

## LETTER

## Ecosystem engineers as selective agents: the effects of leaf litter on emergence time and early growth in *Impatiens capensis*

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### Abstract

By physically modifying the abiotic environment, ecosystem engineers can have dramatic effects on the distribution and abundance of species in a community. However, ecosystem engineering can also change the selective environment and evolutionary dynamics of affected species, although this remains relatively understudied. Here, we examine the potential for an ecosystem engineer – oak trees – to affect the evolutionary dynamics of the herbaceous, understory annual, *Impatiens capensis*, through leaf litter deposition. Using a quantitative genetic experimental approach, we found that: (i) the presence of leaf litter significantly affected a suite of germination, growth and phenological traits in *I. capensis*; (ii) *I. capensis* does not exhibit performance trade-offs across litter and bare soil environments in the form of negative across-environment genetic correlations; (iii) the presence or absence of leaf litter significantly alters the pattern of natural selection germination timing and hypocotyl length; and (iv) the frequency of leaf litter environments can dramatically change which combinations of hypocotyl length lead to highest mean fitness across both bare soil and leaf litter environments. More generally, our results demonstrate the potential for ecosystem engineers to alter both the ecological and the evolutionary dynamics of the species they affect.

### Keywords

Across-environment genetic correlations, ecological genetics, ecosystem engineering, fitness surfaces, genotypic selection, leaf litter, selection gradients, trade-offs.

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### INTRODUCTION

All organisms physically modify their abiotic environment throughout the course of their lives. Determining whether these physical modifications of the environment affect other species, and the magnitude and strength of these effects, has become a major goal for ecology. In a pair of highly influential papers, Jones *et al.* (1994, 1997a) argued that interactions between species mediated by physical modification of the environment not only had dramatic effects on species richness and abundances, but were relatively understudied in comparison with more conventional trophic interactions such as predation, competition and so on. In an attempt to place the tremendous diversity of phenomena that could be considered ‘physical modification of the environment’ into a general framework, Jones *et al.* (1997a)

proposed the concept of ecosystem engineering, and defined ecosystem engineers as ‘organisms that directly or indirectly control the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials’.

Although the concept of ecosystem engineering initially generated debate over whether or not intent was implied on the part of the engineering species (Jones *et al.* 1997b; Power 1997a,b), and whether or not the concept should be limited to keystone species (Reichman & Seabloom 2002a,b; Wilby 2002), the controversy associated with it appears to have subsided. In addition to organisms that are considered classic examples of engineers such as termites, prairie dogs, beavers, and gophers (Dangerfield *et al.* 1998; Alkon 1999; Ceballos *et al.* 1999; Reichman & Seabloom 2002b; Wright *et al.* 2002, 2003), engineering effects have

been described for mollusks (Gutierrez *et al.* 2003), fish (Flecker & Taylor 2004), insects (Feller 2002; Lill & Marquis 2003), polychaete worms (Schwindt *et al.* 2004), grasses (Perelman *et al.* 2003; Fogel *et al.* 2004), burrowing shrimp (Berkenbusch & Rowden 2003) and many other species (see Table 1 of Wright & Jones 2004). To date, many of these studies have evaluated the effects of ecosystem engineers with purely ecological criteria – often by evaluating species richness or abundances in engineered and non-engineered plots.

An under-appreciated and under-examined role of ecosystem engineers is their capacity to alter the evolutionary dynamics of the other species in the community that they affect (Jones *et al.* 1994, 1997a; Skelly & Freidenburg 2000). By altering habitat conditions and physically modifying the environment, ecosystem engineers have the potential to alter the evolutionary dynamics of the entire suite of species that they affect. Ecosystem engineers can affect the evolutionary dynamics of species that inhabit engineered and non-engineered sites in at least three different ways: (i) if those species face genetic trade-offs across engineered and non-engineered environments, either in fitness or in other ecologically important traits (Via & Lande 1985, 1987; Via 1987; van Tienderen 1991; Gomulkiewicz & Kirkpatrick 1992; Gavrilets & Scheiner 1993a,b); (ii) if the presence or absence of ecosystem engineers significantly alters the pattern of natural selection on those species (Stinchcombe & Rausher 2001); and (iii) if the relative frequency of engineered and non-engineered environments alters fitness surfaces for traits (cf. Gomulkiewicz & Kirkpatrick 1992). While these possibilities are well known for studies that examine the evolution of traits in heterogeneous environments and the evolution of phenotypic plasticity, to our knowledge they have not been applied to understand the microevolutionary response of a species to the actions of an ecosystem engineer. However, ecosystem engineers, by definition increase environmental heterogeneity (at least at a spatial scale including engineered and non-engineered patches: Jones *et al.* 1997a; Wright & Jones 2004) and thus likely drive trait evolution in species influenced by engineers. Ultimately, understanding the evolutionary consequences of ecosystem engineers will be necessary to fully evaluate their role in the dynamics of communities.

Here, we examine how an important ecosystem engineer of deciduous forests of the north-eastern USA, oak trees, and more specifically the leaf litter that they deposit, affect the microevolutionary dynamics of the understory herbaceous annual *Impatiens capensis*. The capacity of deciduous trees to act as an ecosystem engineer because of their leaf litter was recognized in the original papers articulating the ecosystem engineering concept (e.g. Table 1 of Jones *et al.* 1994; Fig. 1e of Jones *et al.* 1997a). In forested sites, trees

can function as an important ecosystem engineer, because the leaf litter that is deposited seasonally physically modifies the germination and early growth environment experienced by seeds and seedlings of herbaceous understory plants, in addition to its effects through decomposition. Besides reducing the amount of light which hits the soil layer (Facelli & Pickett 1991b) and presenting a physical barrier to growth (Bergelson 1990), leaf litter modifies the spectral quality of that light (i.e. the R : FR ratio: Bliss & Smith 1985), and the humidity and temperature of the germination environment (e.g. Bliss & Smith 1985; Fowler 1986; Facelli & Pickett 1991a,b; Thompson 1994).

In addition to the long recognized effects of leaf litter on plant community structure (see e.g. Bergelson 1990; Facelli & Pickett 1991a; Facelli 1994; Foster & Gross 1998; Xiong & Nilsson 1999), two lines of preliminary evidence suggest that the presence or abundance of leaf litter could affect the evolutionary dynamics of *I. capensis*. First, in a well-studied pair of sun and woodland populations of *I. capensis*, genotypes collected from the woodland population (which has more leaf litter) have significantly longer hypocotyls (Dudley & Schmitt 1995; Donohue & Schmitt 1999). The studies to date on this pair of sun and woodland populations, however, have focused on the evolutionary consequences of variation in intraspecific density of *I. capensis* plants that competed for light and other nutrients, and did not address the potential consequences of physical modifications to the environment caused by leaf litter. Second, in additional surveys of other local populations of *I. capensis* in Rhode Island and Massachusetts, USA, we have noticed that seedlings emerging through leaf litter appear to have longer hypocotyls and emerge slightly later in the season (J.R. Stinchcombe and E. von Wettberg, personal observation). However, these results are only suggestive because several other factors besides the physical effects of leaf litter vary between these populations; accordingly, a direct experimental approach manipulating leaf litter is necessary to evaluate its evolutionary consequences. To evaluate how the engineering effects of leaf litter could alter the evolutionary dynamics of *I. capensis*, we sought to answer four questions: (i) Does *I. capensis* face performance trade-offs between the bare soil and leaf litter environments? (ii) Does the genetic architecture of morphological and phenological traits change between bare soil and leaf litter environments? (iii) How does leaf litter affect the pattern of natural selection on germination and elongation traits? and (iv) How does the frequency of leaf litter environments affect which combinations of hypocotyl length lead to highest mean fitness across both bare soil and leaf litter environments? Our results illustrate that ecosystem engineers not only induce plastic changes in the species that they affect, but also significantly alter the pattern of

natural selection on ecologically important traits and the fitness surfaces for those traits.

## MATERIALS AND METHODS

### Study system and natural history

Jewelweed (*I. capensis* Meerb. Balsaminaceae), is an herbaceous, self-compatible annual commonly found in North American deciduous forests and wetlands. Populations of *I. capensis* typically germinate and elongate under a wide variety of leaf litter conditions, from heavy leaf litter in woodland sites, to little or no leaf litter in open sites. In Oak-Hickory forests of the northeastern USA, *Impatiens* seeds typically disperse throughout the summer and fall, and are subsequently covered with falling leaves in late autumn through winter. The following spring, seedlings emerge either directly from the soil or through a layer of leaf litter and elongate rapidly prior to closure of the overhead canopy if one exists.

### Experimental design

To study the possible evolutionary consequences of ecosystem engineers on *I. capensis*, we grew plants that either emerged and elongated through leaf litter or bare soil, and examined how leaf litter altered the pattern of natural selection on morphological and phenological traits. Experimental plants were drawn from 45 recombinant inbred lines (RILs) of *I. capensis* that had been created by crossing a single inbred line collected from a woodland population to a single inbred line collected from an open population. The F1 of this cross was allowed to self-fertilize, and *c.* 100 of the resulting F2 plants were propagated by single-seed descent for six generations to produce the RILs (for more details on the creation of these lines, see Heschel *et al.* 2004). The genetic structure of such lines is similar many natural *Impatiens* populations in which rare outcrossing events may be followed by several generations of self-fertilization (Paoletti & Holsinger 1999).

On 11 June 2003, we planted 12 replicate seeds from each of the 45 RILs into 12.7-cm diameter round pots filled with Scott's 360 Coir Growing Medium (Scotts-Sierra Horticultural Products, Marysville, OH, USA). Seeds from these 45 RILs had been collected and stratified in distilled water for *c.* 4 months at 4 °C prior to planting. (This stratification technique, which is necessary for laboratory maintenance of the RILs, does not allow an evaluation of the effects of leaf litter on overwinter survival.) After planting, we randomly selected half of the pots from each line to be covered with *c.* 2.54 cm of white and red oak (*Quercus alba* and *Q. rubra*) leaf litter which had been gathered from a nearby suburban lawn that was adjacent to a natural *I. capensis* population; this

litter depth is within the range of naturally occurring litter depths in *Impatiens* populations (J. Stinchcombe, personal observation; E. von Wettberg, unpublished data). Pots were then split into three spatial blocks in the greenhouse, such that four replicates per line-treatment combination were in each block, for a total of 1080 plants in a randomized blocked design (two treatments  $\times$  45 lines  $\times$  three blocks  $\times$  four replicates). Pots were placed immediately next to each other, yielding an intraspecific density of *c.* 62 pl m<sup>-2</sup>. We elected to use a greenhouse approach because it facilitated randomly assigning leaf litter or bare soil treatments to individual plants (which would be difficult in the field) and because equalizing other environmental factors that could conceivably affect germination and elongation traits (soil quality, light and moisture availability, etc.) allowed us to focus solely on the effects of leaf litter. We elected to focus solely on the engineering effects of leaf litter, rather than other effects (e.g. canopy closure, wind and rain disturbance, etc.) because our traits of interest, emergence time and hypocotyl length, are most likely to be of importance early in the growing season, prior to overhead canopy closure.

Two days after planting, each block was surrounded by a border row of plants and then aluminum foil to prevent incident lateral light from reaching plants. Pots were censused five times for seedling emergence from the leaf litter or soil in the first 2 weeks of the experiment to estimate time to emergence for each plant. Throughout the experiment, plants were bottom-watered daily with Ebb-Flo irrigation (i.e. each bench was bottom-watered in its entirety, simultaneously) to ensure that soil moisture levels were the same in the leaf litter and control treatments and across blocks. All plants were fertilized uniformly with Peter's 20-20-20 (N-P-K; Scotts-Sierra Horticultural Products) as needed. On 27 August 2003, we harvested all the plants from the experiment, and measured hypocotyl length, the length of the first two internodes and total height on all plants. A growing season of this length (77 days) equals the median lifespan of experimental *I. capensis* plants grown in woodlands sites under low and natural densities, and in sun sites grown under natural densities (Donohue *et al.* 2000a; our reanalysis of their lifespan data). For two randomly determined blocks, we also counted the number of branches per plant and estimated reproductive fitness as the sum of flowers, fruits and pedicels for each plant (see Heschel *et al.* 2004). We used the sum of flowers, pedicels and fruits as an indicator of current reproduction (flowers), recent reproduction (fruits) and past reproduction in which the seeds have already explosively dehisced (pedicels). Dry biomass for all plants was determined after drying the above-ground parts of plants at 65 °C for *c.* 48 h.

By using real leaf litter in our experiment, there is the possibility that some of the effects of leaf litter are due to

nutrient or chemical leaching into the soil. While the use of artificial leaf simulacrum would avoid the potential for decomposition and chemical leaching, it is unclear whether it would mimic the naturally occurring effects of leaf litter on light availability and spectral quality, humidity, and physical interference. While we cannot formally exclude the possible effects of leaching and decomposition, we expect that differences between the two treatments are mainly due to the physical effects of leaf litter for two reasons: first, our experiment was of relatively short duration (77 days) for these effects to occur, and second, because we believe that the nutrient and chemical effects of potting soil and fertilizer treatments should predominate over any effects because of leaf decomposition.

### Statistical analysis

For preliminary analyses, we sought to determine whether the leaf litter treatment led to a plastic response in any of the morphological and phenological traits we measured by comparing the mean values in each treatment. Our analyses focus on two traits expressed early in the life cycle that we had chosen *a priori* (emergence time and hypocotyl length) as well as a suite of potentially correlated traits expressed later in development. We used mixed-model ANOVA (Proc Mixed in SAS; SAS Institute, Cary, NC, USA) to determine whether significant differences existed between the leaf litter and bare soil treatments. In these models, block, treatment and the block  $\times$  treatment interaction were included as fixed effects, with RIL and RIL  $\times$  treatment included as random effects. Block was considered a fixed effect because we did not wish to generalize about spatial variation in the traits of interest based on the variation present in the greenhouse. We also included the number of days a seed had been stratified (i.e. elapsed days from collection from the parental plant to the experimental planting) as a covariate in these models to control for any effects of seed age on germination and early growth traits.

To determine if *I. capensis* faces performance trade-offs between the bare soil and leaf litter environments, we evaluated the across-environment genetic correlations for our two focal traits (emergence time and hypocotyl length), absolute reproductive fitness, and the suite of correlated traits that we measured. The across-environment genetic correlation was estimated in the context of a mixed-model ANOVA for the trait, performed with the restricted maximum likelihood (REML) option of Proc Mixed (Fry 2004; Sgrò & Blows 2004). To test the significance of these genetic correlations, we compared the  $-2 \log$  likelihoods of the full mixed model ANOVA to subsequent models in which the across-environment genetic correlations were constrained to equal 0 or 1 (Fry 2004). While it is possible to estimate and test the significance of across-environment genetic correla-

tions using traditional mixed-model ANOVA approaches (Fry 1992) the likelihood framework is preferable because it does not assume that within and among line variance components are equal in both environments (Fry 2004). As before, days of stratification was included as a covariate in these analyses.

To determine if the leaf litter treatment affected the genetic variance-covariance matrix (G-matrix) for the suite of traits we measured, we used two approaches. First, we estimated the G-matrix by REML for each environment separately. We attempted to estimate the entire G-matrix for each treatment in a single analysis as described by Fry (2004), but these analyses failed to converge. Accordingly, we estimated the G-matrix in an element-by-element fashion in each environment: genetic variances were estimated for each trait separately from the line variance component in analyses of single traits. To estimate the genetic covariance between traits, we estimated the line variance component for the sum of the two traits, and then subtracted the genetic variance of each trait and divided by two (following Mezey and Houle 2005). One drawback of this estimation approach was that the G-matrices we estimated by REML were not positive definite, precluding further analysis of them by traditional principal component analysis (PCA) or testing for common principal components (see below).

The second approach we used to determine whether the leaf litter treatment affected the G-matrices was to use the program CPCrand (Phillips & Arnold 1999; available from <http://darkwing.uoregon.edu/simpphil/software.html>). CPCrand tests a series of hierarchical hypotheses about matrix similarity – whether two matrices share one, two or up to  $p-2$  principal components in common (for  $p \times p$  matrices; Phillips & Arnold 1999), share all of their principal components (i.e. have common principal components), are proportional to each other or are equal to each other. CPCrand uses a randomization approach to compare the actual test statistics for shared principal components, proportionality, and matrix equality to a null distribution obtained by randomizing genetic families or lines across treatments; each hypothesis in the ‘jump up’ procedure is tested against the null hypothesis of unrelated matrix structure. We supplied CPCrand with the phenotypic data for our experiment and utilized the 5000 randomizations and the ‘jump up’ procedure to test for varying degrees of G-matrix similarity (see Donohue *et al.* 2000b; Conner *et al.* 2003 and Caruso *et al.* 2005 for other examples of this approach).

One advantage of the CPCrand approach is that it is possible to use matrix bending to eliminate the problem of non-positive definite matrices. However, analysis of all eight traits with our data required a high degree of matrix bending, which has yet to be fully verified when applied in

concert with the randomization approach of CPCrand (CPCrand documentation). Accordingly, we removed two traits from these analyses (total height and absolute reproductive fitness), which dramatically reduced the degree of matrix bending required (bending coefficient of 0.0222 for analysis of six traits as opposed to 0.2361 for an analysis of all eight traits). In addition, the G-matrices estimated and compared by CPCrand are estimated from ordinary least-squares ANOVA rather than REML estimation.

To determine whether leaf litter affected the pattern of natural selection on germination and early growth traits we used genotypic selection analysis (Rausher 1992; Stinchcombe *et al.* 2002). In this analysis, mean relative fitness for an RIL is regressed on the RIL mean of the trait(s) of interest, and the resulting estimate of natural selection is unbiased by environmentally induced covariances between traits and fitness. Here we regressed relative fitness on time to germination, hypocotyl length, and the traits we measured that were genetically correlated to these two focal traits (first and second internode length). [First internode length has also previously been shown to be under differential selection between sun and woods sites in *Impatiens* grown at similar densities (Donohue *et al.* 2000a), although these sites also differ in many other characteristics besides the effects of leaf litter.] To determine whether the leaf litter treatment altered the relationship between these traits and fitness, we included in this model treatment as a class variable and all treatment  $\times$  trait interactions (i.e. treatment  $\times$  hypocotyl, treatment  $\times$  emergence time, etc). We did not evaluate whether there was stabilizing/disruptive selection or correlational selection on these four traits, and whether it differed between treatments, because of the size and relatively low power of such a model: full analysis for four traits including all linear, squared and cross-product terms, and their interactions with treatment would yield a selection model containing 29 independent variables.

Branch number was analysed in a separate model because it was not genetically correlated with either emergence time or hypocotyl length (genotypic selection analysis is unbiased by exclusion of traits that are not genetically correlated; Rausher 1992). We failed to detect any selection on branch number, and accordingly only present selection analyses for emergence time, hypocotyl length, and first and second internode lengths.

The environmental frequency of leaf litter and bare soil sites will rarely, if ever, be equally distributed across a landscape. We therefore evaluated how the fitness surfaces for one trait (hypocotyl length) would change depending on the relative frequency of leaf litter and bare soil environments. We regressed mean reproductive success, averaged over both environments, on hypocotyl length in the litter treatment, hypocotyl length in the soil treatment, the square of each of these terms, and the cross-product of the two. In

this analysis, the squared terms estimate the strength of stabilizing/disruptive selection on hypocotyl length in each environment, and the cross-product term estimates the strength of correlational selection on particular combinations of the two traits. These analyses were performed with mean reproductive success calculated for three frequencies of the leaf litter environment: 5%, 50% (experimental) and 95%. Mean reproductive success for each inbred line for these three scenarios was estimated by weighting their mean reproductive success in the leaf litter and bare soil environments accordingly and summing the two [e.g. for 95% leaf litter frequency,  $W = (w_{\text{leaves}} \times 0.95) + (w_{\text{soil}} \times 0.05)$ ]. This approach is equivalent to evaluating a hard selection model (van Tienderen 1991; Donohue *et al.* 2000a, 2005; Kelley *et al.* 2005), under three different environmental frequencies. To facilitate the interpretation of these analyses, we also interpolated 3-D surfaces representing the relationship between reproductive success and hypocotyl length in the two environments. Fitness surfaces were interpolated using the spline option of the G3GRID procedure of SAS (version 9.1.3; SAS Institute) with a smoothing coefficient of 0.1.

## RESULTS

### Leaf litter significantly affects plant phenology and morphology

The leaf litter treatment had dramatic effects on plant phenology and morphology (Table 1). Seeds planted into pots covered in leaf litter emerged significantly later than those planted into bare soil pots (a difference of  $\approx 0.58$  days, Table 1). In addition, the early growth characteristics were significantly altered by leaf litter: plants emerging through leaf litter had significantly longer hypocotyls (1.44 cm longer or  $\approx 15\%$  of mean hypocotyl length in the bare soil treatment). The effects of emerging through leaf litter extended to later developmental traits, including significantly shorter first internodes (0.61 cm,  $\approx 6\%$  shorter than in the bare soil treatment) significantly fewer overall branches and lower dry biomass (Table 1). We failed to detect any significant differences in the length of the second internode, total height or absolute fitness, although there was a suggestive trend for lower absolute reproductive fitness in the leaf litter treatment. In total, these results indicate that early emergence through leaf litter significantly affects germination, elongation, and adult traits in *I. capensis*, and leads to significantly reduced above-ground biomass.

### Genetic trade-offs across environments are absent

One way in which ecosystem engineers can affect the evolutionary trajectory of the species they affect is if those

**Table 1** Mean phenotypic values morphological and phenological traits of plants grown in the leaf litter and bare soil treatments

Trait (units)	Leaf litter mean (SE)	Bare soil mean (SE)	$F_{1,44}$	$P$ -value
Time to emergence (days)	<b>5.88 (0.10)</b>	<b>5.30 (0.10)</b>	<b>26.09</b>	<b>0.0001</b>
Hypocotyl length (cm)	<b>10.81 (0.17)</b>	<b>9.37 (0.16)</b>	<b>95.40</b>	<b>&lt; 0.0001</b>
First internode length (cm)	<b>9.49 (0.19)</b>	<b>10.10 (0.19)</b>	<b>26.28</b>	<b>&lt; 0.0001</b>
Second internode length (cm)	10.53 (0.28)	10.42 (0.27)	0.45	0.51
Branch number*	<b>8.21 (0.30)</b>	<b>9.22 (0.29)</b>	<b>18.09</b>	<b>0.0001</b>
Total height (cm)	103.68 (1.16)	103.13 (1.13)	0.26	0.61
Dry biomass (g)	<b>2.20 (0.05)</b>	<b>2.29 (0.05)</b>	<b>4.59</b>	<b>0.04</b>
Absolute reproductive fitness	20.44 (1.89)	23.28 (2.30)	1.35	0.25

Mean values presented are least-square means from mixed-model ANOVAs, as described in the text. Significant differences between treatments are shown in bold.

\*Denominator degrees of freedom for the  $F$ -test for branch number was 43, because of poor germination of one recombinant inbred line in the leaf litter treatment.

species face performance trade-offs across engineered and non-engineered environments. In the case of *I. capensis*, we find no evidence of genetic trade-offs across environments for any of the traits we studied – in each case, there is a significant, positive genetic correlation between traits expressed in the bare soil environment and those same traits expressed in the leaf litter environment. The across-environment genetic correlations ranged from 0.45, in the case of emergence time to 1 in the case of hypocotyl length (Table 2). For two of the traits that we examined, emergence time, and absolute fitness, the across-environment genetic correlations significantly was  $< 1$ , while the across-environment genetic correlation for first internode length showed a marginally significant difference from 1. The absence of negative genetic correlations we detected in our experiment might be related to the problem of detecting trade-offs in size- and fitness-related traits affected by general vigour (Fry 1993), or possibly because *I. capensis* faces genetic trade-offs in performance in

**Table 2** Across-environment genetic correlations between traits expressed in the leaf litter and bare soil environments

Trait	$r_{ge}$	Probability	
		$r_{ge} = 0$	$r_{ge} = 1$
Emergence time	0.45	0.065	$< 0.0001$
Hypocotyl length	1	$< 0.0001$	0.5
First internode length	0.94	$< 0.0001$	0.08
Second internode length	0.996	$< 0.0001$	0.5
Branch number	0.93	$< 0.0001$	0.22
Total height	0.88	$< 0.0001$	0.19
Dry biomass	0.89	$< 0.0001$	0.17
Absolute reproductive fitness	0.83	$< 0.0001$	0.017

The genetic correlation was estimated by restricted maximum likelihood method, and its significance tested by comparing the  $-2$  log likelihoods of models in which the across-environment genetic correlation was either unconstrained or constrained to equal 0 or 1.

response to other aspects of ecosystem engineering imposed by trees (light or water availability, wind modification, etc.) besides leaf litter. These data indicate that for the preponderance of traits studied, the same loci contribute to them in each environment, supporting two important results: (i) selection on any of these traits, in either environment, will lead to a strong correlated response in the other environment; and (ii) *I. capensis* will only face genetic constraints in its evolutionary response to leaf litter if selection is acting on these traits in opposite directions (Lande 1979).

### Leaf litter does not dramatically alter genetic architecture

The estimated genetic variance–covariance matrices for the eight traits we measured are presented in Table 3. In general, the traits we examined showed qualitatively similar patterns of genetic variation (diagonal of Table 3). Although the two matrices appear to show different patterns of covariation, it is not possible to assess these matrices quantitatively with PCA or common principal component (CPC) analysis because the estimated G matrices are not positive definite.

To compare patterns of genetic variation and covariation in the two treatments, we used the CPC approach implemented by CPCrand (Phillips & Arnold 1999), after omitting two traits, total height and absolute reproductive fitness that necessitated a high degree of matrix bending. Results from 5000 randomizations suggest the two G-matrices estimated by CPCrand share at least four principal components (i.e. the hypothesis of four common principal components could not be rejected: likelihood ratio test = 40.4876,  $P = 0.39$ ). The two G-matrices showed a marginally significant deviation from a model of common principal components (likelihood ratio test = 77.91,  $P = 0.09$ ) and a significant deviation from proportionality (likelihood ratio test = 239.56,  $P = 0.011$ ).

**Table 3** Estimated genetic variance–covariance matrices for the leaf litter (L) and soil (S) environments respectively

	Emergence time	Hypocotyl length	First internode length	Second internode length	Branch number	Total height	Dry biomass	Reproductive fitness
Emergence time	L: 0.5551 S: 0.4548							
Hypocotyl length	L: 0.0004 S: - 0.2449	L: 0.4331 S: 0.9088						
First internode length	L: - 0.093 S: - 0.0468	L: - 0.1207 S: 0.0666	L: 1.5147 S: 1.4205					
Second internode length	L: - 0.0771 S: 0.0481	L: 0.0191 S: - 0.0990	L: 1.7491 S: 1.4219	L: 2.2829 S: 2.7841				
Branch number	L: 0.4048 S: 0.0597	L: - 0.0585 S: - 1.2702	L: - 0.1898 S: - 0.7155	L: 0.4608 S: - 0.8881	L: 2.5681 S: 3.4009			
Total height	L: 0.9063 S: - 0.2357	L: 2.6084 S: - 2.5903	L: 4.1744 S: - 0.8971	L: 5.6368 S: 0.5071	L: 9.574 S: 0.7751	L: 48.9807 S: 27.573		
Dry biomass	L: - 0.0727 S: - 0.1141	L: 0.0343 S: 0.0430	L: 0.1040 S: 0.0502	L: 0.2677 S: 0.0614	L: 0.1506 S: 0.1615	L: 1.3485 S: - 2.2055	L: 0.0889 S: 0.0504	
Reproductive fitness	L: - 0.7136 S: - 1.3811	L: 2.0311 S: - 6.2843	L: - 2.7951 S: - 6.3494	L: 2.7812 S: - 1.0505	L: - 0.6417 S: - 3.6352	L: 44.6723 S: 6.9295	L: 0.5979 S: - 1.9599	L: 96.4947 S: 74.3481

Genetic variance and covariance terms were estimated by restricted maximum likelihood method. Variances and covariances were rounded to four decimal places.

### Leaf litter significantly alters natural selection on a suite of traits elongation traits

Leaf litter, by dramatically modifying the seed and seedling environment of *I. capensis*, has the potential to alter the strength and direction of natural selection on emergence timing and early growth. In an analysis of both treatments by ANCOVA, we found that selection was acting significantly on emergence time and hypocotyl length, with marginally significant evidence for selection on first internode length. In addition, we detected significant evidence that the pattern of selection on hypocotyl length differed between the two treatments (hypocotyl  $\times$  treatment interaction; Table 4a). Separate analyses by treatment revealed that selection significantly favoured longer hypocotyls in the leaf litter treatment, but not in the bare soil treatment (Table 4b); this trend is clearly visible in plots of the selection differentials (Fig. 1), which show the relationship between hypocotyl length and fitness in each environment, uncorrected for other correlated traits. These data suggests that hypocotyl length is selectively neutral in the bare soil treatment, but that longer hypocotyls led to a fitness advantage in the leaf litter treatment, as would be expected.

Separate analyses by treatment suggested significant selection against delayed emergence times in the leaf litter treatment, but not in the bare soil treatment (Table 4b), although both of these estimates are negative. Significant heterogeneity in these estimates was not detected in the ANCOVA (Table 4a). These data suggests that leaf litter

accentuates the fitness benefits of early emergence in *I. capensis*. Additionally, that selection acts against emergence time in the experiment leaf litter treatment suggests that the mean difference in emergence date 0.58 days (see above) was in fact biologically significant. The separate analyses of selection by treatment also suggest that in the bare soil environment genotypes with shorter first internodes and longer second internodes have higher fitness (Table 4b).

### Frequency of litter environments alters fitness surfaces

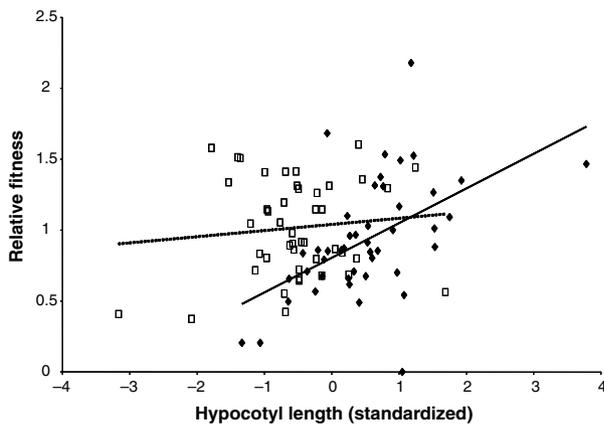
The frequency of leaf litter and bare soil environments will rarely, if ever, be evenly distributed. Accordingly, we determined how a greater or lesser frequency of leaf litter environments would affect the fitness surfaces for hypocotyl length in the bare soil and leaf litter environments. When leaf litter environments are rare, or at 5% frequency, natural selection appears to favour genotypes that are capable of producing long hypocotyls in each environment (back corner of Fig. 2a). In addition, there is some evidence suggesting that selection favours genotypes that have intermediate hypocotyls in each environment, but acts against genotypes that either have short hypocotyls in both environments or mismatched hypocotyls (i.e. relatively long in one environment, but relatively short in another; Fig. 2a; Table 4a).

When leaf litter and bare soil environments are at equal frequency (i.e. the experimental design), the joint pattern of selection on hypocotyl length in the two environments is as

**Table 4** Selection analyses for emergence time and hypocotyl length, and correlated traits. (a) Overall ANCOVA for relative fitness, testing for selection on emergence time and hypocotyl length in the experiment as a whole, as well as significant differences in the pattern of selection between treatments. (b) Parameter estimates for selection gradients in each treatment

Source of variation	d.f.	<i>F</i>	<i>P</i> -value	
(a)				
Treatment	1	<b>5.74</b>	<b>0.0189</b>	
Emergence time	1	<b>4.56</b>	<b>0.0359</b>	
Hypocotyl length	1	<b>12.11</b>	<b>0.0008</b>	
First internode length	1	3.20	0.0773	
Second internode length	1	2.21	0.1412	
Emergence time × treatment	1	0.37	0.5451	
Hypocotyl length × treatment	1	<b>7.30</b>	<b>0.0084</b>	
First internode length × treatment	1	2.69	0.1046	
Second internode length × treatment	1	1.18	0.2804	
Error	80			
			Leaf litter	Soil
Trait			$\beta$ (SE)	<i>P</i> -value
(b)				
Emergence time		<b>-0.1239 (0.06)</b>	<b>0.0499</b>	-0.06897 (0.07) 0.2995
Hypocotyl length		<b>0.2841 (0.06)</b>	<b>0.0001</b>	0.03576 (0.06) 0.5743
First internode length		-0.00825 (0.08)	0.9222	<b>-0.1915 (0.07)</b> <b>0.0132</b>
Second internode length		0.02313 (0.09)	0.7990	<b>0.149 (0.07)</b> <b>0.0494</b>

Significant effects are shown in bold, marginally significant effects in italics. Traits were standardized to a mean of zero and variance of one prior to analysis.



**Figure 1** Selection differentials for hypocotyl length in the leaf litter treatment (filled diamonds) and the bare soil treatment (open squares). The portrayed data indicate total selection on hypocotyl length, including direct selection and indirect selection on other correlated traits.

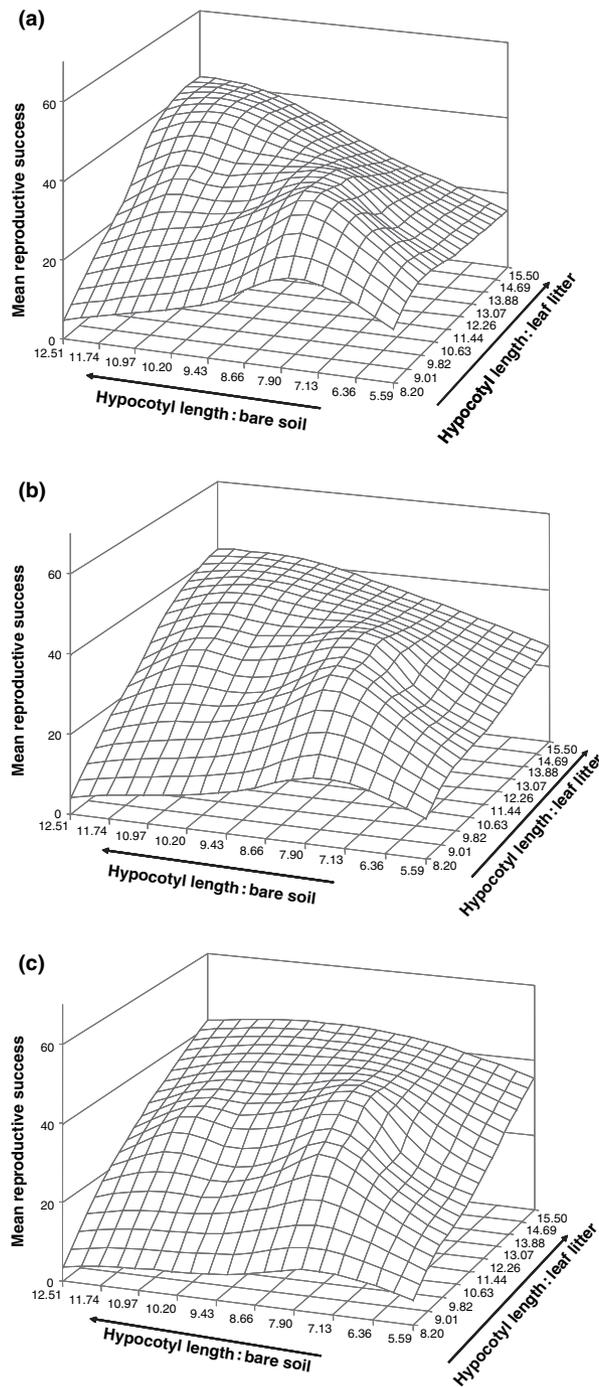
would be predicted from Fig. 1: selection acts to increase hypocotyl length in the leaf litter, but is not acting on hypocotyl length in the bare soil environment (Fig. 2b, Table 5b). In addition, there is marginal evidence that selection on hypocotyl length in the leaf litter is slightly non-linear; this pattern is likely due to the curvilinear plateau in the fitness contours for hypocotyl length in the leaf litter

that occur when hypocotyl length in the bare soil is *c.* 7.9 cm.

For high frequencies of leaf litter (95%), natural selection acts only on hypocotyl length in the leaf litter environment (Fig. 2c, Table 5c). Selection favours longer hypocotyls in the leaf litter environment, regardless of hypocotyl length in the soil environment and variation in hypocotyl length in the soil environment appears to have no effect on fitness. In contrast to the case in which leaf litter was rare, there is neither selection for hypocotyl length in the soil when it is a rare environment, nor any evidence for correlational selection on the joint distribution of these traits.

## DISCUSSION

Our data clearly indicate that leaf litter in deciduous forests of the northeastern USA has the potential to dramatically alter the ecological and evolutionary dynamics of *I. capensis* through its effects of modifying the germination and early growth environment. Leaf litter not only induced several plastic phenotypic changes in a number of morphological and phenological traits (Table 1), but also altered the pattern of natural selection on hypocotyl length (Table 4). The genetic architecture of these traits in *I. capensis* – i.e. their genetic variances and covariances within and across environments – will also dramatically influence the effects of leaf litter on the evolutionary dynamics of the traits we studied. All the traits we examined exhibited strong, positive genetic



**Figure 2** Fitness surfaces for hypocotyl length in the leaf litter and soil environments, for three frequencies of the leaf litter environment: (a) leaf litter environments are rare (5% frequency); (b) leaf litter and bare soil environments are equally frequent (50% each); and (c) leaf litter environments predominate (95% frequency). Note the orientation of the axis for hypocotyl length in the bare soil is increasing from right to left.

correlations across environments and similar patterns of variation and covariation with each other. Accordingly, natural selection for a trait in an engineered environment will lead to a correlated response in non-engineered environments – even those traits are not under selection in that environment. Below we discuss the evolutionary genetics of emergence time and hypocotyl length in response to ecosystem engineers in detail, as well as the general potential of ecosystem engineers to shape the evolutionary dynamics of communities.

### Evolutionary genetics of emergence time and hypocotyl length

The presence of leaf litter, and its overall environmental frequency, will have dramatic impacts on the evolutionary dynamics of emergence time and hypocotyl length. For both traits, we detected a qualitatively similar set of results – a plastic response to leaf litter, strong positive genetic correlations between the traits in both environments, and differences in either the magnitude or significance of natural selection on these traits in the two environments.

Natural selection acting against delayed emergence time for plants under leaf litter is intuitive – plants that delay emergence time are likely at a disadvantage in the competitive size hierarchy, and with fewer seed resources remaining once they begin to de-etiolate. Although the density at which we grew plants was lower than the high density treatments of past experiments (e.g. Donohue *et al.* 2000a,b), densities in natural populations are frequently in this range (e.g. Schmitt *et al.* 2003; J.R. Stinchcombe, M.S. Heschel and J. Schmitt, unpublished results) and plants began interacting with each other and competing for light  $\approx$  5 weeks into the experiment. Our results are qualitatively similar to those described by (Schmitt & Ehrhardt 1990), who found density-dependent selection on emergence time: in both cases, in the more stressful environment (leaf litter or higher density, respectively), selection favours early emergence.

The strong positive genetic correlation between emergence time in the two environments suggests that any selection for faster emergence times in the leaf litter environment will lead to a correlated response in the bare soil environment. The genetic correlation between emergence time in the litter and soil would preclude independent phenotypic evolution in these environments (e.g. Via & Lande 1985, 1987; Via 1987; van Tienderen 1991; Gomulkiewicz & Kirkpatrick 1992; Via & Hawthorne 2005), suggesting that our observations of delayed emergence in sites with leaf litter are not because of genetic differentiation. Our observations of delayed emergence time in the field in litter sites could thus merely be plastic responses, although this hypothesis requires further experimental testing.

**Table 5** Directional, stabilizing, and correlational estimates of the fitness surfaces for hypocotyl length in the leaf litter and bare soil environments under three assumptions of the frequency of leaf litter environment: (a) Leaf litter environments are rare (5% frequency); (b) leaf litter and bare soil environments are equally frequent (50% each); and (c) leaf litter environments predominate (95% frequency)

Trait	$\beta$ (SE)	<i>P</i> -value	$\gamma$ (SE)	<i>P</i> -value
(a) 5% Leaf litter frequency				
Hypocotyl length, leaf litter	<b>5.69 (2.09)</b>	<b>0.010</b>	-1.43 (0.81)	0.084
Hypocotyl length, bare soil	-1.69 (1.75)	0.340	<b>-2.34 (1.15)</b>	<b>0.048</b>
Leaf hypocotyl $\times$ soil hypocotyl	-	-	3.64 (1.91)	0.064
(b) 50% Leaf litter frequency				
Hypocotyl length, leaf litter	<b>7.064 (2.04)</b>	<b>0.001</b>	-1.34 (0.79)	0.097
Hypocotyl length, bare soil	-1.74 (1.70)	0.314	-1.81 (1.12)	0.114
Leaf hypocotyl $\times$ soil hypocotyl	-	-	2.52 (1.86)	0.184
(c) 95% Leaf litter frequency				
Hypocotyl length, leaf litter	<b>8.44 (2.36)</b>	<b>0.001</b>	-1.25 (0.91)	0.179
Hypocotyl length, bare soil	-1.78 (1.97)	0.370	-1.27 (1.29)	0.330
Leaf hypocotyl $\times$ soil hypocotyl	-	-	1.40 (2.15)	0.519

Linear terms ( $\beta$ ) estimate directional selection on an individual trait, quadratic terms estimate stabilizing/disruptive selection on an individual trait ( $\gamma$ ) and cross-product terms correlational selection.

Hypocotyl length appeared to have the largest plastic response to leaf litter, in percentage terms of any of the traits we measured (Table 1). However, despite the plastic response of hypocotyl length to leaf litter, the across-environment genetic correlation in hypocotyl length was not significantly different from one (Table 2), indicating that the same loci contribute to hypocotyl length in each environment. As such, natural selection for longer hypocotyls in the leaf litter is likely to lead to a correlated response in the bare soil environment, even though we failed to detect any fitness effects of hypocotyl length in this environment. The absence of detectable selection on hypocotyl length in the soil environment suggests either that there are costs of hypocotyl length in this environment that become more pronounced, or that the benefits of hypocotyl length are reduced, or some combination of increased fitness costs and reduced fitness benefits. We failed to detect any evidence of costs of increased hypocotyl length in the soil environment – for instance, genotypes with longer hypocotyls did not have shorter internodes or overall plant height (J.R. Stinchcombe, unpublished data), suggesting that early growth does not come at a cost of later growth. Moreover, our assessment of the joint pattern of natural selection on hypocotyl length in both environments suggested that even when bare soil environments are a 95% frequency, there is still no detectable pattern of selection acting against hypocotyl length. A more likely scenario is that hypocotyl length is essentially a neutral trait under the bare soil, low-density conditions of our experiment, but shows enhanced benefits under leaf litter conditions. In leaf litter environments, longer hypocotyls probably aid in escaping the leaf layer and in allowing plants to maintain their position in the size hierarchy, especially if they experience a temporal delay in emergence. These conclu-

sions are supported by our analysis of the fitness surfaces for hypocotyl length when the leaf litter environment predominates: under these conditions, hypocotyl length in the soil remains neutral, but selection favours increased hypocotyl length in the leaf litter, regardless of hypocotyl length in the soil.

### Ecosystem engineers as community-wide selective agents

The consequences of ecosystem engineers have typically been studied by evaluating their effects on species richness in a community or the abundance of a few to several species. However, by physically modifying the environment, ecosystem engineers are also potentially affecting the evolutionary dynamics of a suite of species in a community (e.g. Thayer 1979) by dramatically altering the selective environment (*sensu* Antonovics & Levin 1980; Brandon & Antonovics 1996). Because they affect several species at once, ecosystem engineers and their consequences present an ideal test scenario for the challenge of understanding the ecological and evolutionary dynamics of complex, multispecies communities. For instance, are the evolutionary consequences of leaf litter for *I. capensis* representative for other woodland and open herbaceous species? Are the effects of leaf litter on the evolutionary dynamics of annual and perennial species similar? Does leaf litter impose a similar pattern of natural selection on the suite of species in these habitats, and how many of these species exhibit a similar genetic architecture for traits affected by leaf litter? Answering questions such as these will be essential to determine whether there are any general patterns to the evolutionary consequences of ecosystem engineers.

In their original article, Jones *et al.* (1994, p. 383) briefly considered the evolutionary consequences of ecosystem

engineers, but primarily focused on the fitness consequences of engineering on the engineers themselves or larger macro-evolutionary patterns such as diversification, adaptive radiation, and extinction. [We note that much of niche-construction theory bears on similar issues, but focuses heavily on feedback to the engineer or 'niche constructor' (Odling-Smee *et al.* 2003; Laland *et al.* 2004; but see Keller 2003).] Although ecosystem engineers may impose selection because of their direct activities (e.g. beavers felling trees non-randomly depending on tree secondary chemistry: Bailey *et al.* 2004), to our knowledge few previous investigations have examined how the physical modification of the environment *per se* (i.e. dam building, leaf litter accumulation, etc.) influences the evolutionary dynamics of affected species (but see Thayer 1979; Skelly & Freidenburg 2000). Understanding the evolutionary consequences of ecosystem engineers could also lead to a better understanding of their ecological consequences as well, for at least three reasons. First, natural selection imposed by ecosystem engineers, and the presence and magnitude of genetic correlations in species affected by them, will both directly affect the retention and loss of quantitative genetic diversity in populations. Genetic diversity in populations, especially plant species has been shown in several recent studies to affect a suite of other phenomena traditionally considered to be purely ecological in nature, e.g. disturbance resistance (Hughes & Stachowicz 2004), species richness, evenness and community composition of arthropods (Duney *et al.* 2000; Johnson & Agrawal 2005), and nutrient cycling (Schweitzer *et al.* 2004). Second, the traits that respond to selection imposed by ecosystem engineers could be the same traits that influence ecological interactions between the affected species in the community – for example, emergence time and hypocotyl length in *Impatiens* could conceivably affect interspecific competitive interactions between *Impatiens* and other herbaceous species that emerge through leaf litter. In this manner, an evolutionary response to the selective impact of an ecosystem engineer could indirectly alter ecological interactions among the suite of affected species. Third, the mechanisms driving the ecological consequences of leaf litter typically appear to be species differences in germination and establishment traits (for a recent meta-analysis see Xiong & Nilsson 1999). Germination and establishment traits, however, are likely to be genetically variable within and between most plant populations. Accordingly, genetic variation in these traits within and between populations, has the potential to create spatial heterogeneity in the community-wide consequences of engineers. Determining the evolutionary consequences of ecosystem engineers, and how often or whether these changes have indirect ecological consequences, remains an important empirical challenge.

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