

## Interpreting phenotypic variation in plants

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**Plant ecologists and evolutionary biologists frequently examine patterns of phenotypic variation across variable environments or genetic identities. Too often, we ignore the fact that most phenotypic traits change throughout growth and development of individual plants, and that rates of growth and development are highly variable. Plants growing in different environments are likely to grow at different rates, and will be of different sizes and stages of development at a particular age. When we compare plants as a function of plant size or developmental stage, as well as a function of age, we broaden our understanding of phenotypic variation between plants.**

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Environmentally-induced phenotypic variation (phenotypic plasticity) in plants is often considered to be a functional response that maximizes fitness in variable environments. The assessment of variability in plant morphology (e.g. biomass partitioning) and physiology (e.g. nutrient use efficiency) is critical in testing ecological and evolutionary models that make predictions about the functional or adaptive nature of phenotypic plasticity (e.g. plant strategy theory<sup>1</sup>, the resource-ratio hypothesis<sup>2</sup>; optimal partitioning models<sup>3</sup>; and evolutionary interpretations of phenotypic plasticity<sup>4</sup>). For example, differences in the partitioning of biomass to leaves between plants of the same species grown in high versus low light has been cited as evidence for optimal partitioning<sup>5</sup>.

Differences among species in the amount of morphological plasticity exhibited in response to varying resource availability have been used to support the notion that plasticity may be an adaptation to patterns of resource availability in the habitat in which a particular species evolved<sup>6</sup>. The comparisons among indi-

vidual plants on which these conclusions are based have generally been conducted at common points in time or at common plant ages.

### Assessing phenotypic variation: what we often miss

G.C. Evans<sup>7</sup> argued over 20 years ago that comparing plant traits as a function of plant age may lead to serious complications in interpreting data. He noted that many phenotypic traits of plants change dramatically over the course of plant growth and development – a phenomenon he referred to as ‘ontogenetic drift’. For example, total biomass in different plant parts, such as leaves, stem and roots, clearly increases in concert with overall growth; additionally, the proportional distribution of biomass among these parts is rarely constant for extended periods<sup>7</sup>. In some herbaceous plants, the ratio of root to shoot biomass is initially very high because of early root growth and establishment in the soil, but then drops rapidly over the course of the first few weeks of growth<sup>8</sup>. Physiological traits can also differ markedly between individuals of different sizes, or at different stages of ontogeny<sup>9,10</sup>.

The absence of appreciable change during ontogeny is probably the exception rather than the rule for traits related to resource acquisition, allocation and partitioning<sup>7,11</sup>. Furthermore, plants growing in different environments often grow at different rates, and thus will be of different sizes and developmental stages at a given age. Thus, plants of a particular age can frequently be ontogenetically dissimilar. The interpretation of variation in many phenotypic traits will, therefore, depend on whether comparisons are made as a function of plant age, size or developmental stage (Box 1). For example, Evans strongly suggested that environmentally-induced changes in traits representing any aspect of plant biomass partitioning need to be examined as a function of plant size in order to draw any conclusions as to the functional significance of the phenotypic variation.

### Functional adjustment or ontogenetic drift?

Although Evans warned that functional interpretations of phenotypic variation due to genotype or environment can be compromised when comparisons are made at a single common age, very few of the data used to support models of plant strategy or optimal partitioning have been interpreted in a manner congruent

with Evans’ suggestions. However, these issues have been considered in detail by many researchers examining plant reproductive effort<sup>12,13</sup> and morphological patterns in animals<sup>14</sup>. Misinterpretations of the functional role of phenotypic variation in physiological and vegetative characteristics of plants can arise when the relationships between phenotypic expression, plant development and growth rate are not considered. Box 1 shows four hypothetical scenarios that illustrate possible relationships among developmental patterns and growth rates, and the potential for contrasting interpretations of experimental results. Throughout, ‘treatment’ differences among plants refer to environmental, genetic or inter-specific causes of variation.

In the first example in Box 1, the pattern of change in phenotypic expression throughout growth and development is fixed, but since growth and developmental rates vary, phenotypic expression varies at any point in time. Thus, phenotypes differ when compared at a common time, but are identical when compared at a common size or developmental stage.

This example has tremendous bearing on studies testing optimal partitioning models<sup>3</sup> of plant growth. A great deal of support for these models has been garnered from studies in which the proportional allocation of biomass to leaves, shoots and/or roots was compared as a function of plant age<sup>15</sup>. For example, shade-grown plants often appear to invest a greater proportion of their resources into leaf area than do those grown in high-light (e.g. have a higher leaf area ratio<sup>7,16,17</sup>). However, allocation patterns change throughout ontogeny, and shade-grown plants usually have slower growth rates than those in high-light. Consequently, observed differences in leaf area ratio between low- and high-light plants are confounded with differences in growth rates<sup>7</sup>. Is increased leaf area ratio in low-light plants the result of functional adjustments as predicted by optimal partitioning models, or rather a consequence of slow growth rates and delayed development? If increases in the relative production of leaf area in low-light represents functional adjustments in allocation, as optimal partitioning models predict, then a plant grown under low light should have a greater leaf area ratio than a high-light plant when both plants are compared at the same size<sup>7</sup>.

When leaf area ratio has been compared among same-sized plants, the differences in allocation patterns due to light environment often disappear, even when the leaf area ratio varies as predicted by optimal partitioning models when comparisons are made at a common

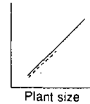
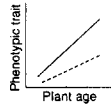
**Box 1. Same-age versus same-size (stage) comparisons of plant phenotypes**

Variable growth rate

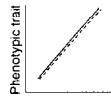
Same age comparison

Same size (stage) comparison

Variable phenotypic expression throughout growth and development

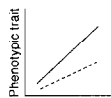


Fixed pattern of change in phenotypic expression throughout growth and development

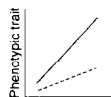


Variable growth rate

Variable phenotypic expression throughout growth and development



Variable pattern of change in phenotypic expression throughout growth and development



In this case, growth rates and phenotypic expression throughout growth and development are variable, but the pattern of change in phenotypic expression throughout growth and development is fixed. Phenotypes differ when compared at a common time, but are identical when compared at a common size or developmental stage. This situation is fairly common (Refs 17–25).

In these cases, growth rates, phenotypic expression throughout growth and development, and the pattern of change in phenotypic expression throughout growth and development, are all variable. Variability at both levels can result in any of three distinct scenarios. In the first scenario, phenotypes that do not differ at a common age may be found to differ as a function of plant size or developmental stage<sup>7,20</sup>. In the second case, comparisons at a common time reveal phenotypic differences, but comparisons at a common size or developmental stage reveal that variation in the trait actually occurs in the opposite direction than would be inferred by comparisons at a common time<sup>7</sup>. In the third scenario, qualitative interpretations do not vary as a function of the axis used for comparison, but quantitative interpretations of phenotypic expression can be markedly different for comparisons at a common plant age versus comparisons at a common plant size or developmental stage<sup>17,18,27,28</sup>.

Whenever plant growth rates are variable (as a function of environmental conditions or genetic identity) and phenotypic expression changes throughout growth and development, comparisons of phenotypes at a common plant age may differ from comparisons of phenotypes as a function of plant size or developmental stage. Each graph above compares the effects of two environments or two genotypes on the expression of a phenotypic trait. The first graph in each pair represents common age comparisons, and the second graph represents common size (or developmental stage) comparisons; the treatment or genotype represented by the solid line grows faster than that represented by the dashed line. Comparisons at a common age will be identical to those at a common size (stage) whenever growth rates and/or phenotypic expression throughout development are constant. Since these conditions are rarely met, it is critical to consider which axis is more appropriate for a given question (see Box 2).

plant age<sup>17–20</sup>. Furthermore, other commonly measured traits such as root:shoot ratio (Refs 21–24) and %N (an estimate of nitrogen use efficiency<sup>25</sup>) also exhibit marked size-dependent changes during growth. This does not mean that all 'treatment'-induced differences in a trait that may be revealed by comparisons at a common plant age are an illusion or irrelevant. For example, differences in leaf area ratios at a given plant age may determine the outcome of competitive interactions among plants<sup>26</sup>, but these differences may not result from 'treatment'-induced changes in the patterns of leaf area production. Rather, they can arise from developmental or allometric relationships that result in plants of different sizes having different leaf area ratios.

*What if there are changes in both growth rate and the pattern of change in phenotypic expression during development?*

The last three possible scenarios in Box 1 depict situations where treatments alter both growth rates and the pattern of change of the phenotypic trait throughout growth and development. In the first of these, shifts in the relationship between a particular trait and plant size are masked by compensatory changes in growth rate such that the trait does not vary among plants of the same age. However, 'treatment'-induced differences in the trait become evident as a function of plant size. For example, Rice and Bazzaz<sup>20</sup> showed that the traits of height and leaf number of an annual plant,

*Abutilon theophrasti*, did not vary as a function of differing light treatments for plants of the same age. However, they found that low-light plants had considerably greater height and leaf number, relative to plant weight, than high-light plants. Thus, they point out that if they had not compared at common plant weights, they might have incorrectly concluded that light treatments did not affect the allocation of resources to stem elongation and leaf production, whereas the comparison at a common weight revealed a very clear effect. Similar cases have been reported by Evans<sup>7</sup> with regard to stem weight ratio and total leaf weight for *Impatiens parviflora* grown in differing light regimes.

In the second example, an even more disturbing scenario is depicted. Here, the patterns of variation in growth rate and in the size-dependence of a trait result in qualitatively different patterns for comparisons at a common age versus a common size. Thus, a trait exhibits a greater value in one treatment, when compared at a common size, but a lower value when compared at any point in time. For example, Evans<sup>7</sup> showed that changes in leaf weight as a function of certain light environments in *Impatiens parviflora* often followed this pattern.

In the last example, comparisons of a trait at a common age or size will provide similar qualitative results, but will differ in the magnitude of response. Thus, plants in a slow-growing treatment may have a lower value of a trait at a particu-

lar age, but the difference between treatments is greatly reduced when they are compared at a common plant size. For example, Poorter and Pothmann<sup>27</sup> showed that the overall qualitative interpretations of interspecific differences in a number of traits such as specific leaf area or specific growth rate were not affected by the choice of plant age or plant size as the basis for comparison. However, the quantitative magnitude of differences among species did change depending upon the choice of comparison. This result has been echoed in other studies on environmental effects on specific leaf area<sup>18</sup>, leaf weight allocation<sup>17</sup>, and on the production of leaf area (Ref. 28; in this study, a developmental index was substituted for biomass). Thus, quantitative interpretations of results will be affected by whether comparisons are made on the basis of age or size even though qualitative ones will not. In fact, it is only when a trait is known to show no ontogenetic drift or when growth and developmental rates are invariant that one may be certain that the interpretation of a 'treatment'-induced change in a trait will not depend on whether that trait was compared as a function of age or size.

**Experimental design and data analysis**

*Allocate replicates over time*

Currently, most studies of phenotypic variation are designed to compare phenotypes at a single or few point(s) in time, usually including a large end-of-season

harvest. Incorporating variation in plant growth and development in such studies will entail a shift in experimental design. To examine explicitly the pattern of change in phenotypic expression over growth and development, we must collect data more often, perhaps using fewer replicates. For example, if a researcher has enough material for 20 replicates of each treatment, one must decide whether to harvest all 20 replicates at the end of the season, to harvest one plant every week for 20 weeks, or some compromise between the two. More frequent harvests facilitate the comparison of treatments throughout growth and development as well as through time (i.e. throughout the season), thus allowing one to distinguish phenotypic plasticity as a result of plasticity in growth rate versus plasticity in how the phenotypic trait changes throughout plant development<sup>29</sup>.

#### Choosing a standard of comparison

As in any research, the choice of methodology reflects the goals of a study (see Box 2). Comparisons at a common age are appropriate for real time processes such as herbivory, competition, community structure and natural selection. For example, the outcome of the competitive interactions between two individual plants may be a function of leaf area display at a given time even if the pattern of leaf area display changes drastically during plant development<sup>30</sup>. Comparisons at a common size are important in studies of allocation and functional adjustments in biomass partitioning and resource acquisition. Other developmental indices, such as node number, plastochron index<sup>28</sup>, growth phase<sup>11</sup> (juvenile, reproductive), height and diameter of plants<sup>31</sup>, may be more appropriate depending upon the question. In all of these cases, these methods allow one to explicitly assess the degree to which patterns of variation in a trait may be influenced by plant development. Regardless of which standard of comparison is deemed appropriate for any particular question, explicit examination of patterns of change in phenotypic traits during growth and development, in contrast to comparisons at just one point, whether at a particular age or size, enhances the functional interpretation of phenotypic variation.

#### Statistical tools

The choice of a standard of comparison will determine what statistical tools are most appropriate. For example, if time is the axis against which phenotypic traits are compared, type 1 regression techniques are appropriate, since we can assume that real time is a

### Box 2. Some alternative standards for comparing phenotypic traits

#### Single phenotypic traits

Individual phenotypic traits may vary in relation to the age, size or developmental stage of a plant. As a result, the interpretation of environmental or genetic variation may differ depending upon whether comparisons are conducted among individuals of the same age, size or stage. The choice of one of these standards depends critically upon the question addressed in the study, and the three are briefly compared below:

Standard	Uses
Chronological	Comparisons at a common point in time are important in relation to 'real time' processes, such as plant-plant and plant-animal interactions, and for the analysis of seasonal patterns, such as reproductive output in relation to the length of the growing season. Examples include leaf nitrogen levels in herbivory studies, flowering loads and pollinator activity, and total fitness in annual plants susceptible to end-of-season frosts.
Growth	For traits that exhibit size-dependent changes during growth, especially those directly related to biomass accumulation, comparisons at a common size (e.g. total plant biomass) are important. Examples include proportional biomass allocation (see also below), whole plant nitrogen uptake and leaf area production (see Fig. 1c). Size-dependent comparisons are particularly relevant for tests of economic models of optimal biomass allocation.
Developmental	Traits that vary during development, particularly if they are related to nodal development or plant developmental stage, may be compared at a common stage (e.g. leaf plastochron number, rosette versus bolting stage) to separate the effects of the rate and ontogenetic pattern of development on phenotypic expression. Examples include reproductive output in relation to life history stage and aspects of leaf development.

#### Two (or more) functionally related phenotypic traits

Many analyses of phenotypic responses to environmental effects involve examining the relative changes in two (or more) phenotypic characters, such as root:shoot and reproductive:vegetative biomass ratios, or height/diameter or leaf nitrogen content/photosynthesis relationships. Interpretations of functional relationships between two or more traits depend critically on the amount of ontogenetic drift exhibited by each individual trait (see Fig. 1d). Explicit analysis of these allometric relationships provides a direct method of interpreting both the changes occurring in each trait independently, and in relation to each other.

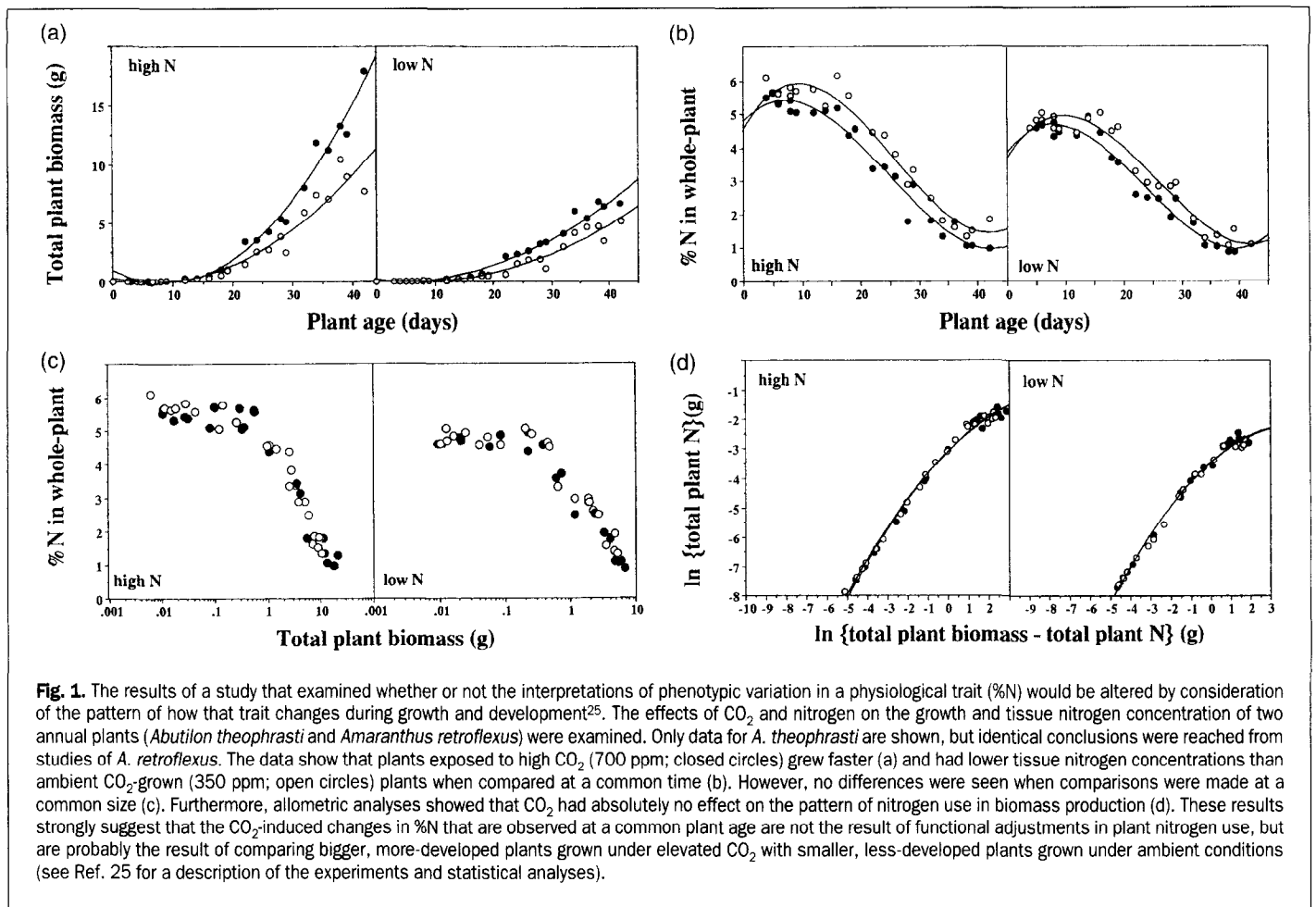
truly independent variable (i.e. will not be altered because of phenotypic expression) and can be measured without error. If the relationship is linear, type 1 linear regression techniques (e.g. analysis of covariance, repeated measures analysis of covariance, comparisons of fitted regression parameters) will suffice. If the relationship is nonlinear, type 1 nonlinear regressions may be compared using methods described by Mead and Curnow<sup>33</sup> and Potvin *et al.*<sup>34</sup>.

If plant growth or developmental characters are chosen as the standard of comparison, type 2 regression techniques are appropriate, as neither variable can be considered truly independent and measured without error. Type 2 linear regression techniques (modifications of type 1 linear regression techniques listed above) can be found in many statistical packages. However, many allometric relationships in plants are nonlinear (i.e. indicative of complex allometry rather than simple allometry<sup>32</sup>), and thus preclude the use of type 2 linear regression techniques. In these instances, type 1 nonlinear regression techniques described above may be employed. In any case, data should be appropriately transformed to achieve normal distributions and homogeneous variances before using standard regression techniques.

#### An example: tissue nitrogen concentration and elevated CO<sub>2</sub>

Plants often respond to elevated atmospheric CO<sub>2</sub> levels with reduced tissue nitrogen concentrations relative to ambient CO<sub>2</sub>-grown plants when comparisons are made at a common plant age<sup>35</sup>. It has been assumed that this phenotypic pattern represents a functional adjustment that optimizes plant nutrient content when the relative availability of CO<sub>2</sub> and nitrogen is altered<sup>36</sup>. However, enriched atmospheric CO<sub>2</sub> accelerates the growth rates of many plant species<sup>37</sup>. Furthermore, plant nitrogen concentrations are often highest in seedlings and subsequently decrease during growth. Does the reduction in plant nitrogen content in elevated CO<sub>2</sub> conditions represent a functional adjustment in this phenotypic trait to changing resource availability, or is it a consequence of differences in nitrogen concentration between bigger, more developed plants and smaller, less developed plants?

This question was addressed in a study where two species of annual plants, *Abutilon theophrasti* and *Amaranthus retroflexus*, were grown with atmospheric CO<sub>2</sub> levels of 350  $\mu\text{mol}\cdot\text{mol}^{-1}$  or 700  $\mu\text{mol}\cdot\text{mol}^{-1}$  and with high or low fertilizer applications<sup>25</sup>. By harvesting individual plants every two days starting three days after



**Fig. 1.** The results of a study that examined whether or not the interpretations of phenotypic variation in a physiological trait (%N) would be altered by consideration of the pattern of how that trait changes during growth and development<sup>25</sup>. The effects of CO<sub>2</sub> and nitrogen on the growth and tissue nitrogen concentration of two annual plants (*Abutilon theophrasti* and *Amaranthus retroflexus*) were examined. Only data for *A. theophrasti* are shown, but identical conclusions were reached from studies of *A. retroflexus*. The data show that plants exposed to high CO<sub>2</sub> (700 ppm; closed circles) grew faster (a) and had lower tissue nitrogen concentrations than ambient CO<sub>2</sub>-grown (350 ppm; open circles) plants when compared at a common time (b). However, no differences were seen when comparisons were made at a common size (c). Furthermore, allometric analyses showed that CO<sub>2</sub> had absolutely no effect on the pattern of nitrogen use in biomass production (d). These results strongly suggest that the CO<sub>2</sub>-induced changes in %N that are observed at a common plant age are not the result of functional adjustments in plant nitrogen use, but are probably the result of comparing bigger, more-developed plants grown under elevated CO<sub>2</sub> with smaller, less-developed plants grown under ambient conditions (see Ref. 25 for a description of the experiments and statistical analyses).

germination, and using nonlinear regression techniques to analyse the data<sup>34</sup>, it was found that: (1) high CO<sub>2</sub>-grown plants had reduced nitrogen concentrations and increased biomass relative to ambient CO<sub>2</sub>-grown plants when compared at a common time (Fig. 1a and b); (2) tissue nitrogen concentrations did not vary as a function of CO<sub>2</sub> level when plants were compared at a common size (Fig. 1c); (3) the rate of biomass accumulation per rate of increase in plant nitrogen was unaffected by CO<sub>2</sub> availability (Fig. 1d). These results indicate that, at least for these plants, CO<sub>2</sub>-induced reductions in plant nitrogen concentration that were observed at a given point in time were probably not due to functional adjustments in plant nitrogen content, but were probably the result of accelerated plant growth in high-CO<sub>2</sub> conditions coupled with a fixed pattern of change in plant nitrogen content as plants get bigger. This example clearly demonstrates the importance of considering the relationship among phenotypic traits, plant growth and plant development when testing hypotheses about the functional role of phenotypic variation.

**Conclusion**

Understanding the degree and direction of phenotypic changes in plants in

response to resource availability is a major goal of plant ecology. Because plants keep their primary morphological surfaces on the outside (i.e. open organization), it has been assumed that they can easily branch and add new parts, whereas the closed organization of animals is thought to impose tight developmental constraints on morphological plasticity<sup>38</sup>. Thus, in contrast to animals<sup>14</sup>, the developmental constraints on phenotypic variation in plants have not been emphasized. Although strong interactions between phenotypic expression, development and growth rate in plants have been recognized for decades<sup>7</sup>, most functional and evolutionary hypotheses of plant response to resource limitations (e.g. optimal partitioning models, plant strategy theory) do not fully incorporate these relationships. A greater appreciation for the degree of phenotypic change during development can only lead to a fuller understanding of the functional significance of phenotypic variation in plants.

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coral-zooxanthellae associations in coral reefs, even though our understanding of the community impact of these associations is almost entirely speculative. Moreover, while the evolutionary role of positive interactions has become clear over the past decade (e.g. the evolution of eukaryotic cells, and flowering plants and their pollinators), positive interactions remain absent from general models of community dynamics and organization. How can an evolutionary play featuring strong positive interactions take place on an ecological stage where positive interactions are insignificant? Textbooks, however, strongly support our contention that positive interactions are currently largely overlooked by community ecologists. Whereas ecology textbooks earlier this century devoted as much attention to positive interactions as they did to competitive ones, modern textbooks hardly mention positive interactions in a community context<sup>10</sup>.

Recent theoretical (e.g. Refs 11,12) and empirical (e.g. Refs 13,14) work has suggested that positive indirect interactions and feedback mechanisms in food-webs may be common important forces in natural communities. In this article, however, we focus on the direct, non-trophic positive interactions that early ecologists suggested were critical aspects of community dynamics and organization<sup>1,2</sup>. Direct positive interactions occur when neighbors modify physical and/or biotic conditions and lead to positive effects. Although these positive interactions have been largely ignored by theoretical ecologists, evidence from a wide range of communities has begun to emerge during the past five to ten years indicating that direct positive interactions may be common, predictable and pervasive forces in natural communities and in physically harsh environments in particular. Here, we examine a small subsample of this evidence and re-evaluate the role of direct positive interactions in ecological communities.

### Do positive interactions affect recruitment?

Positive interactions during recruitment in desert plants were hypothesized thirty years ago, based on spatial patterns suggesting that neighbors buffer one another from potentially limiting physical stresses<sup>15,16</sup>. But ecologists have tended to view these interactions as idiosyncratic features of deserts rather than examples of general principle and, until recently, have not experimentally tested these ideas. Nurse-plant effects and positive density-dependent recruit survivorship, however, have recently been found in other harsh physical environments.

## Positive interactions in communities

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**Current concepts of the role of interspecific interactions in communities have been shaped by a profusion of experimental studies of interspecific competition over the past few decades. Evidence for the importance of positive interactions – facilitations – in community organization and dynamics has accrued to the point where it warrants formal inclusion into community ecology theory, as it has been in evolutionary biology.**

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Early ecological theory included both positive and negative interactions among species as important driving forces in the structure and organization of natural communities<sup>1,2</sup>. More recently, the role of competition in natural communities has received considerable attention (see Refs 3,4), while positive interactions have received little attention and are largely ignored in current models of community organization<sup>5,6</sup>. We broadly define positive interactions as all non-consumer interactions among two or more species that positively affect at least one of the

species involved; thus, we include facultative and obligatory facilitations and mutualisms. Whereas the ecology and evolutionary biology of mutualisms has attracted recent attention<sup>7</sup>, the role that they play in the structure and organization of natural communities has not.

The lack of recent attention paid to the role of positive interactions in communities is at least partly due to their uncritical acceptance by early ecologists and the preoccupation of contemporary community ecologists with competition (but see Ref. 8). In addition, much of the early development of ecology which highlighted positive interactions pre-dated the common use of field experiments in ecology and thus received little critical testing<sup>9</sup>. Moreover, fascination with competition has focused attention on communities where competition is conspicuous, potentially distracting ecologists from even recognizing positive interactions. Consequently, while facilitative and/or positive interactions are part of most working ecologists' conventional wisdom, and while anecdotal examples can be shown in most communities, the general importance of positive interactions to community diversity, structure and productivity is rarely acknowledged.

Modern ecology's view of positive interactions is particularly puzzling given the prominent role that they play in many communities and their importance as evolutionary forces. Few ecologists would deny the potential importance of mycorrhizal associations in forests and