

ESSAY REVIEW

How to quantify competitive ability

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Abstract

1. Understanding the role of competition in structuring communities requires that we quantify competitive ability in a way that permits us to predict the outcome of competition over the long term. Given such a clear goal for a process that has been the focus of ecological research for decades, there is surprisingly little consensus on how to measure competitive ability, with up to 50 different metrics currently proposed.
2. Using competitive population dynamics as a foundation, we define competitive ability—the ability of one species to exclude another—using quantitative theoretical models of population dynamics to isolate the key parameters that are known to predict competitive outcomes.
3. Based on the definition of competitive ability we identify the empirical requirements and describe straightforward methods for quantifying competitive ability in future empirical studies. In doing so, our analysis also allows us to identify why many existing approaches to studying competition are unsuitable for quantifying competitive ability.
4. *Synthesis.* Competitive ability is precisely defined starting from models of competitive population dynamics. Quantifying competitive ability in a theoretically justified manner is straightforward using experimental designs readily applied to studies of competition in the laboratory and field.

KEYWORDS

competitive ability, competitive dominance, competitive effect, competition model, competitive response, interspecific competition, population dynamics, response surface

1 | INTRODUCTION

To quantify the influence of competition on species presence, absence and abundance, ecologists need to be able to identify the species that will win and the species that will lose in competition over the long term (i.e. over multiple generations). The ecological literature on competition is vast, covering decades of empirical research, many reviews of both empirical methods (Brooker & Kikvidze, 2008; Connolly, 1997; Cousens, 1991; Freckleton & Watkinson, 1999, 2000; Gibson, Connolly, Hartnett, & Weidenhamer, 1999; Goldberg & Scheiner, 2001; Inouye, 2001; Weigelt & Jolliffe, 2003) and results (Aschehoug, Brooker, Atwater, Maron, & Callaway, 2016; Connell, 1983; Goldberg, Rajaniemi, Gurevitch, & Stewart-Oaten, 1999; Gurevitch, Morrow, Wallace, & Walsh, 1992; Schoener, 1983), and

the development of over 50 different metrics of competitive ability based on measurements of individual performance (Weigelt & Jolliffe, 2003). Despite the tremendous research attention, however, the question of how to identify the ultimate winners and losers in competition from empirical studies remains unclear (Trinder, Brooker, & Robinson, 2013). For example, the most recent comprehensive review of interspecific competition between plants (Aschehoug et al., 2016) concludes that the hundreds of studies that have examined the impacts of interspecific competition on the performance of individual plants “...have told us little about how such competitive effects ramify to populations.” This observation matches messages from influential reviews of empirical studies from previous decades (Connell, 1983; Goldberg & Barton, 1992; Goldberg et al., 1999; Gurevitch et al., 1992; Inouye, 2001; Schoener, 1983). This is not to

say that we have not increased our understanding of competitive interactions. But the empirical methods and analyses on which this understanding is based are not suited to predicting which species will win and which species will lose in competition over the long term.

There are several reasons for a lack of progress in predicting winners and losers in competition at the population-level over the long term. First, most studies of competition are based on the growth of individual plants in competition over short periods of time (e.g. a growing season). Inference about long-term competitive ability at the population level is often then extrapolated based on verbal or graphical models of competition, with predictions that will often not match population dynamic outcomes (Freckleton, Watkinson, & Rees, 2009). Second, and following from the reliance on verbal or graphical models in the literature, it is widely believed that there are different ways that species can be competitively superior (Aschehoug et al., 2016; Goldberg, 1990, 1996; MacDougall & Turkington, 2004; Wang, Stieglitz, Zhou, & Cahill, 2010), leaving no clear path to identify the ultimate winner in competition. For example, species can be argued to win based on being better at suppressing the performance of other individuals (competitive effect), or alternatively, at tolerating competition from other individuals (competitive response; Goldberg, 1990, 1996). Following on from this idea is the suggestion that quantifying competitive ability requires a pluralistic approach (Aschehoug et al., 2016)—a notion amplified by the many metrics of competitive ability that have been proposed and used over at least the last five decades (Weigelt & Jolliffe, 2003). Finally, suggestions for improving empirical approaches for studying competition reinforce the idea that existing methods are inadequate (Trinder et al., 2013), and ecologists instead require even more complicated and labour-intensive methods, which remain largely unused (Hart & Marshall, 2013; Inouye, 2001; Law & Watkinson, 1987).

Despite the weight of these concerns, and the large amount of effort already expended on improving studies of competition, we believe that progress is possible by taking a different approach. First and foremost, what has been missing from previous reviews, critiques and the empirical work itself, is a precise, quantitative definition of competitive ability that is known to determine the long-term winner and loser in competition under the conditions in which competitive ability is measured. Fortunately, recent developments in coexistence theory make an unambiguous definition possible. With competitive ability precisely defined, it is then possible to sort through the many prior recommendations on how to measure competition to identify the minimal requirements necessary to empirically quantify competitive ability.

This paper is intended as a guide for empirical ecologists who wish to translate the results of empirical studies of competition into predictions of long-term competitive outcomes. Our primary goal is to present a quantitative definition of competitive ability that is theoretically justified and on this basis describe the minimal requirements for quantifying competitive ability in empirical studies. In addition to addressing this primary goal, we describe the implications of the quantitative definition for our general understanding of the determinants of competitive dominance, and expand our discussion

to advocate a general approach to quantifying competitive ability in more complex scenarios.

2 | COMPETITIVE ABILITY DEFINED

The outcome of competition at the species level over the long term depends on competition between individuals, which has consequences for population dynamics via growth and seed production. Competition between species thus plays out over generations and crucially, individual-level growth in response to competition in a single year does not translate simply to long-term competitive outcomes. Therefore, the measurements required to determine species' competitive abilities can be identified by working backwards from the competitive population dynamics. This necessarily requires a model of competitive population dynamics. To illustrate, we use a particular model, but our approach and conclusions are general: across a range of models capable of describing dynamics of competing species in different systems in both discrete and continuous time, the same determinants of competitive ability emerge (Appendix S1; Chesson, 2012). Here, we focus on discrete-time models as they tend to better match the constraints of measuring empirical systems, and can also be converted to continuous time analogues if appropriate.

We focus on the Beverton–Holt competition model, which describes annual plant competitive population dynamics in the field (Beverton & Holt, 1957; Firbank & Watkinson, 1985; Leslie & Gower, 1958; Levine & Hille Ris Lambers, 2009; Watkinson, 1981):

$$N_{i,t+1} = N_{i,t} \frac{\lambda_i}{1 + \alpha_{ii}N_{i,t} + \alpha_{ij}N_{j,t}} \quad (1)$$

$N_{i,t}$ is the density of individuals of species i at time t , λ_i is the per-individual fecundity in the absence of competitors (which is the discrete time equivalent of the intrinsic rate of increase; Leslie & Gower, 1958), and the competition coefficients α_{ii} and α_{ij} describe the per capita effects of conspecific and heterospecific competitors on reproduction respectively. The two-species model includes a second equation with subscripts reversed to describe the population dynamics of species j . The same model can also be used to describe change in biomass, $N_{i,t}$, from 1 year to the next in a perennial system by defining λ_i to be the multiplicative growth rate of biomass in the absence of competitors, and where the interaction coefficients describe reductions in biomass production by conspecific and heterospecific biomass. This model, and models of competitive population dynamics in general, can also be extended to account for the influence of other demographic processes such as germination and seed survival (Appendix S1).

On the basis of this model, the competitive ability of species i can be obtained following methods developed by Chesson (Appendix S1; Chesson, 2000, 2012; Godoy & Levine, 2014), yielding the following expression:

$$\frac{\lambda_i - 1}{\sqrt{\alpha_{ij}\alpha_{ii}}} \quad (2)$$

The numerator of expression 2 is species i 's growth rate in the absence of competitors. The denominator is the geometric mean of the interaction coefficients when species i is the recipient of competition (note order of subscripts on the competition coefficients). The denominator can be understood as species i 's average sensitivity to competition, or, in other words, the ability of species i to tolerate competition by maintaining offspring production under crowded conditions. A second expression with subscripts reversed quantifies the competitive ability of species j .

The species with the highest value of expression 2 is the competitive dominant, meaning that if we ignore niche differences, it will competitively exclude the other species (Appendix S1, Figure SA1). Thus, expression 2 quantifies competitive ability in a theoretically justified manner based on the outcome of competitive population dynamics. The more the species differ in the value of expression 2, the faster the inferior species will be competitively excluded. The definition also applies when there are priority effects (i.e. positive frequency dependence, as might occur with allelopathic interactions, for example), or when species are niche differentiated (i.e. negative frequency dependence, Mordecai, 2011). If the species are sufficiently niche differentiated to allow coexistence, the species with greater competitive ability will typically be numerically dominant (unlikely cases where the inferior competitor nonetheless has the greater single-species carrying capacity can generate exceptions to this rule, Appendix S1). The main message from this expression is that competitive dominance is conferred by the combined ability of species to have high growth in the absence of competition (λ_i , the numerator of the expression), and to be able to tolerate competition from both conspecific and heterospecific neighbours ($\sqrt{\alpha_{ij}\alpha_{ji}}$, the denominator of the expression). Importantly, this message holds true across a range of competition models (for which we provide equivalent expressions in Appendix S1), which emphasizes that the determinants of competitive ability in phenomenological models are quite general.

3 | UNDERSTANDING THE DETERMINANTS OF COMPETITIVE ABILITY

There are three important implications of this analysis for our understanding of competitive ability. First, suggestions that growth in the absence of competitors is not part of competitive ability (e.g. Shipley, 1993) are not supported by theory. In simple terms, growth in the absence of competitors sets the baseline on which the effects of competition act, such that all else being equal the more inherently productive species will win (Appendix S1, Figure SA1). This is also true for competition described by Lotka–Volterra equations in which the competition coefficients are scaled by growth in the absence of competitors (Saavedra et al., 2017). An important implication of this result is that the common approach of comparing competitive ability by controlling for performance in the absence of competitors will draw incorrect conclusions. This is because such an approach forces equal values of λ on both species, even though differences in

λ may ultimately drive differences in competitive ability as shown by expression 2.

Second, comparing the value of expression 2 for each species indicates that differences between species in their sensitivity to competition, not differences in their competitive effects, determine competitive dominance (for a detailed, quantitative explanation, see Box 1). Note that for each species, the denominator of expression 2 includes the interaction coefficients that describe the per capita effects of species i and j on the focal species; the focal species is the recipient of competition with respect to both coefficients (i.e. with respect to both species). Thus, differences between species in competitive ability (differences in the value of expression 2 between species) are determined by whether species have smaller or larger competition coefficients when they are the recipient of competition—that is, differences between species in their *response* to both species i and j (Box 1). Importantly, differences between species in their per capita competitive effects, on which relative yield metrics of competitive ability are based, are completely irrelevant to a species' competitive ability (Box 1; see also Supplementary Information in Levine, Bascompte, Adler, & Allesina, 2017). If species i , for example, exerts large competitive effects (making competition coefficients large when species i imposes competition), this effect falls equally on the performance of individuals of both species i and j . Because effects fall equally, this does not favour one species over the other, and so cannot contribute to competitive ability (Box 1). Note that any species-specific competitive effects contribute to niche differences (or priority effects) (Chesson, 2000), not to the ability of one species to exclude another.

How can the species whose individuals can merely tolerate high densities of competitors eventually win in competition? The answer lies in recognizing that populations composed of individuals that are insensitive to competition will simply continue to increase in numbers to the point that the more sensitive species has negative growth. In other words, insensitivity to competition at the individual level leads to a large population size (i.e. large N_i), which increases the total amount of competition that both species experience, but is more damaging to the more sensitive species. This ultimately leads to exclusion of the species that is more sensitive to competition. So while it is true that species can differ in their competitive effect and competitive response (Goldberg, 1990, 1996; Goldberg & Barton, 1992; Goldberg & Landa, 1991), in contrast to commonly held views, only individuals' responses to competition (if measured correctly, see below) confer the ability of a species to win or lose in competition in the long term. Only in systems where greater density does not translate into greater competitive effects on an individual (e.g. contest competition for sites) would this measure of competitive dominance lose relevance.

Finally, expression 2 also makes it clear that the performance of individuals in response to intraspecific competition (α_{ii}) actually contributes to interspecific competitive ability. Following the argument in the previous paragraph, this is because it is only through tolerance of both heterospecific and conspecific competitors that a species can attain sufficiently high densities to exclude their heterospecific

Box 1 Decomposing competition coefficients into differences between species in their competitive effect and response.

Beginning with seminal papers by Goldberg and colleagues (Goldberg, 1990, 1996), ecologists have long appreciated that competitors differ in their response to competition and in their ability to exert competitive effects. However, in the absence of quantitative theory, how species' competitive effects and responses relate to competitive dominance in a population dynamics context is unclear. In the main text, we argue that species differences in their response to competition, not their competitive effects, determine competitive dominance, a point we formalize in this Box.

Following the competition model given by Equation 1, the reduction in species i 's fecundity caused by each individual of species j is quantified with a competition coefficient α_{ij} . The value of this competition coefficient reflects both species i 's response to competition and species j 's ability to exert competitive effects (on a per capita basis). To identify the role of competitive effects and responses in determining competitive ability, we partition each interaction coefficient into these two components:

$$\alpha_{ij} = r_i e_j \quad (3)$$

where r_i is the generic response of an individual of species i to any heterospecific or conspecific individual, and e_j is the generic per capita competitive effect of an individual of species j on any heterospecific or conspecific individual (Godoy et al., 2014). This partitioning does not permit species-specific components of the interaction that would contribute to niche differences or priority effects, but our conclusions also hold when these processes operate (as in Equation 2).

Following Equation 3, species that have large competitive effects will be associated with large interaction coefficients when they exert competition (i.e. when they are represented by the second of the two subscripts on the competition coefficients). Meanwhile, species that are highly responsive to competition will be associated with large competition coefficients when they are the recipients of competition (i.e. when they are represented by the first of the two subscripts on the competition coefficients). For example, the following set of competition coefficients were created by assuming species j has four times the competitive effect as species i ($e_i = 0.2$, $e_j = 0.8$), and species i is one half as responsive to competition as species j ($r_i = 0.25$, $r_j = 0.5$):

$$\begin{bmatrix} \alpha_{ii} & \alpha_{ji} \\ \alpha_{ij} & \alpha_{jj} \end{bmatrix} = \begin{bmatrix} 0.005 & 0.1 \\ 0.2 & 0.4 \end{bmatrix}$$

Note that the ratio of the geometric means of the values within columns reveals the ratio of competitive responses, while the ratio of the geometric means of the values within rows reveals the ratio of competitive effects. From this set of interaction coefficients, we would conclude that species i is less responsive (i.e. less sensitive) to competition while species j exerts greater competitive effects. This interpretation and terminology is consistent with Goldberg and Landa (1991). It should also be clear that differences between species in their competitive effects or competitive responses will cause correlations between interaction coefficients, because the values of r and e for each species contribute to multiple competition coefficients.

In the main text of the paper, we interpret the expression for competitive ability (Equation 2) to mean that only species' fecundity in the absence of competitors and *response* to competition determine competitive dominance; there is no role for the species' competitive effects. This can be seen by expressing the competitive imbalance as the ratio between the two species' competitive abilities as given by Equation 2 (following the average fitness difference of Chesson, 2000) and replacing the competition coefficients with the product of competitive effects and responses as in Equation 3:

$$\frac{\lambda_i - 1}{\sqrt{r_i e_i r_i e_i}} / \frac{\lambda_j - 1}{\sqrt{r_j e_j r_j e_j}} \quad (4)$$

The competitive imbalance then simplifies to the following expression:

$$\frac{\lambda_i - 1}{r_i} / \frac{\lambda_j - 1}{r_j} \quad (5)$$

with an obvious role for differences between species in their competitive response, while the differences between species in their competitive effects have cancelled out, making it clear that competitive effects have no role in determining competitive dominance.

competitors (Appendix S1, Figure SA1). Consequently, measurements of the strength of intraspecific competition as well as interspecific competition are necessary to quantify interspecific competitive ability.

The logic of our phenomenological treatment of competition parallels that from mechanistic models of competition, exemplified by Tilman's R^* theory (Chesson, 2000; Tilman, 1980, 1982). Here, the dominant competitor is not the species whose individuals consume

the greatest quantity of the resource, which would correspond to a large per capita competitive effect as in Box 1. Rather, it is the species whose individuals can tolerate the lowest level of the limiting resource and still have positive growth.

4 | HOW TO EMPIRICALLY QUANTIFY COMPETITIVE ABILITY

The quantitative definition of competitive ability allows us to identify the minimal experimental design required to quantify competitive ability empirically. Importantly, and as we discuss further below, the requirements for quantifying competitive ability are not as onerous as recent recommendations for studies of competition might suggest (Gibson et al., 1999; Inouye, 2001). It is because we have generated a precise, quantitative definition of competitive ability, something not presented in previous critiques, that we are able to sort through the many recommendations for studying competition, to identify the key features required of empirical studies.

Empirically quantifying competitive ability requires estimating the parameters in expression 2 for each competing species (Figure 1). To do so, one simply needs to measure the growth of a separate, single individual of a focal species in the absence of competitors, in the presence of conspecific competitors, and in the presence of heterospecific competitors. A minimal experimental design would compete two individuals in each of the competition treatments, with replication as appropriate (Figure 1, minimal design), to allow one to estimate the intra- and interspecific interaction coefficients from a regression model (Figure 1b). However, growing focal

individuals with a range of competitor densities is preferable as it enables one to discriminate between different functional forms of competition to identify the most appropriate model for the system under study (e.g. Beverton-Holt vs. Ricker, etc., Appendix S1; Hart & Marshall, 2013; Levine & Hille Ris Lambers, 2009). In general, the duration of the experiment should be long enough to capture the hypothesized mechanisms by which individuals affect other individuals. Conclusions about competitive ability will then apply under the conditions in which competitive ability is measured.

Note that the competition coefficients quantify the rate of decline in offspring production as the density of competitors increases (Figure 1b). Therefore, it is not sufficient to simply compare performance in the presence and absence of competitors as is commonly done in studies of competition (e.g. using log ratios; Weigel & Jolliffe, 2003), but it is instead necessary to fit a competition model (i.e. a linear or nonlinear regression model) to estimate these coefficients. Importantly, these phenomenological competition coefficients are agnostic with respect to the mechanism of competition, and so have the advantage of integrating the effects of all (potentially unknown) mechanisms operating at the time of the experiment into a single value. Repeating the design such that both species are treated as the focal allows the comparison of the value of expression 2 between competitors, which then allows the dominant competitor to be identified, and strength of the competitive imbalance to be quantified.

It is worth briefly placing the design we have described (Figure 1) in the context of the many existing critiques of, and recommendations for, empirical studies of competition. The experiment we describe is an extension of what is sometimes called a partial-additive or a target-neighbour design (Gibson et al., 1999). In the version we

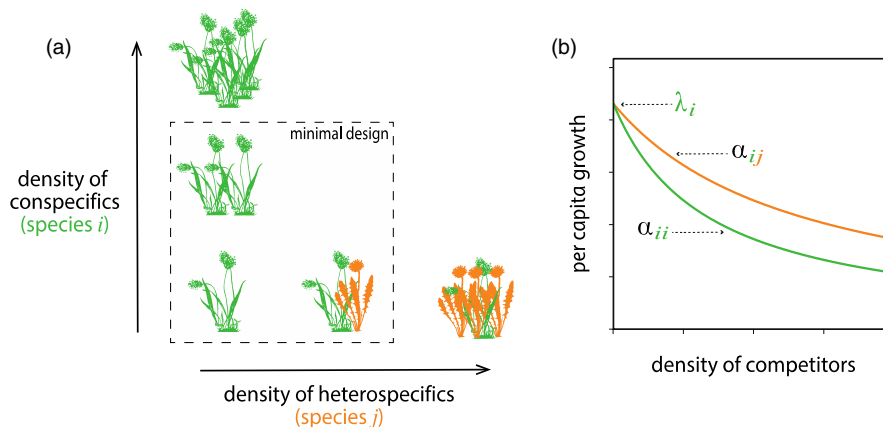


FIGURE 1 (a) Experimental design for quantifying competitive ability, which needs to be repeated for each focal species. Each species must be grown alone (to estimate λ_i), and with conspecific and heterospecific competitors (to estimate α_{ii} and α_{ij} respectively). While competition coefficients can, in principle, be estimated by growing single individuals against each other (minimal design), a more powerful approach would grow focal individuals against gradients of conspecific and heterospecific densities (Freckleton & Watkinson, 2000). (b) Data from the experiment is used to estimate the parameters that determine competitive ability, where λ_i is growth in the absence of competitors, and α_{ii} and α_{ij} quantify the rate of decline of per capita growth with increasing density of conspecific and heterospecific competitors respectively. Different competition models use different functional forms for describing the rate of decline in performance with increasing density of competitors, but the basic determinants of competitive ability are unchanged (Appendix S1). It is worth noting that many studies of competition quantify the absolute decrease in per capita growth in the presence of competitors (i.e. a decrease in performance along the y-axis), but not the rate of decline as is required to quantify competitive ability. Also, many studies control for differences between species in λ (i.e. the intercept), which also precludes identifying the winner in competition

describe the density of the focal individuals is kept low enough to preclude competition between them, and the response to increasing densities of *both* conspecific and heterospecific competitors is assessed. This design has been used in several studies of competition (e.g. Goldberg & Landa, 1991; Hartnett, Hetrick, Wilson, & Gibson, 1993), but has very rarely been implemented or analysed in a way that allows estimates of competitive ability (but see Godoy, Kraft, & Levine, 2014). For example, while the response variable required to quantify competitive ability is simply the multiplicative growth of a focal individual (e.g. $\text{biomass}_{t+1}/\text{biomass}_t$, Figure 1), this response variable is rarely measured. Instead, in an effort to control for differences between species in maximum growth rates (i.e. differences in λ_i) ecologists using this design have tended to standardize growth rates or standardize the response to competition across species (e.g. MacDougall & Turkington, 2004; Shipley, 1993) in ways that make it difficult to estimate λ_i and α_{ij} (see also supplementary information in Levine et al., 2017). When the determinants of the winner in competition are clearly identified as in expression 2, it becomes clear that such standardization is counterproductive to identifying the winner in competition.

In our experience, there is an increasing perception among researchers that overcoming the real and perceived limitations of existing designs for studying competition requires more complicated and labour-intensive response surface experimental designs, especially if one aims to predict the outcome of competition (Gibson et al., 1999; Goldberg & Scheiner, 2001; Inouye, 2001; Law & Watkinson, 1987). To this end, we have implemented these designs in our own studies of competition (Hart, Burgin, & Marshall, 2012; Hart & Marshall, 2013). However, the definition of competitive ability (expression 2) makes it clear that such designs are often overkill for quantifying competitive outcomes. Both the streamlined experimental design we describe (Figure 1) and response surface designs allow one to identify an appropriate competition model for the system being studied, and to estimate the value of each of the parameters in expression 2. The additional power of a response surface design is that it allows one to fit a model that includes higher-order interactions that account for frequency dependence in the strength of competition between species (Freckleton & Watkinson, 2000). In our assessment, ecologists wishing to simply quantify competitive ability need not invest the considerable extra effort in doing a response surface design, unless they are specifically concerned about higher order interactions.

5 | CAVEATS AND A GENERAL APPROACH FOR QUANTIFYING COMPETITIVE ABILITY

Our contribution describes methods for predicting the winner in competition in the presence and absence of niche differences (but see Appendix S1). However, predicting the full population dynamic outcome of competition requires not only identifying which species is competitively dominant but also quantifying niche differences between species. Fortunately, the same general approach of combining

experimental data with models of competitive population dynamics can also be used to quantify niche differences between species, enabling one to predict the full population dynamic outcome of the interaction (Godoy & Levine, 2014).

It is important to note that even with the approach we propose, a strong set of assumptions are involved in extrapolating from short-term and/or small-scale experiments to outcomes of competition over the long term. One important difficulty is ensuring that the fitness components (e.g. biomass, fecundity, survival) measured on individuals over relatively short periods of time capture the individual-level experience of competition over a lifetime (Inouye, 1999). This long-standing challenge is most acute for long-lived species, and also for species with cryptic life-history stages (Goldberg et al., 1999; McPeck & Peckarsky, 1998). This problem can be overcome by renewed emphasis on defining the relationships between short-term performance metrics and the fitness of individuals over their lifetime, and by parameterizing population models that incorporate each of the separate demographic rates that may respond to competition and contribute to population growth (e.g. Chu & Adler, 2015). Our approach also does not overcome other well-documented difficulties in studying competition, such as the influence of pre-existing size differences between individuals on the results of competition experiments (Gibson et al., 1999), and so these considerations still need to be accounted for in both the design and interpretation of competition experiments.

The approach we advocate in this paper is based on a phenomenological assessment of competitive ability, which has the advantage of being able to capture multiple potentially unknown mechanisms of competition. An alternative approach for predicting winners and losers in competition is to develop an understanding of the underlying mechanisms that drive competitive dominance, such as resource competition, an important goal that remains challenging to achieve (Miller et al., 2005; Trinder et al., 2013).

Our assessment assumes that competition occurs in a constant environment, or at least that the predictions for competitive dominance will hold as long as the biotic and abiotic conditions under which competition was measured apply across the spatial and temporal scales of interest. While restrictive, this reflects the common assumption of the vast majority of empirical efforts at quantifying competitive ability (Aschehoug et al., 2016; Connell, 1983; Goldberg et al., 1999; Gurevitch et al., 1992; Schoener, 1983; Weigelt & Jolliffe, 2003), which are often done under a specific set of conditions in the laboratory or field. Given this prevailing assumption, ecologists' difficulties in identifying winners and losers in competition have largely occurred in the absence of consideration of the additional complexity generated by spatially and/or temporally variable environments.

However, although our definition of competitive ability is specific to spatially and temporally homogeneous systems, the general approach we describe is more powerful and can be applied to competition occurring in variable environments. As we have shown, the key steps are to develop a model of competitive population dynamics for the system under study, identify the parameters that confer the

ability to win in competition from the model, and then empirically estimate those parameters in the laboratory or field. Importantly, models of competitive population dynamics can be defined in a way that encompass the processes most relevant to understanding competition between a particular set of focal species, whether that be, for example, competition for space at the germination/establishment phase, or competition across spatially or temporally varying environments (see Bolker, 2008; Otto & Day, 2007, for a general introduction to model specification and fitting). It may not always be straightforward to identify competitive winners in more complicated models, and this remains a challenge for future work (Ellner, Snyder, & Adler, 2016). Nonetheless, the general approach we describe allows one to overcome one of the major impediments to predicting competitive outcomes from empirical data—how to translate measurements on individuals over the short term, into predictions for competing populations over the long term.

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AUTHORS' CONTRIBUTIONS

S.P.H. and J.M.L. conceived of and wrote the paper, with input from R.P.F. All authors contributed substantially to revisions.

DATA ACCESSIBILITY

This paper does not use original data.

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