



OPINION ARTICLE

Empirical tests of trait–function relationships are crucial for advancing trait-based restoration: a response to Merchant et al. (2023)

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Trait-based restoration strategies are gaining significant attention in the scientific community. A recent article in *Restoration Ecology* by Merchant et al. outlined four reasons why traits are underused in restoration practice. In their response to the paper, Gornish et al. highlighted examples of how practitioners do, in fact, use traits in restoration and made recommendations for researchers to better engage with practitioners to leverage existing knowledge. Here, we clarify a preeminent challenge for either perspective: that we continue to lack the empirical data needed to develop and apply the effective trait-based tools envisioned by many researchers. Long-term, spatially replicated studies designed to address context-dependency are needed to address critical knowledge gaps. Co-developing projects with practitioners not only fosters more realistic and relatable study designs but also increases the likelihood of adopting new methods, enabling long-term research that advances theory while improving local outcomes through more accurate trait-based predictions.

Key words: community assembly, context-dependency, ecosystem functionality, functional traits, plant performance, practitioner collaboration

Implications for Practice

- To advance the usefulness of traits in restoration, researchers must first address uncertainties in the science that limit the usefulness or adoptability of trait-based tools.
- Traits may not consistently predict restoration outcomes because their relationships with functions are context-dependent, various trait strategies may similarly influence plant performance and ecosystem function, relevant traits and their trade-offs can be unclear, and plants face multiple simultaneous factors influencing trait selection.
- Key knowledge gaps include understanding how traits affect plant performance and ecosystem functions under different environmental conditions, the trade-offs of targeting specific traits in restoration, and deciding which traits to prioritize in restoration efforts.
- Researchers should prioritize co-developing long-term projects focusing on stable practitioner relationships and understanding context-dependency and uncertainty.

Introduction

There is a long history of using plant characteristics in management to provide ecosystem services (e.g. erosion control and water holding capacity) or improve ecosystem responses to stress (e.g. drought, fire; Whisenant 2002). In restoration specifically, traits are used to select species and ecotypes to address many challenges (Gornish et al. 2023), including species that

may restore function in uncertain and unprecedented conditions (Pérez-Ramos et al. 2017; Fu et al. 2023). In academic circles, the idea that species traits can be used to direct ecological restoration has existed for two decades (Temperton et al. 2004; D’Antonio & Chambers 2006). However, as noted by both Merchant et al. (2023) and Gornish et al. (2023), empirical tests of these approaches are scant (Carlucci et al. 2020).

In their paper, Merchant et al. (2023) advance four reasons why traits are underused in restoration, which are summarized in Table 1. We commend the authors for their efforts to bridge theoretical and practical gaps and agree that addressing these four issues would significantly improve the utility of functional traits in restoration endeavors. However, we contend that the absence of an operational framework (Table 1, reason #2) poses a disproportionately large challenge for the practical application of trait-based approaches to restoration, rendering the other points less impactful without its resolution.

Merchant et al. (2023) proposed three solutions for resolving the operational framework issue, including making species trait–function relationships widely available (solution 2.1), developing tools that connect traits to restoration outcomes (solution 2.2),

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Table 1. Four reasons that restoration ecologists do not employ traits in restoration practice, as proposed by Merchant et al. (2023).

Different goals and approaches: Practitioners use other sources of knowledge
Lack of operational framework: There is no validated way to use functional traits in realistic restoration planning
Plant stock constraints: Plant material supplied by commercial nurseries and seed collectors does not meet the demand of trait-based restoration projects
Lack of trait data: Measuring traits competes with resources that could be spent on other restoration actions

and conducting tests of how trait-driven species mixes influence restoration outcomes (solution 2.3). While evolving databases and models can inform current actions (e.g. seed provenance guidelines; St. Clair et al. 2022), their effectiveness will be limited without empirical work to resolve context dependencies, as described below. Thus, we emphasize the critical need for more empirical tests (solution 2.3) before we can accurately populate trait–function databases (solution 2.1) and parameterize models (solution 2.2). Here, we identify key knowledge gaps in linking traits to function and explore practical approaches to fill these gaps in collaboration with practitioners.

Existing Studies of Trait–Function Relationships Highlight Key Knowledge Gaps

Some studies have found that trait-based restoration approaches work as intended. For instance, in Hawaiian lowland forests, where native species typically exhibit slower growth and resource acquisition compared to non-natives, Ostertag et al. (2015) implemented a large-scale restoration based on the hypothesis that countering the impact of invasive species on carbon and nutrient cycles would favor native species. Their approach involved choosing native species with traits promoting slower decomposition, which led to a reduction in C, N, and P cycling and was associated with decreased invasion rates (DiManno et al. 2023).

Other studies demonstrate that even when trait-based restoration approaches do not achieve expected results, they can still clarify relationships between traits and ecosystem processes. For example, studies attempting to create invasion-resistant communities based on the theory of limiting similarity (MacArthur & Levins 1967) did not show the anticipated competitive dynamics between functionally similar native and non-native species. Instead, different trait-based mechanisms were effective at suppressing the growth of invasive species. In a European grassland, Yannelli et al. (2018) found that early emergence and rapid growth in native species, combined with high sowing density, suppressed invasives due to a priority effect. Similarly, in an annual-dominated California grassland, Funk and Wolf (2016) observed that natives with efficient belowground resource uptake and higher aboveground biomass allocation, not similarity in resource use, were successful in suppressing an invasive grass. These cases underscore that while traits offer valuable insights for restoration, they may

Table 2. Challenges and knowledge gaps associated with mapping traits to restoration outcomes.

Challenges

- (1) Traits do not consistently predict restoration outcomes
- (2) Trait–function relationships are context-dependent
- (3) Different trait strategies can lead to similar function
- (4) It can be unclear which traits or trait trade-offs are relevant for achieving specific restoration outcomes
- (5) Plants respond to multiple factors simultaneously, leading to different selective pressures on traits

Knowledge gaps

- (1) How do traits influence plant performance under different environmental conditions (e.g. grazing and drought)?
- (2) What trade-offs exist when targeting specific traits in restoration?
- (3) Which traits should we include in restoration planning? Should there be a stronger focus on compiling data for less common traits (e.g. seed and root traits)?
- (4) How do traits respond to interacting environmental filters to influence function across space and time?

not always predict outcomes reliably, partly because it can be challenging to identify the most important traits controlling a desired outcome (Table 2, Challenge 1).

Yet other studies find weak or inconsistent links between traits and plant, community, and ecosystem processes. Several reasons for this have been proposed. First, as noted by Merchant et al. (2023), trait–function relationships can be context-dependent (e.g. Balazs et al. 2020; Table 2, Challenge 2). For instance, the predictive power of traits for plant performance, like survival or growth, can change with environmental variables (Fig. 1A) or differ among plant types (Fig. 1B). Similarly, links between traits and ecosystem processes can fluctuate based on environmental factors (Fig. 1C) and differ for various ecosystem functions (Fig. 1D), due to shifting mechanisms driving these processes or varying trait impacts under different conditions (Eviner & Hawkes 2008). To improve the application of traits to ecological restoration, we need a better understanding of which traits drive particular restoration outcomes and how trait–function relationships vary across environmental conditions (Table 2; Knowledge Gap 1).

Second, a given functional outcome can be achieved by different plant strategies, weakening the relationship between a single plant trait and function (Table 2, Challenge 3). For example, plants can enhance aboveground productivity by increasing leaf N to optimize leaf-level photosynthetic rates (Funk et al. 2021) or by diluting leaf N concentration to increase the total amount of leaf area (Funk & Wolf 2016). In this case, both high and low N concentrations could lead to enhanced aboveground productivity but are likely to have opposite impacts on soil N cycling rates. Root traits also illustrate this complexity. Plants can acquire resources via many thin roots (high specific root length) that efficiently explore soil or by outsourcing resource uptake to microbial symbionts that live in roots with large diameters (Bergmann et al. 2020). As a result, this leads to weak

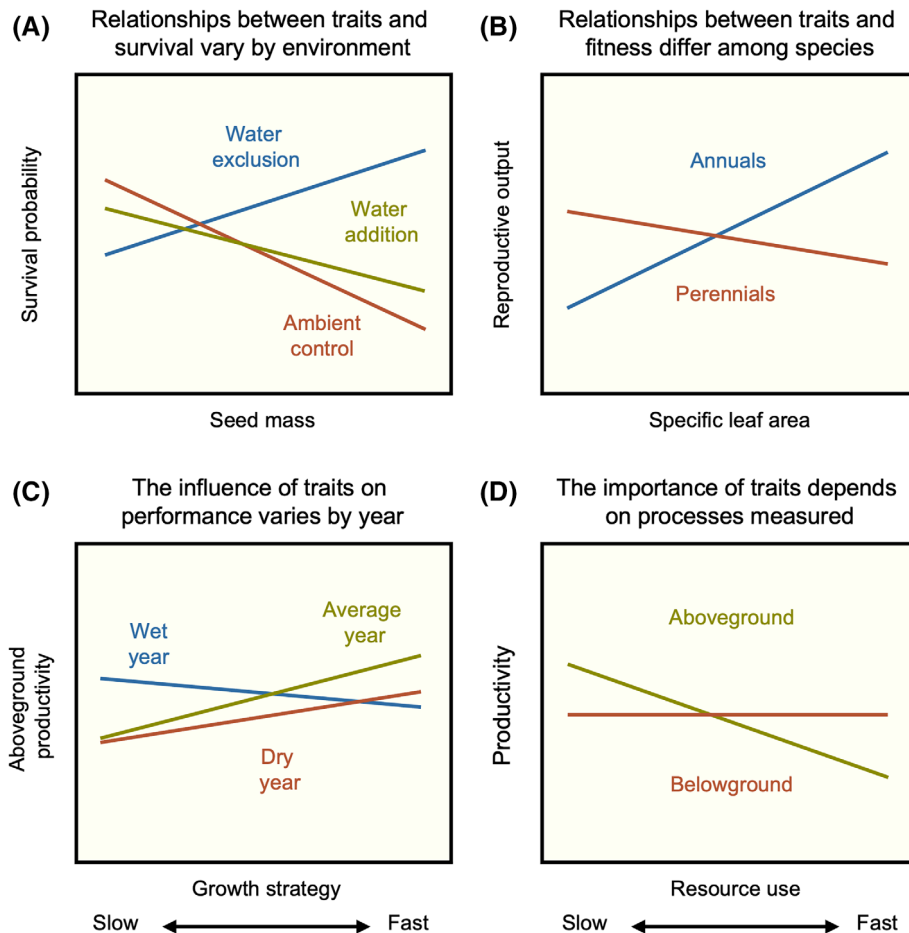


Figure 1. Examples of weak or inconsistent links between functional traits and plant performance (panels A and B) and ecosystem processes (panels C and D). (A) Larson et al. (2021) found that the ability of seed mass to predict survival probability of an emerged seedling depended on rainfall treatment (water addition, water exclusion, and control). (B) In a coastal sage scrub system, aboveground traits, including specific leaf area, were good predictors of reproductive output in annual species, but not perennials (Funk et al. 2021). (C) Aboveground traits associated with a “fast” and “slow” growth strategy predicted aboveground productivity in some years (Wolf et al. 2021). The relationship was significant in a dry (41% ambient rainfall) and average (90% ambient rainfall) year, but not a wet year (118% ambient rainfall). (D) Traits associated with a “fast” and “slow” growth strategy were good predictors of aboveground but not belowground productivity (Aoyama et al. 2023).

relationships between a single root trait and belowground resource uptake. Exploring trait trade-offs, such as between growth and resource-use efficiency, rather than considering individual traits has been an effective method to discern differences in growth strategies among native and non-native plants (Valliere 2019), with important implications for restoration (Table 2; Knowledge gap 2).

Third, despite ongoing advancements in trait databases, studies often rely on a narrow range of traits (e.g. leaf morphology) to clarify ecological patterns (e.g. Halassy et al. 2019; Zirbel & Brudvig 2020; Fu et al. 2023), and these traits may not be the most relevant for achieving restoration outcomes (Table 2, Challenge 4). For instance, seed traits are critical to community assembly and stability (e.g. Larson et al. 2021) and are rarely considered in restoration. Inconsistencies might also stem from a focus on morphological traits, such as tissue density, while overlooking more complex physiological traits, which are harder to measure but may be important drivers of

plant performance, community responses to perturbations, and ecosystem functions. Finally, demographic traits (such as longevity and reproductive output), particularly in combination with functional traits, may be important for predicting community resilience in response to environmental perturbation (Paniw et al. 2021). While expanding data collection on less common traits is crucial for understanding community assembly, resilience, and ecosystem function (Table 2; Knowledge gap 3), it is important to ensure that such data, particularly complex physiological and demographic traits, are accessible to practitioners through publication in open-access journals and outlets geared toward managers (Matzek et al. 2014) and integrated into species selection tools that are practical for practitioners to use.

Finally, traits can respond differently to simultaneous abiotic and biotic factors, weakening relationships between a given trait and function (Funk 2021; Table 2, Challenge 5). For example, in annual-dominated California grassland, low specific leaf area may promote drought tolerance (Harrison & LaForgia 2019) but

make species more susceptible to grazing (Sandel et al. 2011). Additionally, plant performance may be limited by different factors over time, such as water availability during seedling establishment and competition from invasive species in subsequent years (Kempel et al. 2013; Funk et al. 2023; Table 2, Knowledge gap 4). Thus, trait-based restoration could be improved by selecting species with traits that are relevant for multiple life stages and multiple stressors.

How Can We Fill These Knowledge Gaps?

For trait-based approaches to effectively guide restoration, we need more empirical evidence on how traits affect both plant performance and ecosystem functionality. While practitioners are pioneering the use of trait-based approaches (Gornish et al. 2023), the academic community still lacks fundamental data necessary for generating robust trait-based tools that will be useful to practitioners, particularly when it comes to the context-dependency of trait–function relationships. Practitioners are acutely aware of context-dependence, and most are focused on species and approaches that would be most successful at their site. In general, ecological research on trait–function relationships does not extend across enough sites to inform management and occurs in much smaller plots than a typical management-scale activity. The most fruitful way for researchers to address these knowledge gaps will be direct engagement with practitioners to best understand on-the-ground priorities and to assess trait–function relationships in real-world settings (Leger et al. 2021), with replicated management trials over space and time (Vaughn & Young 2010). The development, refinement, and implementation of broadly applicable trait-based tools (Gornish et al. 2023; Merchant et al. 2023) is limited by this knowledge gap, along with other barriers—such as lack of practitioner resources and divergent restoration priorities (Table 1).

To enhance the utility of trait-based approaches in restoration, it is essential to address the knowledge gaps outlined in Table 2. One way to feasibly assess context-dependence is by working with land managers to study relatively similar restoration implementations (replicated trials) over space and time. For example, planting of native perennial grasses into annual-dominated California grasslands has shown that native grasses can have opposite impacts on N cycling at different sites (Eviner & Firestone 2007). Higher replication of measures is needed to understand what may drive this context-dependent effect. Monitoring the long-term impacts of restoration is also crucial. For example, it can take decades for soil C stocks to increase in a riparian restoration (Matzek et al. 2020). Co-developing long-term restoration projects with practitioners has the mutual benefit of enabling the insightful practitioner partnerships advocated by Gornish et al. (2023) and incorporating realistic study designs to test the adoptability of new approaches. For example, long-term demographic studies that explore how traits affect plant performance across different life stages could improve our understanding of how trait–function relationships change over time (Garbowski et al. 2021). As traits crucial for early-stage germination and establishment may differ from those needed for later-stage reproduction and long-term survival

(Gremer 2023), results from these studies will also assist practitioners in selecting species that meet both immediate and long-term restoration objectives.

Resolving the context-dependency inherent in trait–function relationships is crucial before we can effectively use trait-based tools, but we also need to test how effective these tools are from a practical perspective. Several programs exist that allow users to generate planting palettes that will optimize a given restoration outcome using trait databases. Some of these tools select relevant traits given a user's restoration goals (Rayome et al. 2019), while others require the user to identify trait–function linkages (Laughlin et al. 2018). However, because we often do not know a priori which traits will achieve our desired function (Funk & Wolf 2016; Yannelli et al. 2018), the usefulness of these tools for achieving specific restoration targets remains limited. Traits may not need to perfectly predict restoration outcomes to be useful; however, verifying this hypothesis requires empirical testing, ideally in partnership with practitioners. Such collaborative research could explore the practical benefits of trait-based approaches and their reliability across different conditions, helping to refine tools for species selection that address multiple needs, such as drought tolerance and grazing resistance.

Working with practitioners to identify their main challenges will enable targeted research that addresses these knowledge gaps, thereby significantly enhancing restoration programs. Currently, there are concerns about restoring ecosystems to withstand changing environmental conditions, particularly the debate over using local versus non-local genotypes to avoid ecological disruptions (Bucharova et al. 2019). Additionally, there is a push to restore ecosystems for multiple services (e.g. Fiedler et al. 2021). Understanding key functional responses and effects is crucial, as traits can guide the selection of species likely to thrive under altered environmental conditions and management practices, recognizing that multiple traits or pathways might lead to desired outcomes.

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