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Regeneration: An Overlooked Aspect of Trait-Based Plant Community Assembly Models

Julie Larson
Chapman University, jlarson@chapman.edu

Jennifer L. Funk
Chapman University, jlfunk@chapman.edu

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Regeneration: An overlooked aspect of trait-based plant community assembly models

Julie E. Larson* and Jennifer L. Funk

Schmid College of Science and Technology, Chapman University, Orange, CA USA

*Correspondence author. E-mail: jlarson@chapman.edu

Running title:

Regeneration traits and community assembly

Abstract

1. Despite the disproportionate influence that propagule production, dispersal, seed to seedling recruitment, and vegetative reproduction can have on plant population and community dynamics,

progress has been slow in the directed collection of regeneration traits to inform community assembly outcomes.

2. While seed mass is globally available and linked to growth and reproductive output, there are limits to its explanatory ability. In this essay, we call for expanded efforts to integrate a more diverse set of regeneration traits into community assembly models.
3. First, we extend an existing community assembly framework to conceptualize regeneration as a series of transitional processes whose outcomes are influenced by abiotic filters, biotic interactions, and species traits. We then briefly review the literature, highlighting filters and traits of demonstrated or theorized importance for each transition. Finally, we place regeneration in the context of existing and emerging modeling approaches in trait-based community assembly, summarizing key areas of progress needed to integrate regeneration traits into these efforts.
4. *Synthesis*. By incorporating influential regeneration traits into empirical studies and global databases, we can begin to disentangle regenerative mechanisms underlying community assembly outcomes and enhance rapidly developing models of species' abundances, distributions, and responses to environmental change.

Key-words: clonality, determinants of plant community diversity and structure, dispersal, emergence, functional trait, germination, seed mass, seed production, seed persistence, seedling establishment

Introduction

Regeneration is the process whereby mature individuals of a plant population are replaced by new individuals of the next generation through seed production, dispersal, germination, seedling emergence and survival, and vegetative reproduction, each of which has the ability to influence plant population and community dynamics (Grubb 1977). At the population level, these regeneration processes can independently or jointly act as key determinants of population growth and abundance, especially in highly transient or early successional systems (e.g., Silvertown *et al.* 1993; Jongejans *et al.* 2010; Harsch *et al.* 2014; Huang *et al.* 2015). At the community level, species differences in the success or timing of new recruitment into open gaps can set community trajectories following major disturbances and direct species turnover throughout succession, driving ecosystem functions and services (e.g., Hausmann & Hawkes 2010; Aicher *et al.* 2011; Fukami 2012; Fraaije *et al.* 2015). While determining the influence of regeneration processes on community assembly typically relies on measurements of seed and seedling abundances over time and space (Zobel *et al.* 2000; Zeiter *et al.* 2006; Clark *et al.* 2007), this information alone has limited applicability to other species and communities. A more mechanistic understanding of intra- and interspecific variation in regeneration success within and across systems is critical to forecast community assembly outcomes and responses to changing environments.

To explain the responses of individuals, populations, and communities over time and space, ecologists have drawn on functional traits—morphological, physiological, or phenological traits with demonstrated influence on plant fitness in the context of the environment (Violle *et al.* 2007). Because functional traits can be measured across species and have implications for fitness, they offer a common currency to predict the performance of species, composition of communities, and how these shift over time and space. Here, we define regeneration traits as those characteristics with demonstrated implications for regeneration processes (i.e. the extent of clonal reproduction, seed production, seed dispersal, germination, or seedling emergence/survival). Incorporating regeneration traits into predictive frameworks of community assembly has long been recognized as an important goal in ecology (Weiher *et al.* 1999; Lavorel & Garnier 2002). However, while some aspects of functional variation during regeneration are well-characterized across species (e.g., negative association between seed mass and seed output, Westoby *et al.* 2002), there has been relatively little progress in characterizing suites of regeneration traits and trait tradeoffs which differentiate ecological strategies across species and incorporating these traits into models of community and ecosystem processes.

The goal of this paper is to identify recent advances in our understanding of key regeneration processes and outline a research agenda to incorporate regeneration traits into community assembly models. We first provide a brief background on trait-filter community assembly theory, suggesting that this conceptual framework can also be applied to multiple, independent regeneration processes within and across communities. To facilitate the collection and use of regeneration trait data, we review the literature and highlight traits and filters of demonstrated or hypothesized importance to vegetative reproduction, seed production, dispersal, germination, seedling emergence, and establishment. We then place regeneration traits in the context of community assembly models, describing data and empirical needs and highlighting potential challenges. By summarizing the key areas for future progress, we hope to promote the integration of regeneration traits into our understanding of community assembly.

Beyond seed mass: the need to improve community assembly models

Community assembly theory predicts that species from a regional pool are “filtered out” of the local community by dispersal, abiotic, and biotic mechanisms according to the functional traits they possess (Keddy 1992a). At the broadest scale, traits influencing the probability that propagules reach the seedbank will determine which (and to what extent) species are present in the species pool (originally termed dispersal filters, although traits influencing the extent of both propagule production and dispersal ability are implicit; see *Identifying influential regeneration traits and filters*). Environmental conditions further limit which species can persist in a community, which can result in trait similarities (i.e., trait convergence) among species within a given site (termed abiotic or environmental filtering). For example, plant species in drier communities may display a narrower range of traits enabling water conservation and survival (e.g., lower specific leaf area (SLA), higher wood density) than observed in the regional species pool (e.g., Cornwell & Ackerly 2009). Importantly, if multiple strategies are possible (e.g., drought tolerance or drought escape (Ludlow 1989; Freschet *et al.* 2011), abiotic filtering could also result in convergence around multiple trait values reflecting those strategies (i.e. multimodal trait distributions, Laughlin *et al.* 2015). Another layer of complexity is added at the local community scale, where biotic interactions such as competition may further influence the number of species capable of coexisting in a given site (termed biotic filters). For example, particular trait values may dominate in a community because they convey a competitive advantage in the presence of other species, resulting in a competitive hierarchy and trait convergence (e.g., early emerging seedlings preempt limited resources from slower competitors, Verdú & Traveset 2005).

However, if competitive exclusion occurs within a particular niche, but multiple niches are available, limiting similarity theory predicts that trait divergence maximizing niche differences will occur (e.g., coexistence of shallow-rooted natives and deep-rooted perennials) (Kunstler *et al.* 2012; Kraft *et al.* 2015a). Furthermore, biotic interactions could promote higher than expected trait divergence in a given environment if established biota alter the microenvironment in a way that facilitates survival among species whose traits may otherwise exclude them (e.g., plants with high SLA in systems limited primarily by water, Gross *et al*. 2009). Finally, in addition to these deterministic drivers of community assembly, some degree of stochastic, probabilistic processes also influence community composition (Hubbell 2001); the relative importance of these mechanisms will likely depend on the scale at which trait-filter relationships are examined (Chase 2014).

This type of framework should be applicable to traits influencing fitness at any life stage, including regeneration. In the first iteration of this “trait-filter” assembly framework, Keddy (1992a) explored how a germination trait (ability to germinate in mud) affected wetland plant assembly. However, while regeneration traits have been considered sporadically in subsequent conceptual advances and empirical tests of this framework, efforts have largely focused on a handful of vegetative traits (e.g., SLA, wood density, height) which are relatively easy to measure, represent broad resource acquisition and growth strategies (e.g., leaf and wood economics spectrums, Wright *et al.* 2004; Chave *et al.* 2009), and explain a meaningful portion of the variation in plant performance and community composition across resource and productivity gradients (e.g., Poorter & Bongers 2006; Cornwell & Ackerly 2009), presumably by influencing adult growth and survival. Importantly, while SLA, wood density, or plant height may also capture aspects of variation in regenerative strategies across species (e.g., Adler *et al.* 2014), the implications of these traits for regeneration are rarely considered or tested directly. Because traits may have different implications for fitness or abundance across growth, survival, and regeneration, trait-based inferences may shift depending on which demographic transition is most limiting to population growth (e.g., seed mass in Larson *et al.* 2015b). Furthermore, filtering mechanisms across demographic stages may be additive, equalizing, or otherwise interactive. Consequently, restructuring empirical efforts and models to incorporate the influence of widely available traits on regenerative processes could improve assembly model performance. Still, some studies suggest that these vegetative traits vary independently from key aspects of regenerative strategies (e.g., Grime *et al.* 1997; Craine *et al.* 2012a), and may be less useful predictors of regeneration processes. For example, Sonnier *et al.* (2010) found that most leaf traits showed little correspondence to assembly patterns in early successional communities across either stress or disturbance gradients, while plant reproductive height, seed mass, and allocation to reproduction explained community composition in response to one or both gradients.

While comparative efforts initially surveyed a wide range of traits which could differentiate species responses to abiotic and biotic filters during regeneration (e.g., Grime 1981), in the last several decades the focus has shifted away from a range of regeneration traits specific to individual communities and filters (e.g., germination in mud, Keddy 1992b) and towards a few general traits that may correlate with community composition on larger temporal and spatial scales. Specifically, many examinations of community assembly have focused on seed mass as the primary trait representing a plant's regeneration strategy (e.g., Funk *et al.* 2008; Kraft *et al.* 2008; Cornwell & Ackerly 2009). Seed mass is the most widely-collected regeneration trait represented in global databases (e.g., TRY, Kattge *et al.* 2011; BIEN, http://bien.nceas.ucsb.edu/bien/). It is easily-measured and often positively correlated with seedling survival but negatively correlated with seedling growth rate and seed output (reviewed in Moles & Westoby 2006), a tradeoff which has been identified as one of four major dimensions explaining ecological variation among plant species (Westoby *et al.* 2002). It has also been linked to other regenerative functions such as susceptibility to granivory (e.g., Blate *et al.* 1998), germination response to light and temperature (e.g., Milberg *et al.* 2000; Pearson *et al.* 2002), and seedling emergence from depth or through litter (e.g., Loydi *et al.* 2013).

However, despite its widespread use, results from empirical studies have demonstrated that seed mass is not always the strongest predictor of community processes. For example, seed mass may have a lower explanatory power than other traits with respect to dispersal distance (Thomson et al. 2011) seed persistence (Hill *et al.* 2012), or seedling survival (e.g., Funk & McDaniel 2010), and its importance for these processes is likely to vary across groups of species or environments (e.g., Hallett *et al.* 2011). Thus, while seed mass is a valuable ecological tool, it is unlikely that this trait alone can capture variation in regeneration processes within and across communities. Efforts to link regeneration traits to assembly patterns must extend beyond seed mass to incorporate a wider variety of traits which may have direct, if context-dependent, implications for regeneration processes in response to the abiotic and biotic environment.

Consideration of such traits in assembly models could be stalled for a variety of reasons. First, relative to vegetative traits, there is relatively little centralized reference to how regeneration traits should be selected and measured in existing trait handbooks (Cornelissen *et al.* 2003; Pérez-Harguindeguy *et al.* 2013). Because these traits are less familiar to community ecologists, they may also be perceived as difficult or time-consuming to measure. However, while some traits may fit this description (e.g., germination hydrothermal time parameters) or require repeated measurement given intraspecific variability (e.g., dormancy-breaking requirements), these challenges are not unique to regeneration traits (Violle *et al.* 2012). An equally important reason for their absence may lie in the potential complexity of explaining variation in regeneration outcomes. Individual regeneration processes can be influenced by filters on small spatiotemporal scales which could be difficult to capture, and understanding broader regeneration outcomes may require teasing apart the influence of several interacting traits and filters on multiple regeneration processes. These challenges are addressed in greater detail below (see *Integrating regeneration traits into community assembly models*).

Still, recent efforts demonstrate that trait-filter frameworks have the potential to uncover patterns in regeneration and offer valuable insights into community assembly. For example, using 25-year demographic records for 13 co-occurring annual plants, Huang *et al.* (2015) found that a few seed traits reflecting moisture and temperature requirements for germination could be linked to germination success in a given year according to key environmental variables (e.g., temperature during rainfall), and were also linked to long-term patterns of variation in fecundity and vegetative growth traits that reflect broad ecological strategies within communities. Thus, while the importance of particular regeneration processes and traits will vary across systems and species, it appears that regeneration within communities is not wholly stochastic, and that informative patterns are detectable within communities. Below, we review potential traits and filters of interest during regeneration, then discuss their incorporation into assembly models.

Identifying influential regeneration traits and filters

Here, we extend the trait-filter community assembly framework to encompass a range of regeneration processes including vegetative reproduction (clonality), seed production, dispersal, germination, emergence, and seedling establishment (Fig. 1). Each of these processes can have a unique impact on community assembly and may be regulated by different filters. Consequently, for each process within a community, we should identify the most relevant abiotic and biotic filters as well as traits that explain species performance in light of these filters. Theoretically, the culmination of trait-filter interactions during each of these processes will yield predictions of regeneration outcomes within a community; however, the necessary data to test the predictive ability of traits and filters during regeneration is severely lacking. Thus, the first step will be to use this framework as a conceptual map to direct research efforts towards identifying trait-filter relationships which influence regeneration and its component processes across different environments. To initiate these efforts, we briefly outline each regeneration process below.

Clonality

While ecologists often discuss regeneration as being either seed-limited (i.e., seed production, dispersal processes) or establishment-limited (i.e., germination to establishment processes) (e.g., Nathan & Muller-Landau 2000; Myers & Harms 2009; Aicher *et al.* 2011), the dispersal of propagules from vegetative organs (i.e., ramets, genetically identical shoot-root individuals) could have substantial and under-reported impacts on community assembly (Fig. 1; Zobel *et al.* 2010). For example, studies have found that as many as 40% to >99% of new recruits in grassland gaps originate from vegetative reproduction (Bullock *et al.* 1995; Benson & Hartnett 2006). Clonality is especially prevalent in herbaceous species (relative to woody; Aarssen 2008) and in temperate, aquatic, and arctic ecosystems (Klimešová & Herben 2015). Within these ecosystems, however, the abundance of clonal recruits (and their contribution to assembly) also varies. Most notably, while seed dispersal may dominate following severe disturbance with larger gaps to fill (e.g., Bullock *et al.* 1995; Klimešová & Herben 2015), high clonality potential may be a stronger driver of abundance in space-limited, competitive communities (e.g., Mudrák *et al.* 2015) or late successional communities (e.g., Moora *et al.* 2009, but see Klimešová et al. 2011). Furthermore, as our understanding of clonality has expanded beyond a binary trait (i.e. clonal or not, Weiher *et al.* 1999), it has become clear that an array of clonal functional strategies exist which may have complex interactions with abiotic and biotic filters.

Although there are relatively few empirical demonstrations of how clonal traits interact with filters to impact community assembly (Zobel *et al.* 2010; Klimešová *et al.* 2011), growing observational evidence has generated a shortlist of functional traits which could influence clonal recruit abundance in light of key abiotic filters (Fig. 1). For example, bud bank size (i.e., the total number of buds available for the generation of ramets) was strongly, positively correlated with average annual precipitation among grassland communities (Dalgleish & Hartnett 2006), and the location of bud banks (e.g., belowground depth) could mediate species responses to disturbance filters such as grazing or fire (Dalgleish & Hartnett 2009). There is also recent evidence that clonal traits reflecting the rate, location, or persistence of clonal growth may be linked to a few key spectra associated with abiotic filters. Klimešová and Herben (2015) found that a strategy of high clonal multiplication rates and low persistence of parent-clone connections (i.e., rapid colonization and spread) was prevalent in tall, littoral plant communities, while low clonal spread rate and high persistence (i.e., prolonged maternal support) was prevalent in short-statured communities under extreme, stressful conditions. Importantly, multiple clonal strategies have also been detected within communities (Wildová *et al.* 2007); if clonal trait variability influences biotic interactions, it could also be an important mechanism of coexistence within communities (Moora *et al.* 2009; but see Klimešová & Herben 2015).

As with sexual regeneration processes (see below), several key areas of exploration require greater attention moving forward. These include empirical investigations of how bud bank and clonal growth traits influence assembly within communities and across gradients (particularly in comparison to sexual regeneration), and how abiotic and biotic factors affect these relationships. Additionally, clonal trait plasticity (Zobel *et al.* 2010), which can be extensive (e.g., Bittebiere & Mony 2015), is not well characterized. Current trait handbooks contain limited information on the categorical assignment of clonal types (Pérez-Harguindeguy *et al.* 2013), but more traits are characterized in clonal trait databases (a growing resource). For example, the development of the CLO-PLA database of clonal and bud bank traits for Central European plant species (Klimešová & De Bello 2009) has facilitated a growing body of recent work, and should continue to be expanded and replicated in other geographic regions.

Seed production

In plant communities dominated by sexual regeneration, seed production is the first point at which inter- or intraspecific trait variation may shape assembly outcomes (Fig. 1). Functional traits reflecting interspecific variation in reproductive capacity are typically correlated with suites of plant traits representing life history strategies (e.g., Westoby *et al.* 2002). For example, a recent global analysis suggested that species whose population growth relies heavily on high seed production tend to be positioned on the "fast return" end of the LES (e.g., high leaf nitrogen, SLA), while species exhibiting high seed mass, wood density, and leaf longevity are more dependent on high rates of survival in lieu of high fecundity (survival-related traits discussed further below) (Adler *et al.* 2014). Seed mass is a particularly important indicator of potential seed production; it reflects per seed resource investment (e.g., total N and P) and is inversely related to the number of seeds that can be produced (seed output per canopy area) (Henery & Westoby 2001). Thus, seed mass and LES traits may be useful as proxies of variation in seed output across species within a community (Fig. 1).

Like all regeneration processes, however, seed output will vary within and across species in response to abiotic factors such as water, nutrient, and light availability, as well as biotic factors such as competition, herbivory, and pollinator presence (e.g., Leishman *et al.* 1999; Peters *et al.* 2014). In addition to life history traits described above, other traits are needed to predict seed output response to such filters. For example, early emergence has been linked to higher fecundity (Verdú & Traveset 2005), and may further explain seed production patterns in favorable conditions (i.e., when there is little risk of post-emergence hazard-induced mortality); in contrast, minimum plant size for reproduction may be an indicator of seed output ability under high stress conditions (e.g., smaller minimum threshold sizes are better able to maintain or achieve greater seed output under stress; Aarssen 2015).

The phenology of flowering could also influence relative success during seed production and, consequently, community assembly. Abiotic filters such as temperature or soil moisture (and their seasonality or change over time) could favor populations with flowering times coinciding with favorable climatic periods in a community (e.g., Craine *et al.* 2012b; Douma *et al.* 2012), while competition for pollinators or resources during flowering could favor phenological divergence (although this is perhaps less commonly detected, Rathcke & Lacey 1985). For example, Craine *et al.* (2012a) found that species more abundant in warmer, drier upland sites than moist lowland sites tended to have earlier first flowering dates (FFD), perhaps because flowering during high resource availability conveys a critical advantage for viable seed production. However, some challenges remain for the integration of phenology into community assembly models. One uncertainty is when shifting filters should be expected to induce plastic or adaptive phenological responses within species ("flowering time shifts", *sensu* Wolkovich *et al.* 2013) rather than driving species turnover in communities based on mean trait values (a subject currently being addressed by studies on phenology and climate change, Sherry *et al.* 2007; Craine *et al.* 2012b; Wolkovich *et al.* 2014). Furthermore, whether species differences in FFD or the ability to shift flowering time impact reproductive success or abundance in predictable ways remains relatively untested. As recent phenology databases are geographically expanded (e.g., USA National Phenology Network, https://www.usanpn.org/), these are likely to be areas of active exploration.

Finally, in addition to identifying key traits linked to seed production, an important task for empirical studies is to identify conditions under which variation in per capita seed production (and related traits) is expected to have a major influence on community assembly patterns. At the population level, total propagule production will depend not just on a species' fecundity, but also adult abundance (Kroiss & HilleRisLambers 2015), making the standing community a critical consideration. Scaling up, we generally expect that species in the community with greater total propagule production will dominate the seed-bank with a greater opportunity to influence community composition and dynamics. However, the extent to which seed production influences assembly patterns may vary across filters (e.g., disturbance or successional gradients, Sonnier *et al.* 2010), and will ultimately depend on dispersal processes and functional tradeoffs at later stages (see below). Consequently, seed production and underlying traits must be examined in concert with other regeneration processes and traits.

Dispersal

Dispersal has long been recognized as a vital process affecting community assembly (reviewed by Schupp *et al.* 2010; Poschlod *et al.* 2013). Community ecologists often think about dispersal in the context of propagule pressure, which may be a combination of seed production (see above) and dispersal. Dispersal itself, the movement of seeds away from the parent plant, reduces competition between a seedling and its parent and siblings and allows populations or species to reach and colonize new gaps. Although identifying which species can reach the seedbank is critical when evaluating the nature and extent of subsequent recruitment filtering in a community, directly quantifying seed arrival is not always feasible. If dispersal traits can enhance predictions of dispersal probability and seedbank composition in a given community, this allows ecologists another way to differentiate under what conditions seed- or establishment limitation more strongly influences assembly (Kraft *et al.* 2015a).

Explanations of spatiotemporal dispersal patterns have ranged from high stochasticity (e.g., equal dispersal abilities across species; seed arrival influenced by parent abundance and chance events) to predictable directed dispersal according to abiotic filters and plant/disperser characteristics (e.g., Nathan & Muller-Landau 2000; Hubbell 2001; Chase 2007; Shipley *et al.* 2011). While seed arrival will be partly influenced by stochastic factors, emerging evidence of non-random dispersal patterns should invigorate efforts to understand its relative role in communities. For example, Fraaije *et al.* (2015) examined community assembly along a riparian moisture gradient and found that seeds of species more tolerant of dry or wet conditions were more likely to arrive at dry and wet ends of the gradient, respectively, suggesting directed dispersal resulting from an interaction between seed traits and abiotic filters. Non-random dispersal could be dependent on a number of abiotic filters (e.g., wind and water movement) as well as the disperser community (Fig. 1) (reviewed in Schupp *et al.* 2010; Poschlod *et al.* 2013).

Recent studies have advanced our understanding of which particular traits may predict dispersal processes (Fig. 1). Using a large dataset, Tamme *et al.* (2014) found that dispersal syndrome (e.g., water-, wind-, animal-dispersed), plant growth form, and terminal velocity were collectively the best predictors of dispersal distance. Marteinsdottir (2014) also found that two traits (dispersal syndrome and seed mass) strongly influenced long-distance dispersal. In contrast, these and other traits (clonal growth index, dispersal method, height, seed mass, and SLA) were poor predictors of dispersal at the local scale. This result contrasts with those from Thomson *et al.* (2011), who found that height was a good predictor of dispersal distance at the local scale. As these results indicate, it is unclear exactly which traits will be predictive within and across communities, but the distribution and influence of different dispersal traits in communities is likely to depend on abiotic and biotic filters as outlined above. For example, Ozinga *et al.* (2004) found that light and moisture gradients were linked to dominant dispersal syndromes across 123 plant communities, while Copeland and Harrison (2015) similarly found that species found in mesic- and xeric microclimates of a single region tended to exhibit water- and wind dispersal mechanisms, respectively. Interactions between the animal disperser community and seed traits (e.g., dispersal mode or seed palatability traits) could also have particularly important implications for regeneration which are currently under-represented in assembly models. For example, seed caching can result in directed dispersal away from the parent plant and into more favorable microsites for establishment (e.g., Hirsch *et al.* 2012), while scarification and digestion by dispersers can also enhance germination (e.g., Rodriguez-Perez *et al.* 2005).

As trait and dispersal data are collected from different types of communities, we can begin to examine how seed output and dispersal traits collectively influence propagule pressure and, consequently, community dynamics. Methods for collecting traits related to dispersal mode and potential can be found in Pérez-Harguindeguy *et al.* (2013) . More traits are characterized in recent dispersal trait databases, e.g., D3: Dispersal and Diaspore Database, (Hintze *et al.* 2013), which includes an array of dispersal traits for a regional set of species and offers a starting point for trait collection in other areas.

Germination

It is not simply the relative abundance of propagules in the seed-bank, but the fate of those seeds which influences community dynamics. Variation in the extent or timing of germination within and across species can have important implications for community trajectories, particularly following disturbance (e.g., Donohue *et al.*

2010; Wainwright *et al.* 2012). While efforts to compare germination characteristics across species were initiated decades ago (e.g., Grime *et al.* 1981; Baskin & Baskin 1988), such traits have had limited application in community assembly and dynamics. For a given species, the proportion of propagules in the seed-bank which germinate (i.e., initiate radicle penetration through the seed coat) in a given year may depend on traits and filters influencing two specific processes: germination and seed persistence (Fig. 1).

Germination is a complex process influenced by a variety of abiotic filters including soil moisture, temperature, light, and chemicals, which interact with species traits to remove layers of dormancy and induce germination (Fig. 1; reviewed in Long *et al.* 2015). Seed mass may correlate with germination responses under certain filters (e.g., Pearson *et al.* 2002), but community assembly models should also strive incorporate traits that more directly capture how temperature and moisture influence the rate and timing of germination across species and populations. These include indices derived from hydrothermal time germination models such as base water potential, cardinal temperatures (i.e., minimum, optimum, maximum temperatures), thermal time, and hydrothermal time for germination (Bradford 2002; Hardegree *et al.* 2013). These indices can be assessed in a laboratory setting, and offer more informative metrics of germination response compared to germination rates measured at a single temperature or moisture level. Base temperature and water potential, for example, identify the lowest temperature and moisture level (i.e., water potential, MPa) at which a selected percentile of the seed population is expected to germinate (e.g., 50th percentile of germinated seeds produced by a plant population in a given year). Additionally, metrics which capture the width of the germination niche (i.e. the range of conditions in which a population may germinate) could have explanatory power (Donohue *et al.* 2010). However, these traits may not account for additional dormancy layers inhibiting germination, which may be related to physical seed traits (e.g., seed coat hardness), or physiological indicators such as temperature stratification, light fluctuation/quality, fire, or ripening requirements (reviewed in Dalling *et al.* 2011; Long *et al.* 2015). Consequently, the composition of germinants in a given year could depend on complex interactions between abiotic factors and germination traits which make it challenging to anticipate relative germination success (e.g., Larson *et al.* 2015b). Still, using just a few physiological germination traits (e.g., thermal time, optimal temperature and base water potential for germination) along with precipitation and moisture data, Huang *et al.* (2015) were able to explain yearly variation in germination patterns across 13 desert annual species over a 25 year period. This insightful study demonstrates that if the most appropriate filters, traits, and scales are identified, trait-based models can improve our understanding of this important regeneration process.

Seed mortality (i.e., lack of persistence) can also influence the proportion of the propagule pool that germinates via both abiotic (e.g., extreme temperature, moisture) and biotic (e.g., fungal pathogens, granivory) filtering on seed survival (Long *et al.* 2015) (Fig. 1). Seed persistence could be related to physical defenses (e.g., seed coat hardness), chemical defenses (e.g., phenolic compounds, oils), and physiological characteristics (e.g., inherent seed longevity indices, Long *et al.* 2008) (Dalling *et al.* 2011; Hill *et al.* 2012; Hamilton *et al.* 2013). For example, Blate *et al.* (1998) found that rates of seed predation ranged from 0 to 100% across 40 tropical tree species and were negatively correlated with seed coat thickness and hardness, as well as seed mass. Independent of granivory, there may be a tradeoff between seed traits governing the ability to germinate rapidly in an environment and the ability for a seed to persist in the soil (Saatkamp *et al.* 2011; Hill *et al.* 2012, but see Hamilton *et al.* 2013), such that multiple seed-bank strategies (transient vs. persistent) may interact to influence community dynamics over time and space. Such a tradeoff between germination rate and seed persistence could parallel the LES tradeoff between rapid growth and greater longevity (Wright *et al.* 2004); although speculative, the possibility of general strategies with strong implications for seed-bank dynamics warrants further exploration.

Moving forward, a key challenge will be to understand whether the complexity of germination, dormancy, and persistence traits and their interaction with multiple filters can be distilled into general principles relating seed traits to broad germination dynamics within a community. The goal will not necessarily be to achieve species-specific predictions of germination in a given year, but to capture general trends influencing vegetative dynamics. This may initially be a context-specific endeavor with inferences limited to local scales, but as more information is collected, it may be possible to look for general trends over broader spatiotemporal scales (Hardegree *et al.* 2013; Poschlod *et al.* 2013).

Emergence

Emergence is the probability that a germinated seed in the seed-bank will penetrate the soil/litter surface to commence autotrophic growth. Co-occurring species can vary substantially in emergence success (e.g., Evans & Etherington 1991; Larson *et al.* 2015b), which has important implications for community dynamics. However, emergence is among the least studied of recruitment processes and is often combined with germination as the transition from seed to emerged seedling, even though these stages may be unrelated and associated with different filters and traits (James *et al.* 2011; Larson *et al.* 2015b). Like germination, emergence is a complex process to model for individual species, and it is yet unclear whether functional traits may be able to explain patterns of variation. However, efforts in seed and crop sciences have highlighted some relevant filters and potential traits of interest (Fig. 1).

Abiotic and biotic filters influencing emergence may include environmental hazards such as freezing and drought events, fungal pathogens, and mechanical suppression due to soil crusting, litter, moss, or soil burial (Fig. 1; Sydes & Grime 1981; Luzuriaga & Escudero 2008; Loydi *et al.* 2013). Traits describing germination phenology may be important predictors of pre-emergent susceptibility to environmental hazards like freezing (e.g., Boyd & James 2013). Morpho-physiological traits of young radicles or shoots (e.g., tissue density or osmotic adjustment, González & Ayerbe 2011; Larson *et al.* 2015b) and cotyledon or coleoptile shape (Sydes & Grime 1981) are also of potential importance. Although virtually unexplored in comparative ecology, interspecific variation in such traits may be substantial. For example, Evans and Etherington (1991) demonstrated that seedling shoot and root lengths can vary over 10-fold across species in the first week after germination, while trait plasticity in response to soil moisture also varied by species. In woody dicots, seedling functional type (determined by the position, exposure and function of cotyledons, Pérez-Harguindeguy *et al.* 2013) could also influence growth rate and tolerance of damage in young seedlings still dependent on embryonic tissues; however, most evidence of such impact to date has come from older seedlings (see following section). To better understand how these traits influence post-germination survival, studies which examine germinated and emerged seedling pools under different environmental scenarios will be especially helpful.

Leaf and root tissues of mature plants are the most commonly studied functional traits, and it may be possible to infer emergence responses from adult attributes if traits are ontogenetically conserved. However, current evidence suggests that some but not all functional aspects may be conserved between regeneration and adult stages (e.g., Alvarez-Clare & Kitajima 2007; Butterfield & Briggs 2011). For example, if root length of recently emerged seedlings is a trait of interest, seed mass may be a good proxy in models (Fig. 2; see also Evans & Etherington 1991), but root length measured from older seedlings may be a poor indicator, even with seedling age differences as little as 3 weeks (Fig.2). Future efforts should thus seek to explore ontogenetic trait conservation from the time of seed germination and emergence through plant maturity to better understand when commonly measured traits can inform processes at other life stages, such as emergence.

Seedling establishment

Seedling establishment is perhaps the most studied process in regeneration, with known abiotic (water, light, and nutrient availability) and biotic (herbivory, pathogens, competition) filters (Fig. 1; Garwood 1996; Moles & Westoby 2004). Biotic filters may also be facilitatory (e.g., mutualistic soil biota, Van Der Heijden 2004), although beyond N-fixation, symbiosis-related "traits" (e.g., mycorrhizal association) are not often incorporated in community assembly models.

Vegetative traits which have been linked to seedling survival include total leaf/plant dry mass and leaf area (in response to drought, Butterfield & Briggs 2011), stem/leaf tissue density and toughness (in response to light, Alvarez-Clare & Kitajima 2007), leaf physiology and photosynthetic capacity (in response to light, Funk & McDaniel 2010), and rooting depth, root biomass, or taproot presence (in response to drought, e.g., Lloret *et al.* 1999; Butterfield & Briggs 2011). Among woody species, seedling functional type (*sensu* Pérez-Harguindeguy *et al.* 2013) has also been related to seedling growth and survival (as well as other aspects of regeneration), particularly in tropical systems (reviewed by Garwood 1996). In these systems, up to 80% of pioneer species may have epigeal foliar cotyledons (i.e. aboveground and photosynthetic; Ibarra-Manríquez *et al.* 2001), which are linked to faster full sun growth rates even when cotyledons are damaged and may provide a competitive advantage. In contrast, seedlings with hypogeal reserve-type cotyledons tend to have higher survival rates following stem damage (Baraloto & Forget 2007), which could be important in communities with extensive stem herbivory or disturbance. In environments with high risk of early season environmental hazards, such as freezing or drought, seedling survival could also be influenced by germination/emergence phenology, as early-emerging seedlings may be more likely to experience hazardous events that are avoided by late-emerging seedlings (e.g., Graae *et al.* 2011; Boyd & James 2013, but see Verdú & Traveset 2005). In contrast, in other systems with strong competitive filters, studies have demonstrated that earlier emergence could increase seedling establishment through competitive release, with long-term implications of these priority effects for community trajectories (Vaughn & Young 2015) (Fig. 1).

With growing datasets, there is substantial room to improve our understanding of which seedling traits influence assembly across community types and environmental gradients. Specifically, there is a relative shortage of empirical studies testing how interactions among a variety of filters and traits ultimately influence the composition of recruited seedling communities. Such efforts may be complicated by the range of traits which can influence a plant's response to a single filter. For example, different leaf traits may enable response to herbivory through escape (e.g., phenology of seed or leaf production), defense (e.g., secondary metabolites), or tolerance (e.g., photosynthetic activity) (Boege & Marquis 2005). Conversely, a single trait (e.g., photosynthetic capacity) may influence how a plant responds to multiple filters (e.g., herbivory, shade, and drought tolerance, Boege & Marquis 2005; Hallik *et al.* 2009; Funk & McDaniel 2010), adding additional layers of complexity in systems driven by multiple biotic and abiotic filters.

Integrating regeneration traits into community assembly models

Given the potential influence of regeneration processes on plant populations and communities, greater incorporation of regeneration traits into trait-filter assembly models could provide new insight into patterns of community composition and species distributions (e.g., Ozinga *et al.* 2004; Fraaije *et al.* 2015; Rosbakh & Poschlod 2015). We expand on their integration below, highlighting the necessary inputs and potential output of assembly models which emphasize regenerative processes in plant communities. We then outline a path forward, summarizing necessary areas of progress and potential challenges to be considered.

While there are many evolving approaches to trait-based inferences of community assembly processes (e.g., Ackerly & Cornwell 2007; Pillar *et al.* 2009; Spasojevic & Suding 2012; Laughlin & Laughlin 2013; Loranger *et al.* 2016), the required inputs and desired outputs are generally similar (Fig. 3). The ultimate objective of trait-based assembly models is to generate expected trait distributions (and thus, species distributions) that match observed distributions within or across communities of interest (Keddy 1992a). By incorporating regeneration traits, the goal will be to improve model output by including additional aspects of plant function to produce more accurate predictions of distributions and dynamics within communities. In order to generate this output, raw data forming the basis for predicted distributions must be collected and assembled (i.e. data inputs), including both regeneration trait data for regional species pools and abiotic and biotic variables. Before predictions can be generated, however, it is also necessary to empirically identify the key abiotic and biotic filters that operate in a system and develop expected relationships between traits and these filters (i.e. filtering mechanisms). To formulate expected trait-filter relationships, studies often utilize observed species abundances to look for shifts in community-weighted trait means across filter gradients (e.g., Buzzard *et al.* 2015), evidence of trait convergence or divergence within communities and across gradients (Freschet *et al.* 2011), or both (e.g., Kraft *et al.* 2008; Spasojevic & Suding 2012; Roscher *et al.* 2013). Recently, it has also been suggested that more direct approaches should also be used to establish these expectations, e.g., controlled studies which isolate impacts of individual filters on fitness across functionally diverse species from the regional pool (Kraft *et al.* 2015a). Once data are assembled and anticipated filtering mechanisms are identified, community assembly outcomes can be predicted.

As a hypothetical example of the possible inputs, outputs, and scale of assembly models emphasizing regeneration processes, suppose a community of interest includes emerged seedlings in a particular site and year which germinate from the larger species pool (i.e. seedbank) (Fig. 4). A range of abiotic or biotic filters could differentially affect seed germination and emergence from the seedbank, and species' responses to these filters should depend on relevant seed or early seedling functional traits (Fig. 4A). Before these data can be used to generate predictions, however, empirical efforts must first develop an understanding of which filters may be most influential and how traits mediate species' responses to these filters (Fig. 4B). For example, within a particular site, a dry year with low spring soil moisture content could impose a significant environmental constraint on the ability of species to germinate (abiotic filtering); in this case, we might expect species with less negative base water potentials for germination (i.e., high moisture requirements) to be excluded from the seedling community (Bradford 2002). In contrast, in a relatively wet year, all species may be capable of germinating regardless of trait variation, and spring soil moisture may be irrelevant as an environmental filter; instead, we may expect competitive interactions (i.e. biotic filtering) to drive assembly. For example, species which germinate rapidly (e.g., low hydrothermal or thermal times) may emerge earlier and preempt resources (e.g., light), precluding slow-germinating species from establishing in the community (Verdú & Traveset 2005). Based on these hypothesized trait-filter relationships, expected trait distributions within the community could be generated (Fig. 4C).

While this example focuses on emerged seedlings as the community of interest (and consequently, filters which shift over time or patches within a community), regeneration traits could also have important influence on assembly over larger temporal and spatial scales, e.g., as measured through indirect links of regeneration traits to adult abundance. For example, base temperature for germination was strongly linked to adult abundance along a regional temperature gradient (Rosbakh & Poschlod 2015). These examples, at their differing scales, represent a starting point to consider the kinds of data and empirical efforts that will be required to account for regenerative outcomes in trait-based community assembly, and to anticipate the potential challenges. We describe these in greater detail below, highlighting key areas of future progress (Table 1).

Data inputs

As initiated here, a first major step to obtaining relevant trait data is utilizing the literature and exploratory multi-trait surveys to compile shortlists of regeneration traits or metrics with theoretical or demonstrated potential to impact fitness and capture larger axes of functional variation across species during regeneration processes. These efforts will increase accessibility to a wider range of potentially informative traits and provide a foundation for more comparable trait selection in empirical studies exploring regeneration outcomes (Table 1, Action 1). As studies incorporating regeneration traits are initiated, it will also be important to establish standardized trait measurement methods across studies and systems (e.g., as in Cornelissen *et al.* 2003; Pérez-Harguindeguy *et al.* 2013) (Table 1, Action 2) and, ideally, to expand trait databases to make commonly-measured trait lists, measurement guidelines, and data more easily accessible (Table 1, Action 3). For example, regional databases have recently been created for dispersal traits (D3: The dispersal and diaspora database, Hintze *et al.* 2013) and clonal traits (CLO-PLA, Klimešová & De Bello 2009). Similar efforts should be extended both geographically and to traits associated with other regeneration processes. The global TRY database has a growing number of traits linked to all aspects of regeneration, and represents an excellent resource to compile data for a wider range of species in a centralized location (Kattge *et al.* 2011). Furthermore, although the extent and influence of intraspecific trait variation and plasticity are not yet well-understood during regeneration, studies suggest that these sources of variation may be substantial at multiple life stages (e.g., Violle *et al.* 2009; Kulpa & Leger 2013; Bittebiere & Mony 2015; Larson *et al.* 2015a); we suggest that intraspecific trait variation should be explicitly incorporated into studies and databases as much as possible (Table 1, Action 4).

While environmental data is already a staple for assembly models and may be available for many plant communities, regeneration processes could be sensitive to variation in abiotic and biotic factors on smaller temporal and spatial scales (Clark *et al.* 1999). Consequently, when focal communities are highly dependent on these processes, models may need to account for intra- or inter-annual variation in environmental variables rather than mean annual values for a community (e.g., to differentiate between outcomes in wet and dry years, Fig. 4). Collecting abiotic and biotic filter data at multiple spatial scales and time points within communities will allow for means and variability to be calculated, the latter of which could be useful in identifying generalizable patterns over longer or larger scales (e.g., across years, Huang *et al.* 2015). The role of scale in regeneration trait-based model development is discussed further below (see *Filtering mechanisms*).

Filtering mechanisms

In order to apply regeneration trait and filter data towards predictions of community composition and dynamics, we must first develop a mechanistic understanding of how different abiotic and biotic filters influence trait selection (Table 1, Action 5). As regeneration traits are incorporated into community assembly models, we suggest that a highly mechanistic approach be utilized initially. Because each regeneration process outlined above is potentially governed by unique aspects of plant function and filtering, it is critical to underpin assembly models with demonstrations of direct links between traits, filters, and species responses during individual regeneration processes prior to drawing inferences about trait influence on larger regeneration outcomes. Establishing direct links between traits and the demographic processes underlying community assembly has been highlighted as a recent priority in community ecology, as assembly models have historically relied on indirect links between traits and abundance in communities to infer these relationships (e.g., Laughlin & Messier 2015).

However, beyond identifying singular relationships, empirical methods and models must also be developed which capture and disentangle the relative roles of filtering from multiple regeneration processes on community assembly (Table 1, Action 6). Notably, the hypothesized trait-filter relationships displayed in the hypothetical illustration above (Fig. 4) depend on several assumptions: first, that one trait may capture species responses to a single filter, and second, that trait distributions within a community may be reasonably predicted from a single filter (as opposed to simultaneous effects of multiple abiotic and/or biotic filters). However, these assumptions may be unrealistic in natural communities. First, given the likelihood that meaningful functional variation during regeneration (across or within species) is multidimensional in nature (e.g., Larson *et al.* 2015a), multiple independent traits (e.g., base water potential and seed mass) and their interactions could influence responses to a particular filter. Consequently, it will be important to develop models which incorporate information regarding the simultaneous influence of multiple influential traits on regeneration processes. We refer readers to recent approaches to this challenge with respect to both abiotic (e.g., Jamil *et al.* 2013; Laughlin & Messier 2015) and biotic (Kraft *et al.* 2015b) filters.

Second, it is becoming increasingly clear that both abiotic and biotic filters often influence trait and species distributions within communities (e.g., Cornwell & Ackerly 2009; Lasky *et al.* 2014; Kraft *et al.* 2015b). If multiple filters simultaneously constrain regeneration processes, this could result in trait distributions that differ from expectations, especially if interacting abiotic and biotic factors are non-additive (Agrawal *et al.* 2007; Pakeman *et al.* 2009). Furthermore, even if a single filtering mechanism dominates assembly patterns, interpretation can be complicated by the fact that multiple mechanisms could lead to trait convergence (e.g., abiotic filtering or competitive hierarchies) or trait divergence (e.g., competition driving limiting similarity, abiotic filtering driving divergent ecological strategies, or facilitation, Mayfield & Levine 2010). Consequently, there is growing awareness that models must consider and more clearly differentiate between multiple different types of filtering (Kraft *et al.* 2015a) and have the capacity to account for a wider range of possible trait distributions (e.g., multimodality, Laughlin *et al.* 2015). In order to untangle the implications of multiple trait-based filtering processes for regeneration, either within or across regeneration stages, these challenges must be addressed.

A final challenge will be identifying the scales on which filters operate during regeneration. For example, abiotic filters may operate at the scale of the microsite during some regeneration processes (e.g., germination, emergence, establishment), resulting in large environmental heterogeneity within a community (e.g., between hills and depressions, shaded and open). In these cases trait-based abiotic filtering may occur across microsites at the plot-level, but be undetectable at the community-level, where environmental heterogeneity and species niche differences promote coexistence and regeneration trait divergence within the community (Grubb 1977; Grime 2006; Kraft *et al.* 2015a). In contrast, trait-filter influences on dispersal may be less detectable at small scales due to stochastic influences, but more detectable at larger scales (e.g., Miller *et al.* 2014, but see Shipley et al. 2011). This leaves several questions to be explored: What are the appropriate spatial and temporal scales to measure environmental filters and regeneration processes (such as successful seed production, germination, or recruitment)? How do we incorporate finer scales of variation into trait-based models while minimizing complexity? And finally, when and how critical is it to account for this smaller-scale variation with respect to understanding broader regeneration outcomes and influence on community dynamics (Table 1, Action 7)?

Conclusion

The opportunities to enhance and apply our understanding of functional variation in the regeneration niche are enormous, spanning from the expansion of trait surveys and databases to the use of key traits in community assembly models (Table 1). As a first step, we should reinvigorate comparative efforts that were initiated decades ago to identify key regeneration traits across a range of species and environments and, if possible, simplify patterns of trait variation (e.g., Grime *et al.* 1981; Baskin & Baskin 1988). With these data, we may begin to characterize main axes of regeneration strategies and test whether a handful of key regeneration traits can be used to explore a broad range of questions regarding trait-filter interactions and their influence on species abundances and diversity across spatial scales (e.g., microsite, community, and regional variation) and temporal scales (e.g., seasonal, yearly, and cross-successional variation). Existing assembly models offer a range of tools to answer these questions via both direct pathways (through links to individual regeneration processes) and indirect pathways (through links to community abundance and diversity). Given expected shifts in climate, disturbances, and species introductions, predicting assembly patterns and responses of plant communities remains a primary ecological and applied goal; integrating regeneration traits into this understanding represents one of the most critical opportunities for advancement toward the realization of this goal.

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Data Accessibility

This manuscript does not use data

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Table 1 Directions for future research. Advancing our understanding of regeneration traits and their implications for community assembly relies on the realization of several key objectives. Efforts geared towards some of these objectives are already in progress (see text).

Data inputs: Trait measurement & database development

1. **Establish a list of traits to measure.**

   Utilize the literature and exploratory trait surveys to establish common lists of traits which are likely to capture the most important axes of interspecific functional variation during regeneration stages depending on abiotic and biotic context

2. **Establish and compile standard protocols for regeneration trait measurement.**

   These exist for some traits (e.g., seed mass) but not all (e.g., coleoptile tissue density).

3. **Increase data accessibility.**

   Compile trait values of individuals and species into global databases (novel databases or expansion of current databases, e.g., TRY, D3, and CLO-PLA3; Klimešová & De Bello 2009; Kattge et al. 2011; Hintze et al. 2013)

4. **Incorporate intraspecific trait variation and plasticity into data collection efforts**

   Measure traits across environmental gradients in controlled and observational settings to understand the extent of plasticity and intraspecific trait variation, which could be important to inform sampling protocols or to incorporate into assembly models.

Filtering mechanisms: Linking traits to community assembly

5. **Identify traits linking directly to abiotic and biotic filters during key regeneration stages.**

   Conduct controlled and observational experiments to identify key traits linked to regeneration outcomes under the influence of specific filters.

6. **Determine the relative importance of abiotic and biotic filters on regeneration processes.**

   Develop models to test hypotheses regarding the relative and combinational influences of biotic and abiotic filtering mechanisms operating within and across regeneration processes.

7. **Acknowledge and characterize the role of scale in trait-based filtering during regeneration.**

   Examine traits, filters, and regeneration outcomes at different scales to identify conditions where traits can be a practical tool for community assembly predictions.

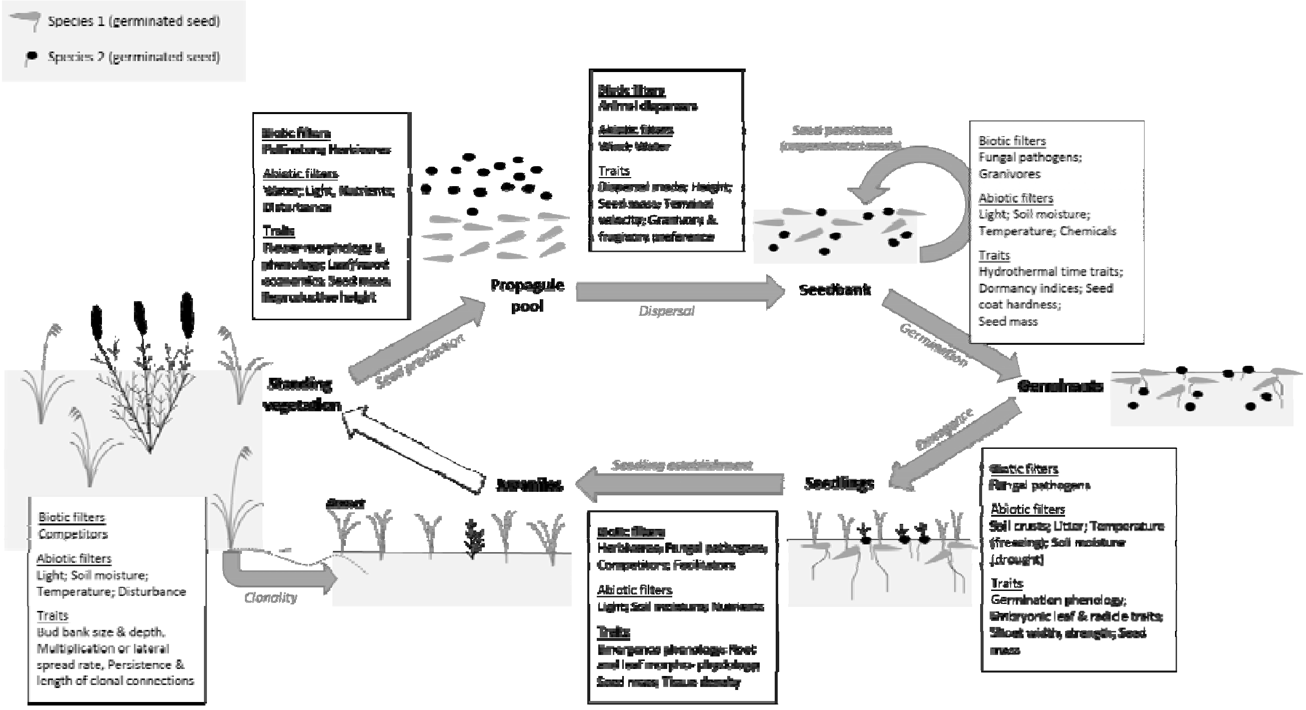

Fig. 1. A “trait-filter” community assembly framework applied across multiple stages of regeneration (grey arrows). Abiotic and biotic filters and functional traits of potential importance are highlighted at each stage of regeneration. These do not represent a comprehensive list; more work is needed to identify relevant filters and traits across environmental gradients. Importantly, the relative importance of different regeneration processes, filters, and traits will vary across community types.

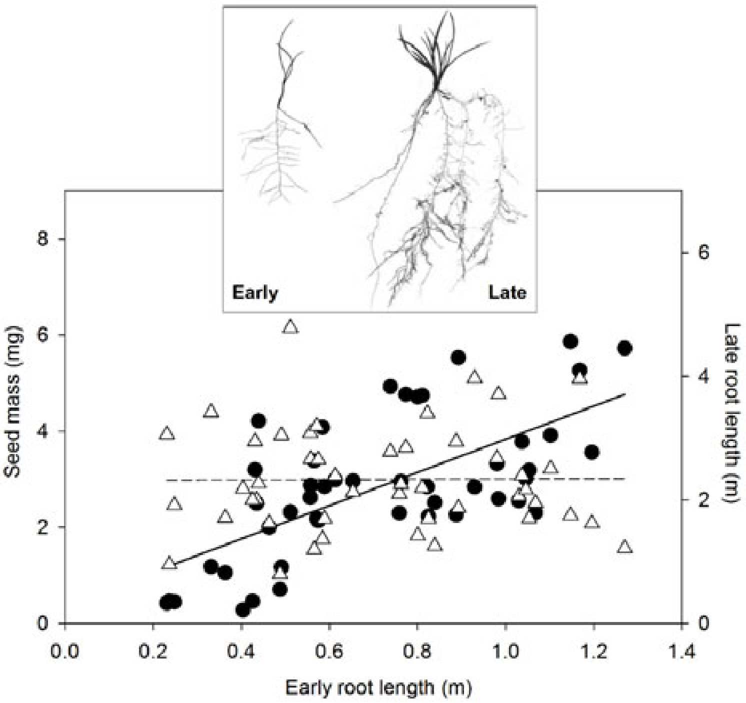

Fig. 2. Relationships between root length of early seedlings (appearance of fully-expanded first leaf) and both seed mass (closed circles) and root length of late seedlings (three weeks following early stage, open triangles). Early root length was strongly correlated with seed mass (Pearson $r = 0.666$, $P < 0.001$; solid line), but not with late root length (Pearson $r = 0.008$, $P = 0.955$; dashed line). Examples of relative seedling development at early and late stages are illustrated in the inset. Data are unpublished analyses using trait data for 47 semi-arid grass varieties (high watering treatment only) from Larson *et al.* (2015b).

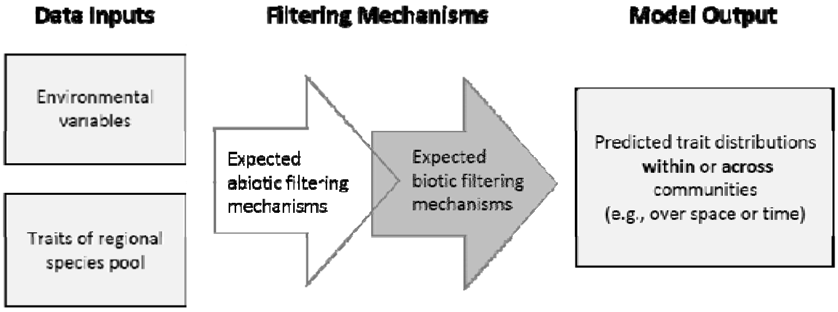

Fig. 3. Inputs and outputs of trait-based community assembly models. Trait and environmental data (i.e. data inputs) provide the basis for models which predict trait distributions within or across communities (i.e. outputs) based on empirical evidence of how abiotic and biotic filters operate on traits in a particular system (i.e. filtering mechanisms).

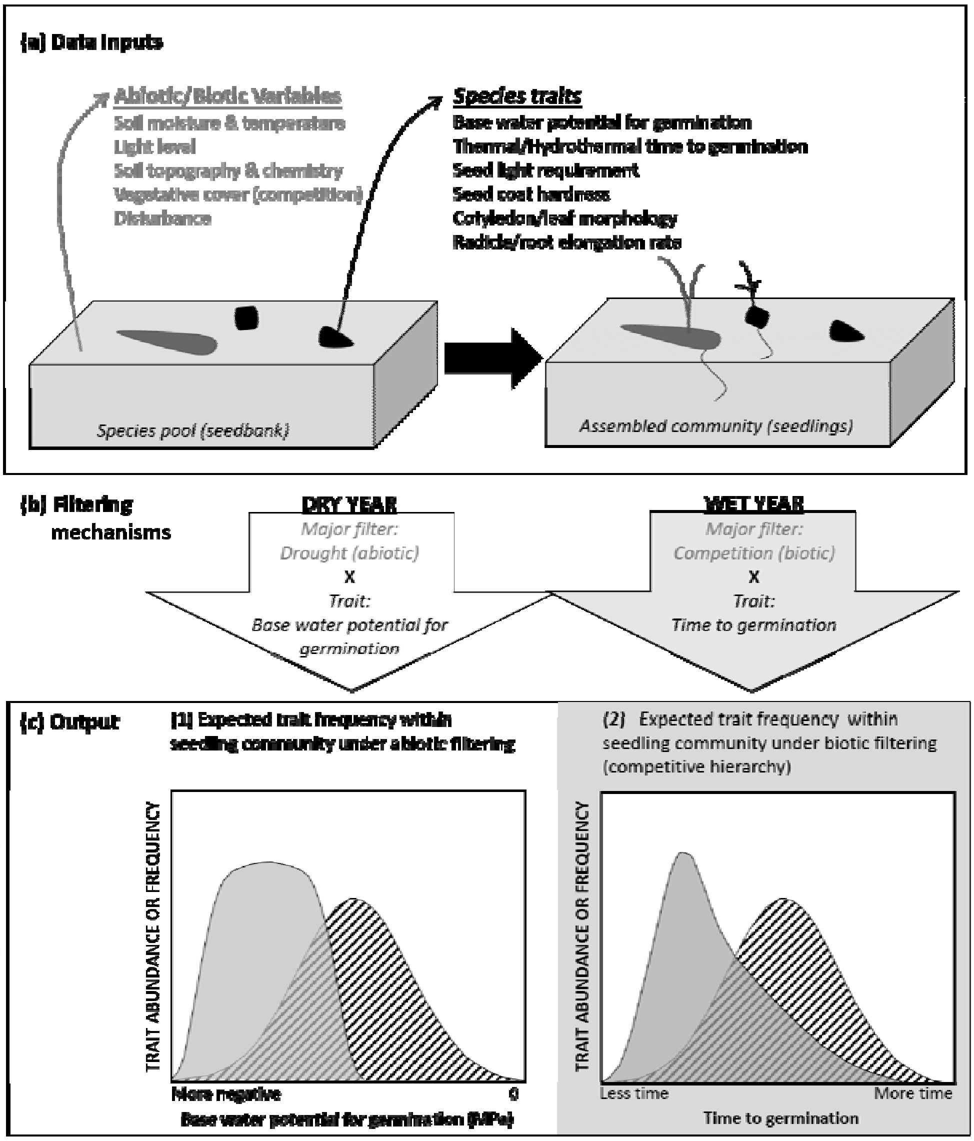

Fig. 4. A hypothetical example incorporating regeneration traits into a community assembly model. (a) If seed to seedling recruitment is a major determinant of community composition, a model may be used to predict how a community of seedlings will assemble from the larger species pool (i.e. seedbank). Expected trait distributions may be generated from relevant filters (abiotic factors which limit germination and emergence, such as moisture, temperature and light, or biotic factors which indirectly effect these resources, such as disturbance and vegetative cover) and traits that influence responses to these filters (e.g., germination response traits, seed and seedling morphological traits). (b) Next, empirical efforts must identify which filters influence seed germination and emergence and how traits respond to these filters (i.e. filtering mechanisms). In temperate systems characterized

by inter-annual variation in weather (e.g., precipitation), influential filters could vary across years. For example, in a dry year, low spring soil moisture content could impose a significant filter on the ability of species to germinate as a function of their base water potential for germination: populations with more negative values (i.e., high moisture requirement) may be excluded. In contrast, in a relatively wet year, all species may be capable of germinating, and spring soil moisture may be irrelevant as an abiotic filter. Instead, competitive interactions over limiting resources (i.e. biotic filtering) may drive assembly if species with particular traits (e.g., rapid germination, or low hydrothermal/thermal times) are capable of emerging earlier and preempting resources (e.g., light) in the community. (c) Based on these hypothesized trait-filter relationships, assembly models might predict (1) exclusion of less negative base water potentials for germination in a dry year and greater trait convergence around more negative values due to abiotic filtering (gray distribution) compared to a null model (hatched distribution), or (2) trait convergence around more rapid germination in a wet year due to biotic filtering (i.e. competitive hierarchy) (gray distribution) relative a null model (hatched distribution).