measurements) with species-level data (eg. from taxonomic treatments), and identification of the native or introduced status and source locality of the individual plants from which trait data are collected. Attention to these issues could immediately open broad opportunities for existing data from studies of contemporary evolution to offer insight into macroevolutionary patterns.

Acknowledgments

The authors thank A. Leotta for assistance with scoring species introduction studies, and H. Sauquet for providing a summary of traits databased in PROTEUS and helpful discussion. This work was supported by the United States Department of Agriculture #2015-67013-23000, and the United States National Science Foundation #1550838.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

**** of special interest**

*** of outstanding interest**

1. Donoghue MJ, Edwards EJ. Biome shifts and niche evolution in plants. *Annu Rev Ecol Evol Syst.* 2014;45: 547–572.
- ** This review emphasizes the need to understand biome shifts and associated adaptations over time on well-resolved phylogenies, with particular attention to which adaptations appear most accessible and able to facilitate biome shifts.
2. Edger PP, Heidel-Fischer HM, Bekaert M, Rota J, Glöckner G, Platts AE, et al. The butterfly plant arms-race escalated by gene and genome duplications. *Proc Natl Acad Sci U S A.* 2015;112: 8362–8366.
3. Morlon H. Phylogenetic approaches for studying diversification. *Ecol Lett.* 2014;17: 508–525.
4. Pennell MW, Harmon LJ. An integrative view of phylogenetic comparative methods: connections to population genetics, community ecology, and paleobiology. *Ann N Y Acad Sci.* 2013;1289: 90–105.
- ** This paper highlights the need to combine phylogenetic inferences with additional data sources, including variation in contemporary populations, to advance understanding of trait evolution.
5. Thompson JN. Rapid evolution as an ecological process. *Trends Ecol Evol.* 1998;13: 329–332.
6. Sax DF, Stachowicz JJ, Brown JH, Bruno JF, Dawson MN, Gaines SD, et al. Ecological and evolutionary insights from species invasions. *Trends Ecol Evol.* 2007;22: 465–471.
7. Ellis EC, Antill EC, Kreft H. All is not loss: plant biodiversity in the anthropocene. *PLoS One.* 2012;7: e30535.
8. Bossdorf O, Auge H, Lafuma L, Rogers WE, Siemann E, Prati D. Phenotypic and genetic differentiation between native and introduced plant populations. *Oecologia.* 2005;144: 1–11.
- * This paper provides a foundational review of the evidence for rapid evolution in plant invaders.
9. Colautti RI, Lau JA. Contemporary evolution during invasion: evidence for differentiation, natural selection, and local adaptation. *Mol Ecol.* 2015;24: 1999–2017.
- ** This paper provides a thorough recent review of the evidence for rapid evolution in introduced species, and important considerations for differentiating adaptive from non-adaptive evolution or sampling artefacts.

- 298 10. Vermeij GJ. Invasion as expectation: a historical fact of life. In: Sax DF, Stachowicz JJ,
299 Gaines SD, editors. Species invasions: insights into ecology, evolution, and biogeography.
300 Sunderland: Sinauer Associates; 2005. pp. 315–339.
- 301 * This chapter explores the idea that species introductions are analogous to other
302 biogeographic transitions over evolutionary history.
- 303 11. Montesinos D, Santiago G, Callaway RM. Neo-allopatry and rapid reproductive isolation.
304 Am Nat. 2012;180: 529–533.
- 305 * This paper explores the idea that species introductions are incipient speciation events.
- 306 12. Lombaert E, Guillemaud T, Cornuet J-M, Malausa T, Facon B, Estoup A. Bridgehead effect
307 in the worldwide invasion of the biocontrol harlequin ladybird. PLoS One. 2010;5: e9743.
- 308 13. Estoup A, Guillemaud T. Reconstructing routes of invasion using genetic data: why, how
309 and so what? Mol Ecol. 2010;19: 4113–4130.
- 310 14. Van Wilgenburg E, Torres CW, Tsutsui ND. The global expansion of a single ant
311 supercolony. Evol Appl. 2010;3: 136–143.
- 312 15. Joshi J, Vrieling K. The enemy release and EICA hypothesis revisited: incorporating the
313 fundamental difference between specialist and generalist herbivores. Ecol Lett. 2005;8:
314 704–714.
- 315 16. Blumenthal DM, Hufbauer RA. Increased plant size in exotic populations: a common-
316 garden test with 14 invasive species. Ecology. 2007;88: 2758–2765.
- 317 17. Blossey B, Notzold R. Evolution of increased competitive ability in invasive nonindigenous
318 plants: a hypothesis. J Ecol. 1995;83: 887–889.
- 319 18. Pannell JR. Evolution of the mating system and ability to self-fertilize in colonizing plants.
320 Mol Ecol. 2015;24: 2018–2037.
- 321 19. Pannell JR, Auld JR, Brandvain Y, Burd M, Busch JW, Cheptou P-O, et al. The scope of
322 Baker's law. New Phytol. 2015;208: 656–667.
- 323 20. Dlugosch KM, Alice Cang F, Barker BS, Andonian K, Swope SM, Rieseberg LH. Evolution
324 of invasiveness through increased resource use in a vacant niche. Nature Plants. 2015;1:
325 15066.
- 326 21. Colautti RI, Barrett SCH. Rapid adaptation to climate facilitates range expansion of an
327 invasive plant. Science. 2013;342: 364–366.
- 328 22. Agrawal AA, Fishbein M, Halitschke R, Hastings AP, Rabosky DL, Rasmann S. Evidence
329 for adaptive radiation from a phylogenetic study of plant defenses. Proc Natl Acad Sci U S
330 A. 2009;106: 18067–18072.
- 331 23. Wiens JJ, Lapoint RT, Whiteman NK. Herbivory increases diversification across insect
332 clades. Nat Commun. 2015;6: 8370.
- 333 24. Baker HG. Self-compatibility and establishment after “long-distance” dispersal. Evolution.
334 1955;9: 347–349.

- 335 25. Cang FA, Wilson AA, Wiens JJ. Climate change is projected to outpace rates of niche
336 change in grasses. *Biol Lett.* 2016;12: 20160368.
- 337 26. Ackerly D. Community Assembly, Niche Conservatism, and Adaptive Evolution in Changing
338 Environments. *Int J Plant Sci.* 2003;164: S165–S184.
- 339 27. Ackerly DD, Schwillk DW, Webb CO. Niche evolution and adaptive radiation: testing the
340 order of trait divergence. *Ecology.* 2006;87: S50–S61.
- 341 28. Dlugosch KM, Anderson SR, Braasch J, Cang FA, Gillette HD. The devil is in the details:
342 genetic variation in introduced populations and its contributions to invasion. *Mol Ecol.*
343 2015;24: 2095–2111.
- 344 29. Dlugosch KM, Parker IM. Founding events in species invasions: genetic variation, adaptive
345 evolution, and the role of multiple introductions. *Mol Ecol.* 2008;17: 431–449.
- 346 30. Uller T, Leimu R. Founder events predict changes in genetic diversity during human-
347 mediated range expansions. *Glob Chang Biol.* 2011;17: 3478–3485.
- 348 31. Ellstrand NC, Schierenbeck KA. Hybridization as a stimulus for the evolution of
349 invasiveness in plants? *Proc Natl Acad Sci U S A.* 2000;97: 7043–7050.
- 350 32. Rius M, Darling JA. How important is intraspecific genetic admixture to the success of
351 colonising populations? *Trends Ecol Evol.* 2014;29: 233–242.
- 352 33. te Beest M, Le Roux JJ, Richardson DM, Brysting AK, Suda J, Kubesová M, et al. The
353 more the better? The role of polyploidy in facilitating plant invasions. *Ann Bot.* 2012;109:
354 19–45.
- 355 34. Rieseberg LH, Archer MA, Wayne RK. Transgressive segregation, adaptation and
356 speciation. *Heredity.* 1999;83: 363–372.
- 357 35. Soltis PS, Soltis DE. The role of hybridization in plant speciation. *Annu Rev Plant Biol.*
358 2009;60: 561–588.
- 359 36. Abbott RJ. Plant invasions, interspecific hybridization and the evolution of new plant taxa.
360 *Trends Ecol Evol.* 1992;7: 401–405.
- 361 37. Adams KL, Wendel JF. Polyploidy and genome evolution in plants. *Curr Opin Plant Biol.*
362 2005;8: 135–141.
- 363 38. Arrigo N, Barker MS. Rarely successful polyploids and their legacy in plant genomes. *Curr*
364 *Opin Plant Biol.* 2012;15: 140–146.
- 365 39. Vandepitte K, de Meyer T, Helsen K, van Acker K, Roldán-Ruiz I, Mergeay J, et al. Rapid
366 genetic adaptation precedes the spread of an exotic plant species. *Mol Ecol.* 2014;23:
367 2157–2164.
- 368 ** This paper provides an outstanding example of the use of current and historical collections
369 to reconstruct allele frequency shift in a plant invasion through time, identifying candidate
370 loci and traits under selection.
- 371 40. Zangerl AR, Berenbaum MR. Increase in toxicity of an invasive weed after reassociation

- 372 with its coevolved herbivore. *Proc Natl Acad Sci U S A*. 2005;102: 15529–15532.
- 373 41. Sargent RD, Angert AL, Williams JL. When are species invasions useful for addressing
374 fundamental questions in plant biology? *Am J Bot*. 2017;104: 797–799.
- 375 ** This paper discusses important considerations when utilizing species invasions to study
376 evolution more generally.
- 377 42. Williams JL, Auge H, Maron JL. Different gardens, different results: native and introduced
378 populations exhibit contrasting phenotypes across common gardens. *Oecologia*. 2008;157:
379 239–248.
- 380 43. Edwards EJ, Donoghue MJ. Is it easy to move and easy to evolve? Evolutionary
381 accessibility and adaptation. *J Exp Bot*. 2013;64: 4047–4052.
- 382 44. West-Eberhard MJ. Developmental plasticity and the origin of species differences. *Proc*
383 *Natl Acad Sci U S A*. 2005;102: 6543–6549.
- 384 45. Puzey J, Vallejo-Marín M. Genomics of invasion: diversity and selection in introduced
385 populations of monkeyflowers (*Mimulus guttatus*). *Mol Ecol*. 2014;23: 4472–4485.
- 386 46. Oduor AMO, Leimu R, van Kleunen M. Invasive plant species are locally adapted just as
387 frequently and at least as strongly as native plant species. *J Ecol*. 2016;104: 957–968.
- 388 47. Keller SR, Taylor DR. History, chance and adaptation during biological invasion: separating
389 stochastic phenotypic evolution from response to selection. *Ecol Lett*. 2008;11: 852–866.
- 390 48. Kane NC, Barker MS, Zhan SH, Rieseberg LH. Molecular evolution across the Asteraceae:
391 micro- and macroevolutionary processes. *Mol Biol Evol*. 2011;28: 3225–3235.
- 392 49. Sauquet H. PROTEUS: A database for recording morphological data and creating NEXUS
393 matrices. Version 1.26 [Internet]. 2016. Available: <http://eflower.myspecies.info/proteus>
- 394 * This database is one of the first collaborative repositories for traits of macromorphological
395 and taxonomic interest.
- 396 50. Sauquet H, von Balthazar M, Magallón S, Doyle JA, Endress PK, Bailes EJ, et al. The
397 ancestral flower of angiosperms and its early diversification. *Nat Commun*. 2017;8: 16047.
- 398 51. Walls RL, Athreya B, Cooper L, Elser J, Gandolfo MA, Jaiswal P, et al. Ontologies as
399 integrative tools for plant science. *Am J Bot*. 2012;99: 1263–1275.
- 400 ** This paper discusses how adopting consistent ontologies for describing traits facilitates the
401 integration of data across studies and fields of inquiry.
- 402 52. Oellrich A, Walls RL, Cannon EK, Cannon SB, Cooper L, Gardiner J, et al. An ontology
403 approach to comparative phenomics in plants. *Plant Methods*. 2015;11: 10.
- 404 53. van Kleunen M, Dawson W, Maurel N. Characteristics of successful alien plants. *Mol Ecol*.
405 2015;24: 1954–1968.
- 406 54. Peppe DJ, Royer DL, Cariglino B, Oliver SY, Newman S, Leight E, et al. Sensitivity of leaf
407 size and shape to climate: global patterns and paleoclimatic applications. *New Phytol*.

- 408 2011;190: 724–739.
- 409 55. Schmerler SB, Clement WL, Beaulieu JM, Chatelet DS, Sack L, Donoghue MJ, et al.
410 Evolution of leaf form correlates with tropical–temperate transitions in *Viburnum*
411 (*Adoxaceae*). *Proc R Soc Lond B*. 2012;279: 3905–3913.
- 412 56. Etterson JR, Delf DE, Craig TP, Ando Y, Ohgushi T. Parallel patterns of clinal variation in
413 *Solidago altissima* in its native range in central USA and its invasive range in Japan.
414 *Botany-Botanique*. 2008;86: 91–97.
- 415 57. Turner KG, Fréville H, Rieseberg LH. Adaptive plasticity and niche expansion in an invasive
416 thistle. *Ecol Evol*. 2015;5: 3183–3197.
- 417 58. Erfmeier A, Tsaliki M, Roß CA, Bruehlheide H. Genetic and phenotypic differentiation
418 between invasive and native *Rhododendron* (*Ericaceae*) taxa and the role of hybridization.
419 *Ecol Evol*. 2011;1: 392–407.
- 420 59. Henery ML, Bowman G, Mráz P, Treier UA, Gex-Fabry E, Schaffner U, et al. Evidence for a
421 combination of pre-adapted traits and rapid adaptive change in the invasive plant
422 *Centaurea stoebe*. *J Ecol*. 2010;98: 800–813.
- 423 60. Zheng YL, Feng YL, Liao ZY, Li WT, Xiao HF, Sui HZ. Invasive *Chromolaena odorata* has
424 similar size but higher phenolic concentration than native conspecifics. *Evol Ecol Res*.
425 2013;15: 769–781.
- 426 61. Eriksen RL, Desronvil T, Hierro JL, Kesseli R. Morphological differentiation in a common
427 garden experiment among native and non-native specimens of the invasive weed yellow
428 starthistle (*Centaurea solstitialis*). *Biol Invasions*. 2012;14: 1459–1467.
- 429 62. Xu C-Y, Julien MH, Fatemi M, Girod C, Van Klinken RD, Gross CL, et al. Phenotypic
430 divergence during the invasion of *Phyla canescens* in Australia and France: evidence for
431 selection-driven evolution. *Ecol Lett*. 2010;13: 32–44.
- 432 63. Barker BS, Andonian K, Swope SM, Luster DG, Dlugosch KM. Population genomic
433 analyses reveal a history of range expansion and trait evolution across the native and
434 invaded range of yellow starthistle (*Centaurea solstitialis*). *Mol Ecol*. 2017;26: 1131–1147.
- 435 64. Kostikova A, Silvestro D, Pearman PB, Salamin N. Bridging inter- and intraspecific trait
436 evolution with a hierarchical Bayesian approach. *Syst Biol*. 2016;65: 417–431.
- 437 * This paper provides an example of a recent approach to integrating intraspecific variation
438 directly into phylogenetic analyses.
- 439 65. Rocha de Almeida AM, Yockteng R, Specht CD. Evolution of petaloidy in the zingiberales:
440 An assessment of the relationship between ultrastructure and gene expression patterns.
441 *Dev Dyn*. 2015; doi:10.1002/dvdy.24280
- 442 66. Rieseberg LH, Blackman BK. Speciation genes in plants. *Ann Bot*. 2010;106: 439–455.
- 443 67. Paterson AH, Schertz KF, Lin YR, Liu SC, Chang YL. The weediness of wild plants:
444 molecular analysis of genes influencing dispersal and persistence of johnsongrass,
445 *Sorghum halepense* (L.) Pers. *Proc Natl Acad Sci U S A*. 1995;92: 6127–6131.

- 446 68. Prentis PJ, Wilson JR, Dormontt EE, Richardson DM, Lowe AJ. Adaptive evolution in
447 invasive species. *Trends Plant Sci.* 2008;13: 288–294.
- 448 ** This paper reviews how invading populations can be leveraged to understand adaptation,
449 with particular attention to genomic approaches.
- 450 69. Kattge J, Díaz S, Lavorel S, Prentice IC, Leadley P, Bönisch G, et al. TRY – a global
451 database of plant traits. *Glob Chang Biol.* 2011;17: 2905–2935.
- 452 * This database houses a global repository of traits of individual plants or their component
453 organs or tissues, with a goal to facilitate understanding of plant adaptations across scales.
- 454 70. Enquist BJ, Condit R, Peet RK, Schildhauer M, Thiers BM. The Botanical Information and
455 Ecology Network (BIEN): cyberinfrastructure for an integrated botanical information network
456 to investigate the ecological impacts of global climate change on plant biodiversity. *PeerJ*
457 *Preprints.* 2016; doi:10.7287/peerj.preprints.2615v2
- 458 * This database houses the largest collection of plant traits to date, including georeferenced
459 observations and measurements of species-level traits. It has a particular goal to facilitate
460 understanding ecological response to climate change.
- 461 71. Cornwell WK, Westoby M, Falster DS, FitzJohn RG, O'Meara BC, Pennell MW, et al.
462 Functional distinctiveness of major plant lineages. *J Ecol.* 2014;102: 345–356.
- 463 72. FitzJohn RG, Pennell MW, Zanne AE, Stevens PF, Tank DC, Cornwell WK. How much of
464 the world is woody? *J Ecol.* 2014;102: 1266–1272.
- 465 73. Pennell MW, FitzJohn RG, Cornwell WK, Harmon LJ. Model adequacy and the
466 macroevolution of Angiosperm functional traits. *Am Nat.* 2015;186: E33–50.
- 467 74. Turcotte MM, Jonathan Davies T, Thomsen CJM, Johnson MTJ. Macroecological and
468 macroevolutionary patterns of leaf herbivory across vascular plants. *Proc R Soc Lond B.*
469 2014;281: 20140555.
- 470 75. Werner GDA, Cornwell WK, Sprent JI, Kattge J, Kiers ET. A single evolutionary innovation
471 drives the deep evolution of symbiotic N₂-fixation in angiosperms. *Nat Commun.* 2014;5:
472 4087.
- 473 76. Zanne AE, Tank DC, Cornwell WK, Eastman JM, Smith SA, FitzJohn RG, et al. Three keys
474 to the radiation of angiosperms into freezing environments. *Nature.* 2014;506: 89–92.
- 475 * This paper illustrates the study of phylogenetic patterns in trait evolution in the context of
476 niche evolution on a large phylogenetic scale. The authors use a combination of existing
477 trait databases as well as their own additional records, which are made publicly available.
478 Many of the traits examined overlap with studies of contemporary evolution of invaders, but
479 introduced populations are not considered in this analysis.
- 480 77. Flores O, Garnier E, Wright IJ, Reich PB, Pierce S, Diaz S, et al. An evolutionary
481 perspective on leaf economics: phylogenetics of leaf mass per area in vascular plants. *Ecol*
482 *Evol.* 2014;4: 2799–2811.
- 483 78. Sims HJ. Morphological rates of angiosperm seed size evolution. *Evolution.* 2013;67:
484 1338–1346.

- 485 79. O'Meara BC, Smith SD, Armbruster WS, Harder LD, Hardy CR, Hileman LC, et al. Non-
486 equilibrium dynamics and floral trait interactions shape extant angiosperm diversity. *Proc R*
487 *Soc Lond B*. 2016;283: 20152304.
- 488 80. Baker HG. Characteristics and modes of origin of weeds. In: Baker HG, Stebbins GL,
489 editors. *The Genetics of Colonizing Species*. New York: Academic Press; 1965.
- 490 81. Guisan A, Petitpierre B, Broennimann O, Daehler C, Kueffer C. Unifying niche shift studies:
491 insights from biological invasions. *Trends Ecol Evol*. 2014;29: 260–269.
- 492 82. Petitpierre B, Kueffer C, Broennimann O, Randin C, Daehler C, Guisan A. Climatic niche
493 shifts are rare among terrestrial plant invaders. *Science*. 2012;335: 1344–1348.
- 494 83. Erwin DH. Macroevolution is more than repeated rounds of microevolution. *Evol Dev*.
495 2000;2: 78–84.
- 496 84. Leroi AM. The scale independence of evolution. *Evol Dev*. 2000;2: 67–77.
- 497 85. Exposito-Alonso M, Becker C, Schuenemann VJ, Reiter E, Setzer C, Slovak R, et al. The
498 rate and potential relevance of new mutations in a colonizing plant lineage. *PLoS Genet*.
499 2018;14: e1007155.
- 500 86. Gordon SP, López-Sepulcre A, Rumbo D, Reznick DN. Rapid Changes in the Sex Linkage
501 of Male Coloration in Introduced Guppy Populations. *Am Nat*. 2017;189: 196–200.
- 502 87. Shine R, Brown GP, Phillips BL. An evolutionary process that assembles phenotypes
503 through space rather than through time. *Proc Natl Acad Sci U S A*. 2011;108: 5708–5711.
- 504 88. Davidson AM, Jennions M, Nicotra AB. Do invasive species show higher phenotypic
505 plasticity than native species and, if so, is it adaptive? A meta-analysis. *Ecol Lett*. 2011;14:
506 419–431.
- 507 89. van Kleunen M, Weber E, Fischer M. A meta-analysis of trait differences between invasive
508 and non-invasive plant species. *Ecol Lett*. 2010;13: 235–245.
- 509 90. Ridley CE, Ellstrand NC. Rapid evolution of morphology and adaptive life history in the
510 invasive California wild radish (*Raphanus sativus*) and the implications for management.
511 *Evol Appl*. 2010;3: 64–76.
- 512 91. Siemann E, Rogers WE. Genetic differences in growth of an invasive tree species. *Ecol*
513 *Lett*. 2001;4: 514–518.
- 514 92. Barrett SCH, Morgan MT, Husband BC. The dissolution of a complex genetic
515 polymorphism: the evolution of self-fertilization in tristylous *Eichhornia paniculata*
516 (*Pontederiaceae*). *Evolution*. 1989;43: 1398–1416.
- 517 93. Hollingsworth ML, Bailey JP. Evidence for massive clonal growth in the invasive weed
518 *Fallopia japonica* (Japanese Knotweed). *Bot J Linn Soc*. 2000;133: 463–472.
- 519 94. Ornduff R. Reproductive Systems and Chromosome Races of *Oxalis Pes-Caprae* L. and
520 Their Bearing on the Genesis of a Noxious Weed. *Ann Mo Bot Gard*. 1987;74: 79–84.

- 521 95. Cheptou P-O, Carrue O, Rouifed S, Cantarel A. Rapid evolution of seed dispersal in an
522 urban environment in the weed *Crepis sancta*. *Proc Natl Acad Sci U S A*. 2008;105: 3796–
523 3799.
- 524 96. Mahy G, Monty A, Maurice S. Phenotypic traits variation among native diploid, native
525 tetraploid and invasive tetraploid *Senecio inaequidens* DC. (Asteraceae). *Biotechnol Agron*
526 *Soc Environ*. 2010;14: 627–632.
- 527 97. Leiblein-Wild MC, Kaviani R, Tackenberg O. Germination and seedling frost tolerance differ
528 between the native and invasive range in common ragweed. *Oecologia*. 2014;174: 739–
529 750.
- 530 98. Colautti RI, Barrett SCH. Population divergence along lines of genetic variance and
531 covariance in the invasive plant *Lythrum salicaria* in eastern North America. *Evolution*.
532 2011;65: 2514–2529.
- 533
534

Figure captions

Figure 1 a) Phylogenetic studies are powerful for generating hypotheses (see Table 1) about macroevolutionary associations between phenotypic or genetic trait states (shown in blue) and potential abiotic or biotic selective environments (shown in green). Tips on the cladogram represent species. b) Contemporary evolution in introduced (I) populations can be leveraged to test these hypotheses. Introduced populations of a lineage are often replicated across multiple environments and vary in both traits and the genetic diversity available for adaptation (including through admixture among native (N) subpopulations, shown here by asterisk *).

Figure 2 a) Traits by TO category from the literature (63 phylogenetic studies, 87 common environment studies of introduced species) and databases (top 200 traits by number of observations from PROTEUS, TRY, and BIEN). Traits with no direct match to a TO term were assigned categories consistent with similar traits or categorized as “miscellaneous”. Lists of individual traits and categorization schemes are available as Supplementary Material 1. b) Word clouds visualizing most frequent terms appearing in list of traits i) investigated in phylogenetic studies, ii) shared between phylogenetic and introduced population studies, and iii) investigated in introduced population (common environment experiment) studies. Word size is indicative of relative frequency within each list; frequency in (ii) is the minimum frequency between lists.

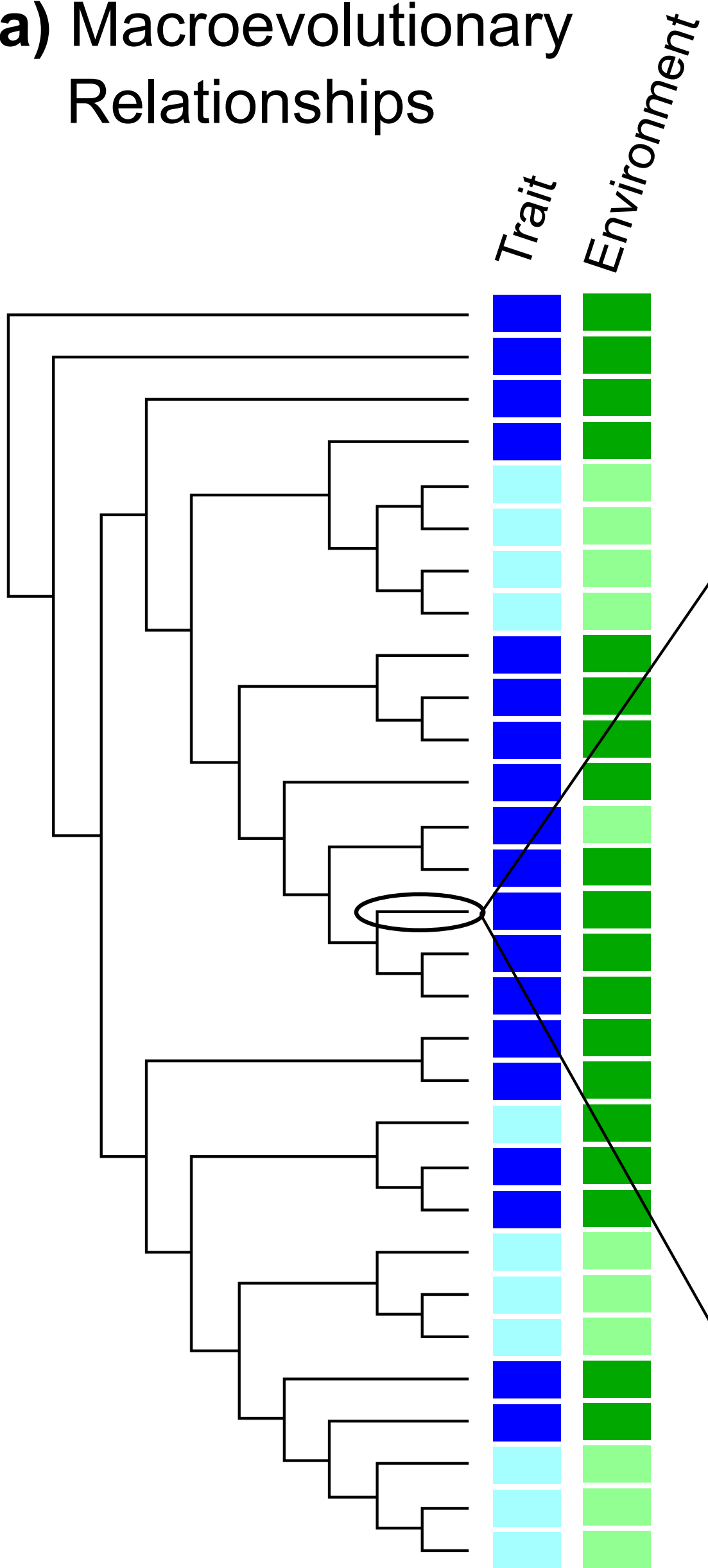
Figure 3 Number of traits showing significant fixed differences (black bars) versus no significant fixed differences (white bars) in introduced populations under any experimental treatment in common environments in the 87 studies reviewed.

SUPPLEMENTARY MATERIAL

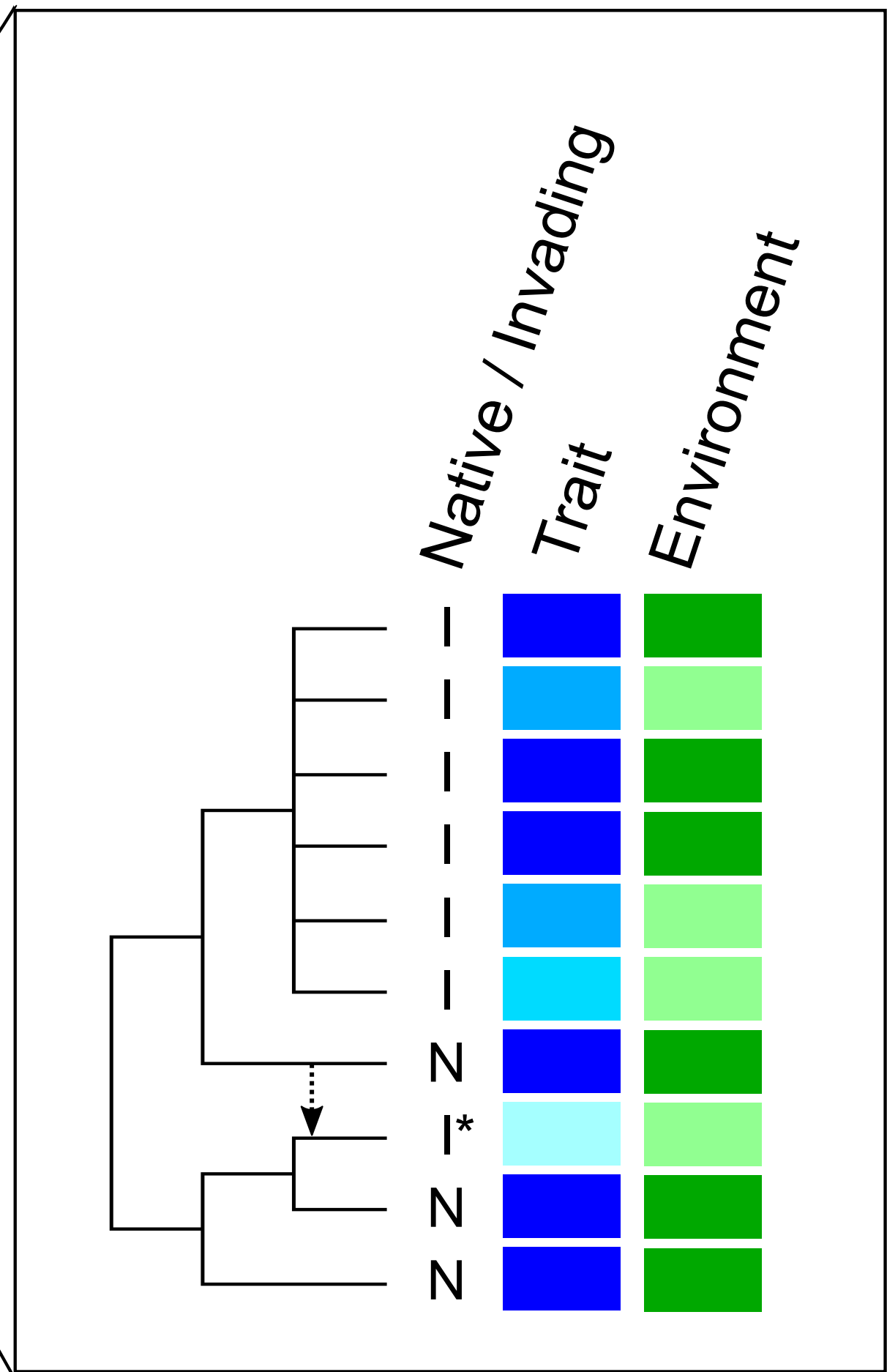
Supplementary Data 1 Citations of studies reviewed for Figs. 2 and 3, with corresponding data for traits examined (phylogenetic and common garden studies), and whether traits were found to have evolved (fixed differences between source populations in common garden studies).

Supplementary Data 2 Categorization scheme after the Plant Trait Ontology for traits examined from the literature and traits databases.

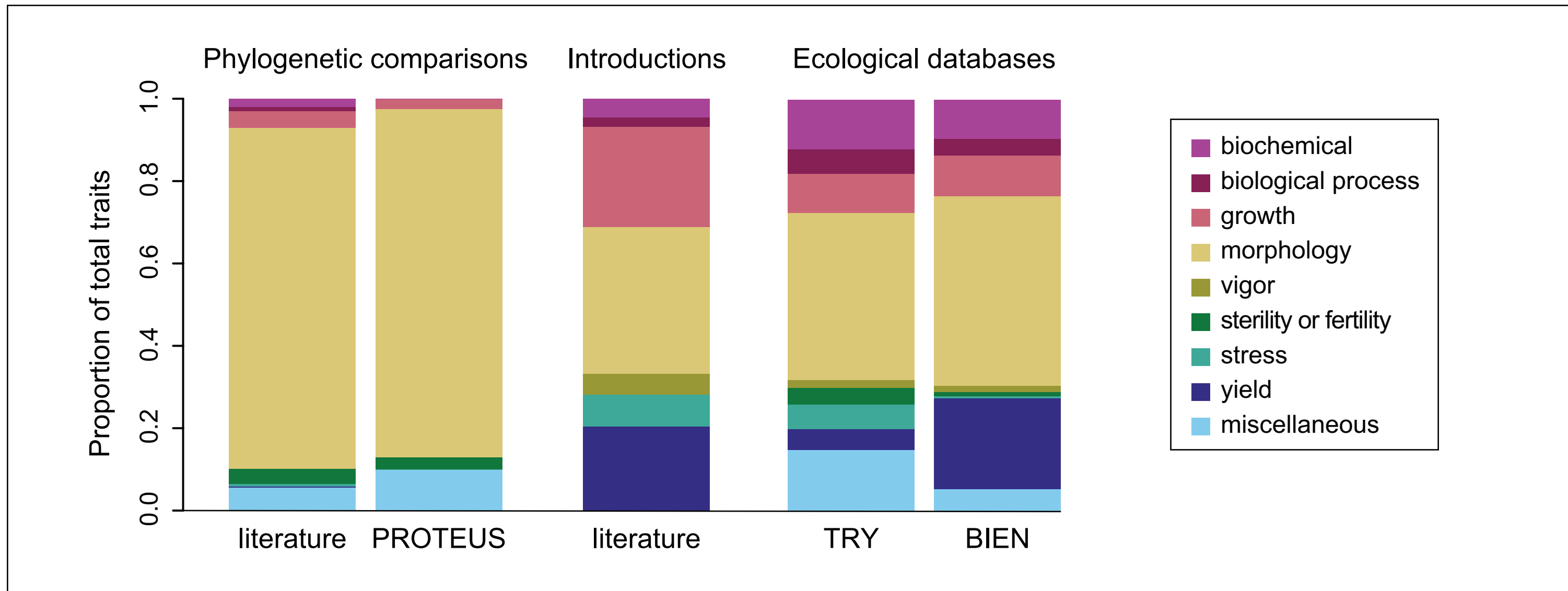
a) Macroevolutionary Relationships



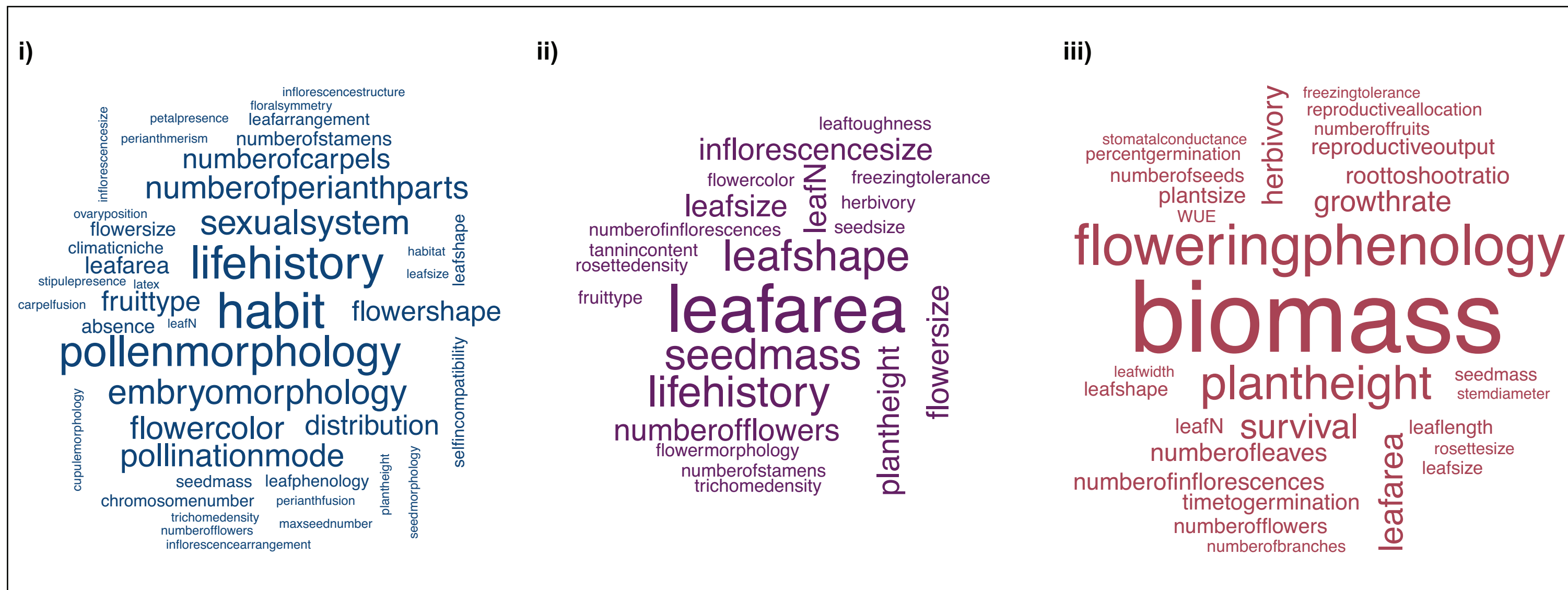
b) Contemporary Evolution in Invading Populations



a)



b)



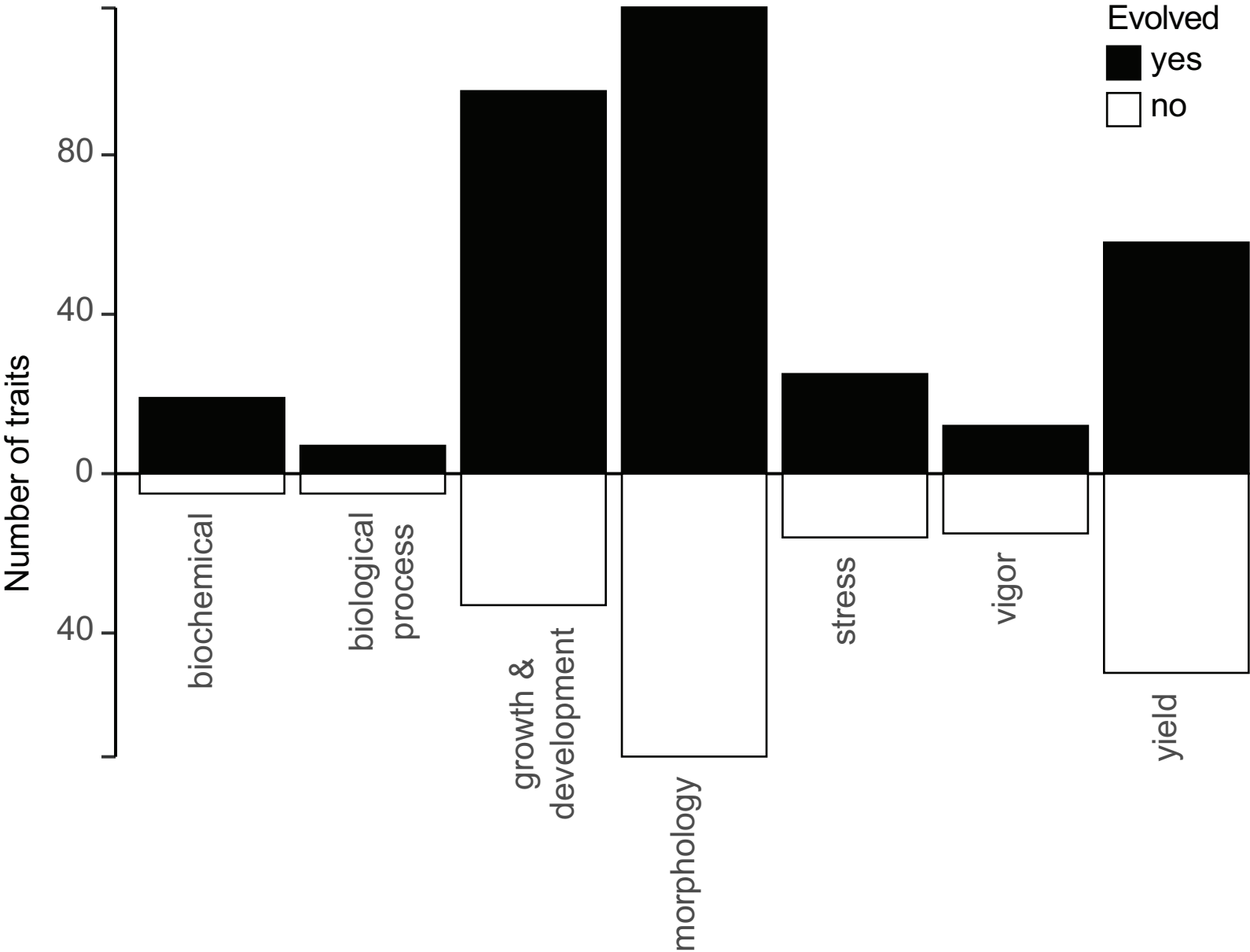


Table 1 Examples of trait evolution hypotheses from phylogenetic comparative perspectives, and evidence from introduced populations which could be used to test them. Example traits include those already of common interest to both phylogenetic comparative and species introduction studies (Fig 2b.ii).

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 <i>Centaurea solstitialis</i> [61], <i>Centaurea stoebe</i> [59], <i>Chromolaena odorata</i> [60], <i>Phyla canescens</i> [62], <i>Rhododendron ponticum</i> [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 <i>Raphanus</i> taxa [90]; tannin content evolution in <i>Sapium sebiferum</i> [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 <i>Eichhornia paniculata</i> [92]; shift to cloning in <i>Fallopia japonica</i> [93], <i>Oxalis pes-caprae</i> [94]; dispersal evolution in <i>Crepis sancta</i> [95]
Trait shifts promote (i.e., happen before) speciation	Increased divergence/reproductive isolation between populations with varying trait states	Life history evolution (perenniality) in <i>Centaurea stoebe</i> [59], <i>Senecio inaequidens</i> [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 <i>Ambrosia artemisiifolia</i> [97], <i>Rhododendron ponticum</i> [58]. See also examples above.
Trait shift is more likely in some plant lineages than others (i.e.,	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

some lineages experience higher rates of trait evolution)		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 <i>Lythrum salicaria</i> [98])