Eco-evolutionary contributions to community trait change in floating aquatic plants

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July 14, 2022

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ABSTRACT:

An entire community of organisms may become modified when its environment changes. These modifications can happen through physiological process (plasticity), evolutionary processes (adaptation) or shifts in species composition (sorting). The outcome of these three sources of change constitutes the community's phenotypic response, but how they combine to drive community trait dynamics is not currently well understood. We have conducted a community selection experiment in which communities of short-lived floating aquatic plants were grown in a range of stressful conditions, and measured changes in their body size. Determinants of phenotypic change were assessed with a full community reciprocal transplant which led to estimates of the contributions of plasticity, adaptation, and sorting. Species were modified during the experiment by both plasticity and adaptation, but in either case the magnitude and direction of change differed among species. Sorting and adaptation were of equal magnitude, but tended to act in opposite directions: in conditions where species with large fronds prevailed, each species evolved smaller fronds, and vice versa. We conclude that community trait dynamics cannot be understood simply by extrapolating the adaptive response of any single species to the whole community.

Keywords: Community trait dynamics, eco-evolutionary dynamics, eco-evolutionary partition, reciprocal transplant, trait change, species sorting, adaptation, phenotypic plasticity, Lemnaceae, duckweed

INTRODUCTION:

A community of organisms that experiences prolonged exposure to a new environment may become altered in response to the new conditions. The community response is characterized by a shift in mean phenotype for a trait common to all species. Such a shift in community mean phenotype may be due to three distinct kinds of process: the physiological response of individuals to a change in the conditions of growth (plasticity), the demographic response of the community through shifts in the relative abundance of species (sorting), and the genetic evolutionary response of each species (adaptation) (Fig. 1). Plasticity, sorting and adaptation, as well as their interactions, may all contribute to any phenotypic change in a multi-species community, and acting collectively they drive community trait dynamics (Guimarães et al. 2017, van Moorsel et al. 2019, Hall et al. 2020).

	Community trait change		
Level of change	Interspecific trait change	Intraspecific trait change	
Type of process	Ecological	Physiological	Evolutionary
Process	**Sorting**	**Plasticity**	**Adaptation**
	Change in community composition through shifts in species relative abundances	*Environmentally induced phenotypic change of individuals due to physiological modification during development or over the course of their lifetime*	*Phenotypic change within species attributable to shifts in genotype frequencies, where genetic variation may be either pre-existing or novel*

Fig. 1. Constituent processes of community trait change.

Historically, ecological and evolutionary processes have been studied in isolation (Slobodkin 1961), but it is increasingly clear that they have the potential to occur on overlapping timescales and can feed back on each other (Thompson 1998, Hendry and Kinnison 1999, Kinnison and Hendry 2001, Hairston et al. 2005, Saccheri and Hanski 2006). For example, ecological change including changes in community composition will often shape the selection environment which drives rapid evolution (Hendry and Kinnison 1999, Reznick and Ghalambor 2001, Carroll et al. 2007) and rapid evolutionary change can feed back to influence ecological parameters like population dynamics (Turcotte et al. 2011) and community structure (Johnson et al. 2009, Hart et al. 2019). The evolution of increased phenotypic plasticity may further alter demographics by promoting persistence in stressful environments (Ghalambor et al. 2007) and either inhibit or promote further evolutionary change by modifying phenotypic variation and its link to genetic variation (Ghalambor et al. 2007, Schlichting and Wund 2014). These findings have stimulated research in the growing field of eco-evolutionary dynamics (Fussmann et al. 2007, Urban et al. 2008, Pelletier et al. 2009, Post and Palkovacs 2009, Schoener 2011), which has as a central goal to understand the relative contributions and interactions of ecological, physiological, and evolutionary processes to community change (Schoener 2011).

Growing interest in the importance of evolutionary change over ecologically relevant timescales has led to the development of partitioning metrics to separate evolutionary from non-evolutionary processes in affecting different properties of populations, communities and ecosystems (Hairston et al. 2005, Ellner et al. 2011, Merilä and Hendry 2014, van Benthem et al. 2017, De Meester et al. 2019). Focusing on community mean phenotype, sometimes referred to as functional identity, is of particular interest given its inclusion of both genetic and non-genetic determinants, its response to environmental change (Garnier et al. 2004, Guittar et al. 2016, Bjorkman et al. 2018), and its direct link to determining ecosystem processes (Grime 1998, Garnier et al. 2004, Mokany et al. 2008).

Estimating the contributions of plasticity, sorting and adaptation to community change is not a straightforward task (van Benthem et al. 2017). Community trait change can be easily partitioned into inter- and intra-specific components, but the intra-specific component may combine both non-genetic and genetic change (Fig. 1). Separating plasticity from adaptation either requires detailed genetic information about the populations, or trait data from large-scale transplant experiments that measure lineage trait expression across environments. A variety of analytical procedures have been used to partition overall community phenotypic change into components that represent these processes (Collins and Gardner 2009, Govaert et al. 2016, van Benthem et al. 2017, Govaert 2018). Collins & Gardner (2009) adapted the Price equation (Price 1970, 1972) to partition community phenotypic change into that between species, between lineages and within lineages. First designed to measure evolutionary change within a population from one generation to the next, the Price equation is readily extended to measure change within multi-species communities over longer time scales and has been used to describe changes in toxin resistance within microbial communities, and carbon uptake by marine phytoplankton in high-CO_2 environments (Collins and Gardner 2009). However, this method requires detailed data on the dynamics of different lineages within species, which is often difficult

to obtain if lineages are indistinguishable from one another. Furthermore, Govaert et al. (2016) pointed out that the Price equation approach cannot determine the cause of phenotypic change within lineages, lumping together both non-genetic change due to phenotypic plasticity and genetic change due the introduction of novel genetic variation via mutation, immigration, or horizontal gene transfer.

The most rigorous method to distinguish between phenotypic plasticity and evolutionary change is with the use of a classical reciprocal transplant experiment, where populations from two environments are cultured in both their 'home' and 'away' environments (Miller and Fowler 1993, Kawecki and Ebert 2004). Fitness and/or phenotype are then measured on the second or third generation of growth in the transplanted environment, minimizing maternal effects and allowing plastic physiological change to be fully expressed, but before shifts in genotype frequencies become relevant. This reaction norm approach has been used to identify local adaptation (Kawecki and Ebert 2004, Hargreaves et al. 2020) and to partition observed differences in traits between populations into contributions from plasticity and evolutionary processes (Govaert et al. 2016, Stoks et al. 2016). Although reciprocal transplants are usually done with a single species, the concept can be extended to a whole community (Govaert et al. 2016). Despite being proposed more than 5 years ago, a multi-generational community reciprocal transplant has to our knowledge yet to be carried out. Here we describe a community selection experiment where whole communities are exposed to modified environments and whose effects are assessed using a full community reciprocal transplant assay.

Floating aquatic plant communities

We assembled experimental communities of four species of floating aquatic plants: the angiosperms *Lemna minor* (here designated Lm),*Spirodela polyrhiza* (Sp) and *Wolffia columbiana* (Wc), and the liverwort *Ricciocarpus natans* (Rn). These are small, morphologically simplified plants that generally consist of no more than a flattened leaf-like frond that may bear one or more submerged roots. The plants reproduce vegetatively in most conditions by releasing a daughter frond every few days from a meristem on the lower surface of the parental frond in the case of the three angiosperms, and by fragmentation in the case of the liverwort. Because they are widespread and abundant, are easily maintained and manipulated in the laboratory or outdoors, and possess highly reduced morphology and simplified physiology, they are being increasingly used as a tractable model system in ecology and evolution (Laird and Barks 2018, Hart et al. 2019, Vu et al. 2019). They are particularly well suited for a community selection experiment since their small size allows for large populations and high replication, and their rapid reproduction permits more than a dozen generations within a single season.

We use community mean frond area as our measure of phenotype since it is a simple and easily measurable trait common to all four species that has ecological relevance, and one that should respond to environmental conditions via physiological, ecological and evolutionary processes. The frond is essentially a photosynthetic sheet whose area may fluctuate to balance light capture and photosynthesis (growth) with the production of daughter fronds (reproduction) (Vasseur et al. 1995). Average frond area varies widely among the four species (Rn has fronds roughly twice as big as Sp, 5x bigger than Lm, and 66x bigger than Wc), and therefore shifts in species composition in a community will greatly change mean frond area as well as the total number of individuals in the community.

Optimal leaf size in plants depends on the interaction of temperature, light, water and nutrient availability and influences fitness through its effect on total light capture and photosynthesis, thermoregulation and transpiration (Parkhurst and Loucks 1972, Anten et al. 1995, Hirose et al. 1997). In land plants, low irradiance tends to lead to the production of larger leaves. This is the case for shade versus sun leaves of the same plant (Rozendaal et al. 2006), mean leaf size for plants within species along environmental gradients (Petritan et al. 2009, Kichenin et al. 2013), and among species adapted to different environments (Hamann 1979, Ackerly and Reich 1999). In species consisting of only a single leaf or frond, this standard physiological response should be compounded since it will also capture shifts in biomass allocation away from roots and into shoots when light is limiting, (Brouwer 1962; Poorter & Nagel 2000). This is the case for Lm whose root:frond area ratio shifts in response to both light and nutrient availability (Cedergreen and Madsen 2002). In addition to these ecological and plastic responses, there is evidence that frond size in Lm has a genetic

basis (Vasseur and Aarssen 1992, Vasseur et al. 1995), and that populations in the field sustain a surprisingly large amount of genetic variation (Vasseur et al. 1993, Cole and Voskuil 1996). Furthermore, frond (or more generally leaf) area has been identified as both a response and effect trait due to its correlations with both environmental variables and rates of photosynthesis and growth (Lavorel and Garnier 2002). That variation in mean frond area can be influenced by several processes, respond to multiple environmental variables, and affect community and ecosystem properties, justifies its use as a focal trait in our community selection experiment.

Design of a community selection experiment

A community selection experiment begins with a source community of several species, collected from its natural environment. The community should ideally be well-adapted to its environment and in a state of evolutionary and ecological equilibrium. The experiment is conducted in two phases. Phase 1 is the selection phase, in which communities are cultured in modified environmental conditions. Phase 2 is the relaxation phase, in which the original conditions are restored to all communities (Fig. 2). In Phase 1, a sample of the ancestral source community is transferred to a modified environment and propagated for several or many generations, leading to a derived community. At the same time, a replicate sample is maintained in the original environment, so that it retains the attributes of the ancestral community. The average value of a character may become modified in the derived community relative to the ancestral community. The processes responsible for this modification are evaluated by a reciprocal transplant assay at the end of the selection phase. To perform this assay, samples from both the ancestral and derived communities are transplanted into both the original and modified environments. After a lag of two or three generations, to allow any carry-over or maternal effects to decay, the phenotypes of all species from the community are scored. The results of the assay can then be used to partition the contributions of sorting, plasticity and adaptation, and their interactions, to overall phenotypic change.

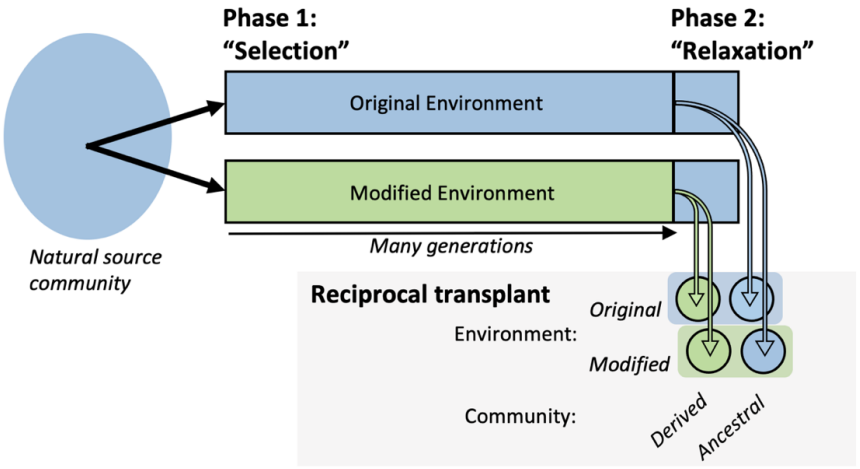

Fig. 2. The design of a basic community selection experiment.

The results of the reciprocal transplant assay can be compared with data from the experiment itself. First, measurements at the beginning of Phase 1 correspond with the ancestral community in the original environment and express the initial state of any given character. Secondly, the equivalent measurements at the end of Phase 1 correspond to the derived community in the modified environment, and express the combined effects of plasticity, sorting and adaptation. Thirdly, any change that has occurred in the modified environment by the end of the second generation in Phase 1 can be confidently attributed to plasticity, because there has not yet been enough time for sorting or adaptation to cause substantial change. Hence, phenotypes at this point are expected to be similar to those expressed by the ancestral community in the modified environment in the

reciprocal transplant assay. Finally, Phase 2 corresponds to the derived community cultured in the original environment, where any persistent change must be attributed to sorting or adaptation. This approach is less rigorous, because it compares the state of the same communities at different times, but it will highlight any unexpected, and potentially questionable, outcome of the reciprocal transplant assay.

In this report, we describe the outcome of a community selection experiment using four species of floating aquatic plants, and measure how mean frond area responds to changes in light and nutrient availability. The objective of our experiment was to monitor phenotypic change in a whole community over several generations and then evaluate the contributions of plasticity, sorting and adaptation.

MATERIALS AND METHODS:

Source community

The source plant community was isolated from a eutrophic pond adjacent to fallowed agricultural fields on McGill University's Macdonald campus, Quebec, Canada (45° 42' N, 73° 94' W). The pond sustains a diverse community of floating macrophytes consisting of three species of duckweed (Lm, Sp and Wc) and one liverwort (Rn). In June of 2018, we took large samples consisting of hundreds of thousands of individuals, taken from 10 microsites around the pond to ensure that our samples were representative of the pond's overall intraspecific genetic diversity. Samples were then combined, thoroughly mixed, and then sorted into the constituent species which would be used to inoculate the experimental communities.

Experimental design

Our community selection experiment consisted of propagating samples isolated from the source community in outdoor mesocosms under a range of environmental conditions. Whereas the simplified description of a general community selection experiment outlined above involves propagating the ancestral community in both original and modified environmental conditions, here we use eight distinct modified conditions in addition to the original environment, essentially running eight separate community selection experiments, allowing us to generalise our results.

The experiment was conducted at the LEAP research facility at McGill's Gault Nature Reserve in Quebec, Canada (45° 32' N, 73° 08' W) (Fugère et al. 2020). 18 180L mesocosms were filled with water piped from Lac Hertel, a pristine mesotrophic lake on the reserve, 1km upstream of the experiment. The water was sieved to remove fish and tadpoles but contained intact communities of zooplankton and phytoplankton. Mesocosms were then seeded with identical mixtures of the four species of macrophytes isolated from the source community and left to settle for one week. The four species were added in equal abundances by wet mass, 35g per species per mesocosm (which translates to roughly 23,000 individuals for Lm, 5,400 for Sp, 87,500 for Wc, and 4,000 for Rn in each mesocosm). A factorial gradient of light and nutrients was then applied to the mesocosms with three levels of each factor. This gives two replicate mesocosms for each of nine unique sets of environmental conditions. The mesocosms were arranged in a split-plot design with nutrient level and replicate randomly positioned within each light level. Light (% shading) and nutrients (dissolved Nitrogen and Phosphorus, DN and DP) were measured at the site of the source community at the time of sampling and the experimental treatment levels were determined so that the intermediate treatment (medium light, medium nutrients) mimicked these conditions. We refer to this treatment level as the "original" environment and the other eight as "modified" environments. The gradient in light availability was established with the use of varying layers of 50% shade cloth, quadrupling between levels (Low= 3%, Medium = 12%, High = 50%, in reference to an unshaded site). The nutrient gradient was established by the addition of inorganic nitrates and phosphates (KNO_3 and H_2KPO_4), maintaining a constant ratio of DN and DP. The natural water from Lac Hertel served as the low nutrient level (DN=200 μgL^{-1}, DP=10 μgL^{-1}), nutrients were quadrupled for the medium level (DN=800 μgL^{-1}, DP=40 μgL^{-1}), and quadrupled again for the high level (DN=3200 μgL^{-1}, DP=160 μgL^{-1}). DN and DP were measured in all mesocosms every two weeks and topped off to maintain the treatment nutrient levels throughout the experiment. Nutrient samples were analysed for DN with a continuous flow analyser (OI Analytical Flow Solution 3100 ©) using an alkaline persulfate digestion method, coupled with a cadmium reactor, following a standard protocol (Patton and

J.R. 2003) and for DP using a standard protocol (Wetzel and Likens 2000). All samples were analysed at the GRIL- Universite du Quebec a Montreal (UQAM) analytical laboratory.

The experiment was conducted in two phases: Phase 1 which applied the nine treatment combinations of light and nutrients to the mesocosms over 12 weeks ("Selection phase", Fig. 3a), and Phase 2 where all mesocosms were reverted to the original (intermediate) conditions for an additional two weeks ("Relaxation", Fig. 3c). Communities were randomly sampled every two weeks to measure frond area and estimate the relative abundance of each species. Communities were first mixed to eliminate spatial aggregation, then sampled by taking three blind scoops using a small net (diameter = 3cm) which yielded hundreds of individuals. From this sample, individuals were sorted by species and exhaustively counted to obtain species relative abundances. Phenotypes were then measured for ten individuals of each species. In the case that samples included fewer than ten individuals for a rare species, we continued to blindly sample, and sort out the species until we obtained sufficient material. The ten were selected again by blindly scooping into each species-specific sample, this time using a bacterial loop which isolates a single individual at a time. These ten individuals of each species were then photographed and analyzed in imageJ to obtain frond area. To minimize variation due to frond age, only mature individuals were included, using only those that already had a daughter frond budding from them. From estimates of species' mean frond area and relative abundances we calculated community mean frond area for each mesocosm as $\sum_{i=1}^{s} (\mathrm{FA}_i \times p_i)$, where FA_i is mean frond area for species i and p_i is the proportion of species$i$ in the community.

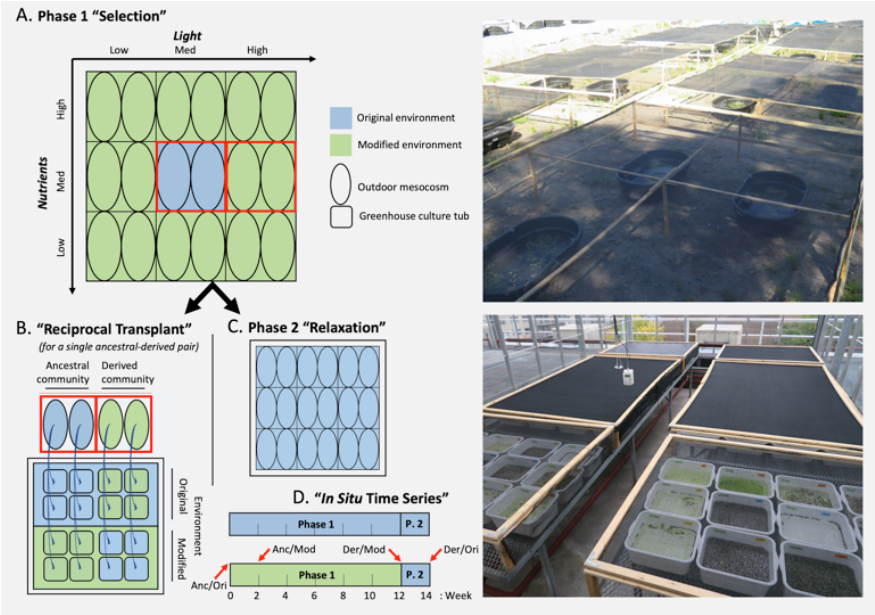

Fig. 3. Experimental design. A) 18 mesocosms with identical initial species compositions were subjected to a crossed gradient of light and nutrients. Two replicate mesocosms were kept in each of eight unique modified environments as well as the original environment (medium light-medium nutrients) which was designed to mimic the environmental conditions of the natural source community from which the plants were collected. After 12 weeks of growth (Phase 1), phenotypic change was assessed using both a reciprocal transplant trial and an in situ time series. B) At the end of Phase 1 samples were taken from all mesocosms to inoculate a reciprocal transplant trial in a research greenhouse. Communities from the original environment are referred to as ancestral and communities from modified environments are referred to as derived. Only one ancestral-derived pair is shown here. C) Phase 2 consisted of returning all mesocosms to the original environmental conditions for an additional two weeks. D) Using both Phase 1 and Phase 2 measurements, we can obtain an in situ time series with an identical structure as the reciprocal transplant data to use as an independent

source of evidence.

Reciprocal transplant trial

At the end of Phase 1, we used a reciprocal transplant trial to assess the consequences of 12 weeks of growth in modified environments on community mean phenotype. At this point we refer to communities grown in Phase 1 modified environments as "derived", and communities grown in the Phase 1 original environment as "ancestral". By assaying all communities, both ancestral and derived, in both original and modified environments, we were able to quantify the contributions of plasticity, sorting and adaptation to overall community change.

Random samples (5% of the mesocosm surface) were taken from each mesocosm at the end of Phase 1 and used to inoculate the reciprocal transplant, located in a research greenhouse in McGill University's Phytotron. For each of the eight derived communities, a pair-wise reciprocal transplant assay was conducted with the ancestral community, assaying both communities in both modified and original environments. Each of the eight derived-ancestral pairs resulted in 16 growth assays – two replicate mesocosms per community, each assayed in two environments, replicated twice (Fig. 3b).

These assay environments were assembled in the greenhouse in 10L tubs filled with natural water and plankton communities from Lac Hertel, the same as in Phase 1. Nutrient and shading treatments were applied in the same way as for Phase 1. The mesocosm samples were used to inoculate the assay tubs at half of the density as that in the mesocosms at the end of Phase 1 to allow for rapid population growth. After two weeks (roughly one to two generations), we measured frond area on 10 randomly sampled individuals of each species. Total number of fronds of all species in all assays were counted at the beginning and end of the reciprocal transplant to obtain the average number of generations.

In situ time series

Phase 2 of the experiment consisted of reverting all mesocosms to the original environmental conditions for an additional two weeks. At week 12, after samples had been taken from the mesocosms to be used in the reciprocal transplant trial, the mesocosms were all reverted to medium light and nutrient levels (Fig. 3c). Light levels were obtained by adding or removing shade cloth. Since during Phase 1, dissolved nutrient levels of all mesocosms consistently dropped below the medium treatment level by the end of each two-week period, Phase 2 levels could be obtained by modifying the final bi-weekly nutrient addition.

The objective of Phase 2 was to obtain a second set of measurements*in situ* to compare with the reciprocal transplant. As for the reciprocal transplant, phenotypes were obtained for both the ancestral and derived communities in both original and modified environments. Measurements of the ancestral community in the original environment were obtained from the week 1 readings at the beginning of Phase 1; measurements of the derived communities in the modified environments were obtained from the week 11 readings at the end of Phase 1; measurements of the ancestral community in the modified environments were obtained from week 3 readings, two weeks (roughly one to two generations) after treatments were first applied; and measurements of the derived communities in the original environment were obtained at the end of Phase 2, two weeks (roughly one to two generations) after all mesocosms were reverted to the original environmental conditions. We refer to this heterogeneous set of measurements as the "*in situ*time series" (Fig. 3d) which serves as a check on the more rigorous reciprocal transplant assay and a separate source of evidence.

Statistical Analysis

At the end of Phase 1, we used a simple 1-way Anova to evaluate if community mean frond area had significantly diverged among the 9 environments. Environment was the fixed factor, and given that there were only two mesocosms per level of environment, mesocosm represents the error variance. To help visualise shifts in species relative abundances over Phase 1, we calculated competition coefficients for each species in each environment using abundance at the final Phase 1 time point. These were calculated based on the classical method for selection coefficients (Bell 2008, p.62) when measuring competition between genotypes

or species, extended to full communities. The competition coefficient of species 1, c_1, is given by

$$c_1 = \frac{r_1 - r_2}{r_2} ln(2) = \frac{1}{g} \ln \left(\frac{\frac{f_{1\ final}}{f_{2\ final}}}{\frac{f_{1\ initial}}{f_{2\ initial}}} \right)$$

where r is the growth rate in doublings per day of either the focal species (1) or the total community (2), g is the number of generations of the total community, $f_1$is the relative frequency of the focal species, and $f_2 = 1 - f_1$ is the relative frequency of all other species bar the focal species.

Although we aimed to replicate the treatment environmental conditions in the reciprocal transplant, given that it took place in smaller volume tubs in a greenhouse as opposed to outdoor mesocosms, other aspects of the environment may have differed that could have affected plant growth. We therefore calculated standardized deviations in mean frond area to compare Phase 2 phenotypes with those from the reciprocal transplant (derived communities in original environment) for all communities. For each species, the deviation in mean frond area from the overall mean was calculated for each treatment combination and standardized by dividing it by the overall mean. These standardized deviations are independent of size and allow the species to be combined in the same analysis. They were calculated separately for the Phase 2 and the reciprocal transplant communities and then compared using linear regression, calculating the coefficient of correlation.

Eco-Evo Anova

The outcome of the community selection experiment was evaluated with a reciprocal transplant consisting of assaying the two community types (ancestral and derived) in each of two environments (original and modified) at the end of which phenotypes were scored on a random sample of individuals from each assay. The phenotype Y of any individual is assumed to be governed by the additive effects of i$^{\text{th}}$Environment E, the j$^{\text{th}}$ Community C, and the k$^{\text{th}}$ Species S, plus their interactions, plus error.

$$Y_{\text{ijkl}} = constant + E_i + C_j + S_k + (EC)_{\text{ij}} + (ES)_{\text{ik}} + (CS)_{\text{jk}} + (ECS)_{\text{ijk}} + e_{\text{ijkl}}$$

The contribution of any source of variation can then be estimated by a three-way factorial Anova. This will enable the contribution of physiological, ecological and evolutionary processes leading to the overall response to be evaluated (Table 1). There are two complications, however. First, the number of individuals may differ among species, giving rise to an unbalanced data structure. Secondly, the relative abundance of the species may differ between communities, giving rise to an unbalanced and disproportional data structure. If these were merely nuisances, the analysis could be rescued by some statistical procedure such as resampling. In fact, both are essential features of the data, representing the ecological structure of the community and how it is altered by exposure to a novel environment.

Such a preliminary three-way Anova would give a rough idea of the structure of the data, but is inadequate given the difficulties we have pointed out. For a more detailed analysis, the three-way classification is broken up into three two-way analyses: 1. The Community-Environment analysis is straightforward because the data structure is balanced. 2. The Species-Environment structure is unbalanced but proportional, because the species have the same abundances in the two assay environments. 3. The Species-Community analysis is more difficult when the species composition of the ancestral and derived communities differ, because the data are then both unbalanced and disproportionate. This inflates the differences between the Community means because of the difference in frequency of the species, and leads to an underestimate of the Species x Community interaction, which may even yield a negative Sum of Squares (SS). One way out of this difficulty is to use an appropriate uniform weighting for each species, which yields an unbiassed estimate of the Species x Community term (see Snedecor & Cochran 1967 section 16.6 p 484; the analysis of unbalanced data is reviewed by Hector et al. 2010). The effect of this procedure, however, is to remove the effect of the change in species composition, whereas we wish to retain it. This can be done by using this adjusted Species x Community SS, from which the effect of any shift in species composition has been removed, while partitioning

the Community SS into additive components that represent ecological and evolutionary processes. The mean phenotypes for the two communities are:

$$Ancestral: \ \mathrm{Y_{anc}} = \frac{\sum \ (n_{i,anc} \ \ Y_{i,\ anc})}{\sum n_i}$$

$$Derived: \ \mathrm{Y_{der}} = \frac{\sum \ (n_{i,der} \ \ Y_{i,\ der})}{\sum n_i}$$

where the abundance of the $\mathrm{i^{th}}$ species is $\mathrm{n_i}$ and its mean phenotype in the $\mathrm{j^{th}}$community is $\mathrm{Y_{ij}}$. Hence the difference in mean phenotype is:

$$N\left(Y_{\mathrm{der}} - Y_{\mathrm{anc}}\right) = \ \sum \left(n_{i,\ der}\ Y_{i,\ der} - n_{i,anc}\ Y_{i,anc}\right) = \sum Y_{i,der}\ \Delta n_i + \ \sum n_{i,anc}\ \Delta Y_i$$

where $\mathrm{N = \Sigma\ n_i}$, $\mathrm{\Delta n_i = (n_{i,der} - n_{i,anc})}$, and $\mathrm{\Delta Y_i = (Y_{i,der} - Y_{i,anc})}$. The first term on the right-hand side is the ecological effect, generated by a shift in species composition, and the second term is the evolutionary effect, generated by a change in species mean phenotype independently of assay environment. The parallel to the Price decomposition of phenotypic change is clear (Price 1970, Collins and Gardner 2009). The first term is a covariance: the change in species abundance $\mathrm{\Delta n_i}$ is caused by differences in growth rate, with $\mathrm{\frac{1}{2}\ EN\ (\Sigma\ Y_{i,der}\ \Delta n_i)/(S\text{-}1) = Cov(Y_{i,der},\ \Delta\ n_i)}$. The second term is the weighted change in mean species phenotype, caused in this case by natural selection (or some other evolutionary process); any physiological change (plasticity) is captured by the Environment main effect. The overall unadjusted Community SS is equal to $\mathrm{\frac{1}{2}\ EN\ (Y_{der} - Y_{anc})^2}$, so this can be partitioned into three components:

$$Community\ Ecology\ : Eco = \ \frac{1}{2}\mathrm{EN}\left(\sum Y_{i,der}\ \Delta n_i\right)^2$$

$$Community\ Evolution\ : Evo = \ \frac{1}{2}\mathrm{EN}\left(\sum n_{i,anc}\ \Delta Y_i\right)^2$$

$$Community\ Interaction\ : Eco\ \times Evo = EN\ \left(\sum Y_{i,der}\ \Delta n_i\right)\left(\sum n_{i,anc}\ \Delta Y_i\right)$$

The Community Ecology term expresses the contribution of shifts in the relative abundance of species (sorting) to the Community SS. The Community Evolution term expresses the contribution of any consistent shift in mean species phenotype. The third term, the Eco x Evo interaction, is a sum of products that is positive if abundance and phenotype score change in the same direction, and negative otherwise. It represents a covariance that might be substantial if, for example, those species that have adapted more successfully (through an increase or decrease of phenotype score) have thereby increased in frequency in the community. These three terms do not lead straightforwardly to estimates of variance components, but a rough measure of the relative contribution of ecological and evolutionary effects can be calculated by neglecting the covariance-like interaction term, expressing the other two as fractions of their total, and multiplying this fraction by the Community variance component.

The Species x Community interaction expresses how the overall phenotypic difference between communities varies among species, independently of environment. The highest-order interaction of Species x Community x Environment expresses variation among species in the extent of specific adaptation to environment, and is estimated by difference.

In practice, any real experiment may differ from this ideal model. The sample of species taken from each Community may not be proportional to its relative abundance, for example because it is desired to measure equal numbers of individuals from each species, or because some species have become so rare that only

very few individuals are available for measurement. We have mitigated these shortcomings by randomly resampling (with replacement) a fixed number of individuals from each species in proportion to its known relative abundance and analysing this random sample. The values of parameters (such as SS and variance components) are then estimated as averages over a large number of independent resamples.

Our community selection experiment used eight distinct modified environments and as such, we analysed each ancestral-modified pair separately. Since the ancestral communities assayed in the original environment are identical for each pair-wise transplant, the same assays were used for all pairings. Given that these analyses are not independent, we obtained estimates of the overall contributions of plasticity, sorting and adaptation to variance by taking the averages of all pair-wise reciprocal transplants. The same Eco-Evo Anova was used to analyse the *in situ* time series data whose results we then compared with those of the reciprocal transplant as a separate source of evidence.

Table 1. Interpretation of three-way Anova of a reciprocal transplant experiment.

Source	Factors	df	Interpretation
Environment E_i	Fixed: 2 states, Original and Modified	1	Physiological plasticity: variation in average individual phenotype between environments (overall reaction norm).
Community C_j	Fixed: 2 states, Ancestral and Derived	1	Eco-evolutionary dynamics: variation in average phenotypes of communities caused by evolution (natural selection within species causing change in species mean phenotype) or species sorting (selection among species causing shift in community composition) or both.
Species S_k	Random: S species	S – 1	Ecological statics: variation among average phenotypes of species attributable to ancestry.

Source	Factors	df	Interpretation
Env x Com $(EC)_{ij}$	First-order interaction	1	The plastic response has become altered in the Derived community, perhaps by selection. This represents specific adaptation if the character measured is fitness and is greater in the Ancestral/Original and Derived/Modified than in the converse combinations. Species sorting is not responsible because species composition is balanced between one set of community-environment combinations (Ancestral/Original plus Derived/Modified) and the other (Ancestral/Modified plus Derived/Original).
Env x Spe $(ES)_{ik}$	First-order interaction	S – 1	Variation in degree and direction of plasticity among species (variation among species' reaction norms).
Com x Spe $(CS)_{jk}$	First-order interaction	S – 1	Variation of species mean phenotype between communities, caused by natural selection (not species sorting) varying among species.
Env x Com x Spe $(ECS)_{ijk}$	Second-order interaction	S – 1	Variation in the extent of specific adaptation among species; equivalently, the modification of the plastic response varies among species.
Residual e_{ijkl}	' Error '	4(N-S)	Idiosyncratic variation among N individuals per sample
Total		4N - 1	

RESULTS:

The plants reproduced vigorously during the growing season with initial doubling times of about 8 days for Lm, 15 days for Rn and 10 days for Sp. A large proportion of Wc initially sank to the bottom in

all mesocosms due to transfer shock but recovered in following few weeks. After five weeks' growth all communities had expanded to cover the entire surface of each mesocosm, and further expansion involved overgrowth and the death of senescent individuals. There were strong and consistent changes in community mean frond area, which, as an average over all environmental treatments, fell by about 20%, and by the end of Phase 1, differed significantly between communities (Fig. 4) (ANOVA, $F_{(1,16)} = 89.6$, $p < 0.0001$).

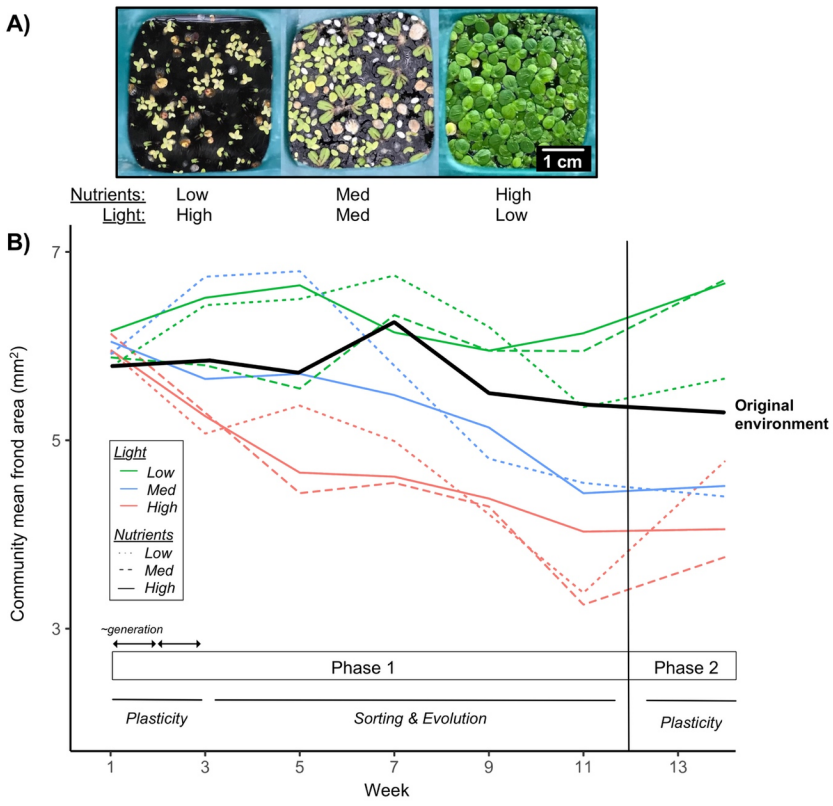

Fig. 4. A) Photos of three communities at the end of Phase 1. B) Community mean phenotype dynamics over 12 weeks of growth in modified environments (Phase 1), followed by an additional two weeks after a reversion to the original environmental conditions (Phase 2). Each line is one of 9 unique environments: 8 modified environments and 1 original environment (medium light-medium nutrients), and the average of two replicate mesocosms. For each mesocosm, community mean frond area is calculated as a species' mean frond area weighted by its relative abundance in the community, summed across all species in the community. Variation in community mean frond area at week 1 is due to idiosyncratic senescence resulting from transfer stress during the 1-week settling time between the initial transfer of plants to the mesocosms (week 0), and when treatments were first applied (week 1).

These differences in community mean frond area were due to both shifts in species relative abundances and phenotypic change within species. By the end of Phase 1, there were large differences between environments in species competitive abilities (Fig. 5). Generally, Lm was the most competitive in all environments and dominated most communities, Rn was most competitive in high light and low nutrient conditions, and Wc in high nutrient conditions, although there were strong interactive effects between light and nutrients making generalisations difficult (Fig. 5). Mean phenotypes shifted consistently for all species over Phase 1, with frond area increasing with increasing nutrient availability and decreasing light (Fig. 6).

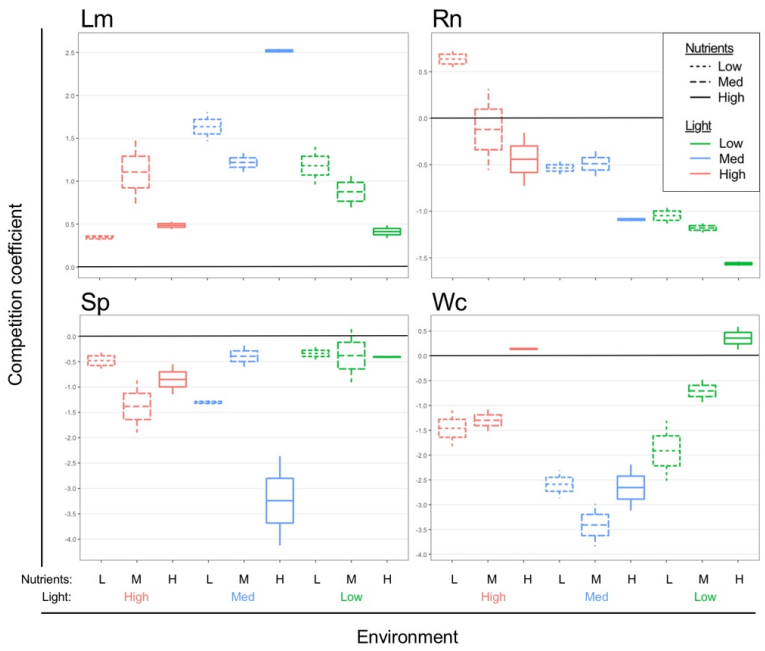

Fig. 5. Competition coefficients after 12 weeks of growth in the original and the eight modified environmental conditions. The horizontal line at 0 indicates no change in relative abundance over Phase 1. (Lm=L. minor, Rn = R. natans, Sp = S. polyrhiza, Wc = W. columbiana.)

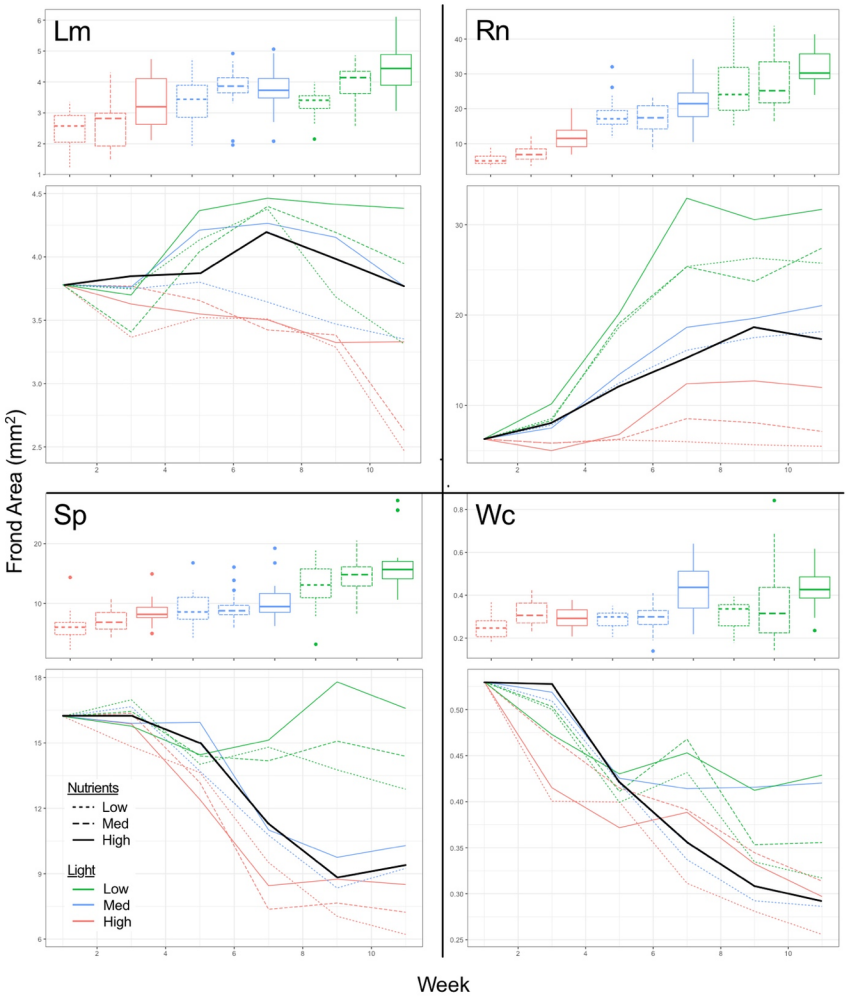

Fig. 6. Changes in frond area of the four species over 12 weeks of growth in the original and the eight modified environments (Phase 1) due to the combined effects of phenotypic plasticity and evolution. Lines are the average of two replicate mesocosms each from which 10 individuals of each species were sampled. The original environment is denoted with a bold black line. Box plots show final differences in frond area among the nine environments for each species at the end of Phase 1 (week 11 measurements only). (Lm=L. minor, Rn = R. natans, Sp = S. polyrhiza, Wc = W. columbiana.)

For both the reciprocal transplant and the *in situ* time series, the overall phenotypic variance among plants is generated by three factors: Species (the four species composing each community), Environment (Original vs Modified) and Community (Ancestral vs Derived). The interpretation of these factors and their interactions is shown in Table 1. The Species effect is the extent to which the evolved differences among species are maintained when the conditions of life change. The main effect of Environment reflects the plastic modification of the phenotype of an individual by the conditions it experiences during its lifetime. The Community term expresses both ecological and evolutionary change and is partitioned into these two components and their interaction.

We used the Eco-Evo Anova to estimate the contributions of each source of variation to overall phenotypic variance for each community. This produces a separate set of estimates for each of the two replicate meso-

cosms in each of the eight modified environments (Table S1). Although the reciprocal transplant and *in situ* time series data are arguably independent, the set of 16 estimates within each are not since the ancestral community assayed in the original environment was identical for each ancestral-derived pairing. For this reason, for both the data sets, we calculated the average contributions of each source of variation to overall phenotypic change across all eight modified environments (Fig. 7).

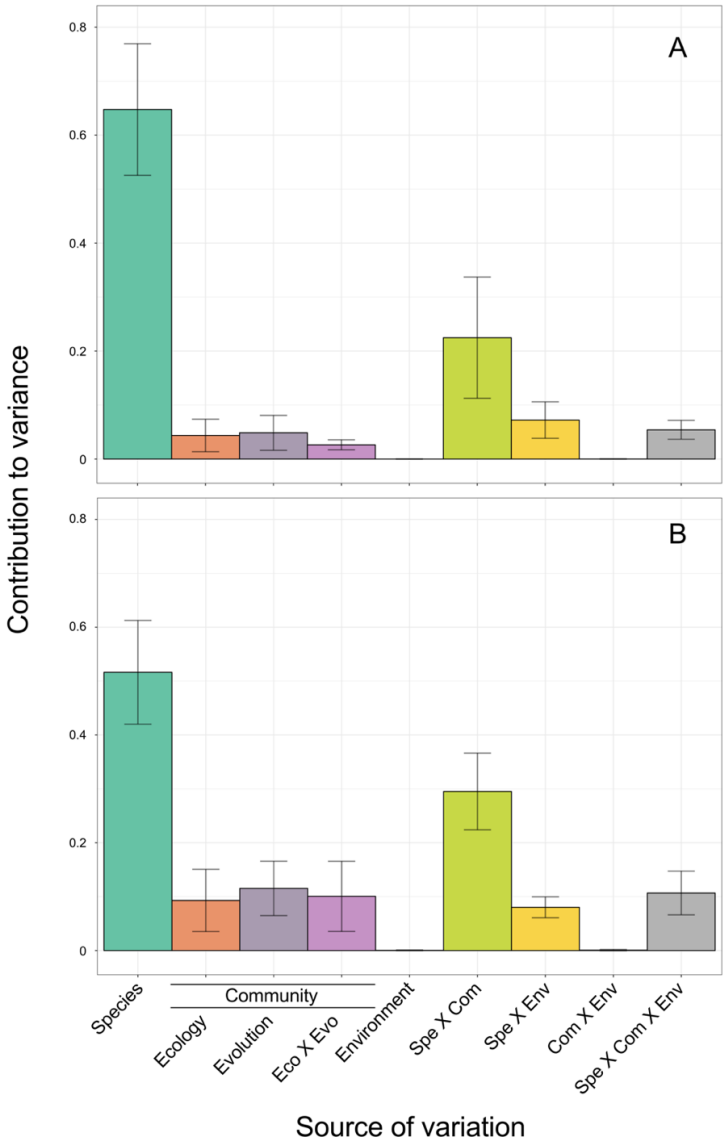

Fig. 7. Contributions of all sources other than residual variance to overall variation in community mean frond area for the ***(A)****reciprocal transplant trial, and* ***(B)*** *in situ time series. Contributions are the result of averaging estimates for two replicate mesocosms for each of eight modified environments. The community term is partitioned into variation due to ecology, evolution and their interaction. Error bars are 95% confidence intervals and show the variation in contributions among the eight modified environments.*

To further compare these two sources of evidence, the reciprocal transplant and the *in situ* time series, we calculated standardised deviations in species mean frond area as a way to compare phenotypic variation among environments for each species in the outdoor mesocosms with those of the greenhouse tubs in the reciprocal transplant. These standardized deviations comparing phenotypes in Phase 2 and the reciprocal transplant (derived communities in original environment) are highly correlated ($r^2 = 0.80$) with a regression coefficient ($b = 0.91$) which overlaps unity (95% C.I. 0.75, 1.08). We conclude that the phenotypes expressed during Phase 2 in the outdoor mesocosms were consistent with those in greenhouse conditions of growth.

DISCUSSION:

In our community selection experiment, we found that community mean frond area responded strongly to changes in both light and nutrients (Fig. 4), driven by both inter- and intra-specific trait change. The primary source of variation in frond area is attributed to Species. The pronounced initial morphological differences between the four species largely persist when light and nutrients are manipulated, so that the Species term accounts for about half of the overall variance among individuals (excluding residual variance) (Fig. 7). Interactions between Species and both Environment and Community are also prominent. For example, there is a general tendency for fronds to become larger at low light levels and high nutrient levels, due to both plasticity and adaptation. This parallels the normal plastic response to light and nutrients of herbaceous terrestrial plants grown from seed (Meziane and Shipley 1999, 2001) and confirms that our observations are consistent with these well-established ecophysiological generalizations. However, different species do not invariably respond to the same extent. For example, Lm and Wc show this expected plastic response to nutrients at low and high light levels, but not at intermediate light, whereas Rn shows this plastic response at medium and high light levels, but not under low light (Fig. S1 & S2). Likewise, Rn and Sp had strong, but opposite plastic responses — whereas frond area increased in low light and low nutrient environments for Sp, it decreased for Rn (Fig. S1 & S2). These Species x Environment interactions were so strong that the overall contribution of plasticity was negligible. Similar interactions have been reported for terrestrial plants (Meziane and Shipley 1999). Likewise, there was considerable variation among species in the extent to which frond size shifted due to adaptation. Whereas all species evolved larger fronds in low light and smaller fronds in high light, the evolutionary response to nutrients was extremely variable resulting in a strong Species x Community interaction (Fig. S1 & S2).

It was more surprising to find that the Community term, expressing both sorting (ecology) and adaptation (evolution), accounted for about one-quarter of the variance, with roughly equal contributions from each (Fig. 7). This result is in line with other studies that have found the rate and effect size of evolution to be of comparable magnitude to that of ecological processes in determining community structure and dynamics (Hairston et al. 2005, Palkovacs et al. 2009, Bassar et al. 2010, Pantel et al. 2015) and further emphasizes the importance of including the possibility of rapid evolution when considering how communities respond to environmental change (Fugère et al. 2020). The interaction between Ecology and Evolution terms was both strong and unexpected. If selection within species (Evolution, representing adaptation) and selection between species (Ecology, representing sorting) act in the same direction, then fronds will evolve to become larger (or smaller) in all species, while larger (or smaller) species become more abundant. We found instead that sorting and adaptation tended to act in opposite directions (Fig. 8); in communities where species evolved smaller fronds, the larger species had a competitive advantage and increased in relative abundance, and vice versa. This response was largely dependent on community productivity — in increasingly stressful environmental conditions (high light and/or low nutrients) that resulted in lower overall community productivity, fronds of all species evolved to become smaller, whereas the larger species (Rn and Sp) outcompeted the smaller species (Lm and Wc). Likewise, in beneficial environmental conditions (low light and/or high nutrients) that resulted in higher overall community productivity, species tended to evolve larger fronds, but the smaller species (lamely Wc) had a competitive advantage. Possible explanations as to why selection may not act in the same direction within and among species include the presence of inter-specific allelopathic interactions, which have been identified for several species of duckweed (Wolek 1974, Jang et al. 2007, Bich and Kato-Noguchi 2012), or other species interactions resulting in negative-frequency dependence (Armitage and Jones 2019). Alternatively, within species selection may have altered frond area due to an environmentally

induced covariance between phenotype and fitness (Rausher 1992), although the reciprocal transplant should theoretically disentangle this covariance by separating the genetic from plastic sources of frond size. Finally, it is possible that less stressful environments (low light, high nutrients) resulted in selection favouring an increase in frond size indirectly by acting on a genetically linked trait, and at the same time enabling the relative proliferation of the smaller species with higher potential growth rates.

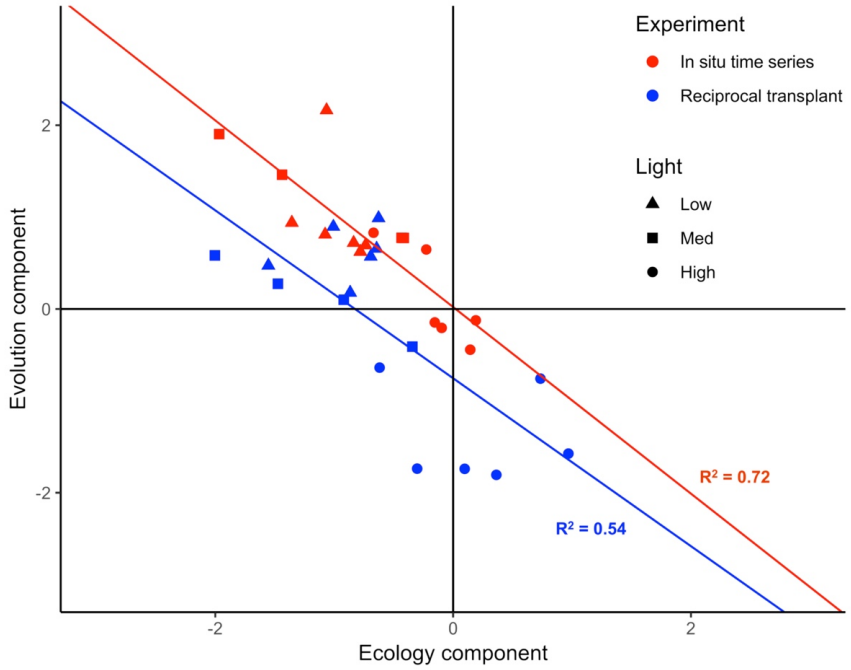

Fig. 8. Correlation between the contributions of species sorting (ecological component) and adaption (evolution component) to variation in phenotype for the reciprocal transplant and general reversion experiments. Each point is a single mesocosm.

Any real experiment will deviate from the ideal community selection experiment as outlined in the introduction. For example, it is unlikely that the source community is in a static state of ecological and evolutionary equilibrium, and therefore the community mean phenotype of the ancestral community in the original environment will undoubtedly change over the course of Phase 1 through seasonal species turnover, ongoing response to variables like day length and temperature, or imperfect replication of the source community's environmental conditions. This was the case for our experiment where mean frond area changed for three of the four species over the course of Phase 1 in the original environment (Fig. 6). In addition, we began Phase 1 with equal relative abundances of all species in each community and not with those of the source community, potentially throwing communities out of equilibrium, which further explains shifts in the community mean frond area over Phase 1 due to sorting. The reciprocal transplant and subsequent partition of variance into its components is based on a comparison between all communities at the end of Phase 1 and therefore does not incorporate any potential change in the ancestral community, but instead attributes variation in phenotype among communities accumulated over the course of Phase 1 to plasticity, sorting and adaptation. Reassuringly, the strikingly similar results between our reciprocal transplant (that discounts change in the ancestral community over Phase 1) and the *in situ* time series, indicates that the change in frond area in the ancestral communities was insignificant compared to the differences between ancestral and derived communities. Both tests produced extremely similar results, both in terms of the relative contributions to variance (Fig. 7), and the negative eco-evo relationship (Fig. 8). These results are further strengthened by the tight correlation of standardized deviations in frond area comparing phase 2 with the reciprocal transplant, despite

obvious environmental differences between the source community, our outdoor mesocosms and greenhouse culture tubs.

The agency responsible for evolutionary change in our experiment is uncertain. Epigenetic changes might be transmitted over several generations because reproduction was exclusively vegetative (Verhoeven and Preite 2014). This would mimic genetic change and over the long-term lead to selection for adaptive plasticity. However, the main effect of Environment is very small, and we have shown that evolved phenotypes were conserved during the transition from Phase 1 to Phase 2, and from Phase 1 to the reciprocal transplant experiment. Alternatively, this evolutionary change could be caused by strong natural selection acting on genetic variation. This would require a large amount of pre-existing genetic variation in the populations given the short time span of the experiment. It could be assumed that populations of such fast growing, asexual species would be made up of only a small number of clones, especially in colder climates where populations likely go through an annual genetic bottleneck in the winter. There is however considerable evidence that duckweed populations maintain a surprisingly high level of within site genetic diversity. In *L. minor* , the most studied of the four species, allozymic and microsatellite sequence analysis of field populations showed in all cases a high degree of within population genetic diversity (Vasseur et al. 1993, Cole and Voskuil 1996, El-Kholy et al. 2015). The most extensive survey (Vasseur et al., 1993) found on average 20 genotypes per site based on 18 loci, 13 of which were polymorphic. Furthermore, Ziegler et al. (2015) concluded from a common garden growth experiment using 39 clones of duckweed from 13 species that the majority of variation in growth rate was attributed to variation among ecotypes/clones and not species. This mirrors our own ongoing work using common garden growth assays where we find greater variation in fitness among individuals of Lm within sites than among sites (unpublished). Given this likely high degree of genetic variation within species in our source community, we conclude that strong natural selection acting on standing genetic variation, and not epigenetic change, is likely to have been the process responsible for phenotypic modification (van Moorsel et al. 2019). In similar work using two of the same species (Lm and Sp), Hart et al. (2019), also found that genotypic evolution over 10-15 generations resulted in phenotypic changes which altered competitive hierarchies and therefore community dynamics. Given the enormous population sizes and short generation times of such floating aquatic plants, it is perhaps not surprising that evolutionary processes should play an important role in structuring their communities.

Our experiment has shown how the average phenotype of a community may become modified over the course of several generations by sorting, plasticity, and adaptation. The overall community response, however, could not be reliably predicted from the response of any given species due to a negative correlation between the ecological and evolutionary effects on phenotypic change. Likewise, considering rapid evolutionary change is essential when predicting community trait dynamics in response to environmental change. These results are in line with other recent studies that have demonstrated the importance of rapid evolution in structuring communities in ways which can alter eco-physiological responses and mediate species interactions (Becks et al. 2012, Pantel et al. 2015, Stoks et al. 2016, Hart et al. 2019, Fugère et al. 2020). We conclude that community trait dynamics cannot be understood simply by extrapolating the adaptive response of any single species to the whole community.

Acknowledgments: We thank Elizabeth Hirsch, who helped with data collection. This experiment was supported by a Discovery Grant from the Natural Science and Engineering Research Council of Canada to GB and an Alexander Graham Bell Canada Graduate Scholarship from the Natural Science and Engineering Research Council of Canada to MDJ.

Authors' contributions: MDJ performed the experiment and contributed to the analysis. GB conceived the study and developed the analytical procedure. The manuscript was prepared jointly by MDJ and GB.

Competing interests: The authors declare no competing interests.

Data availability: Raw data from which all figures were generated will be stored in the Dryad repository before publication of the article.

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SUPPLEMENTARY MATERIALS

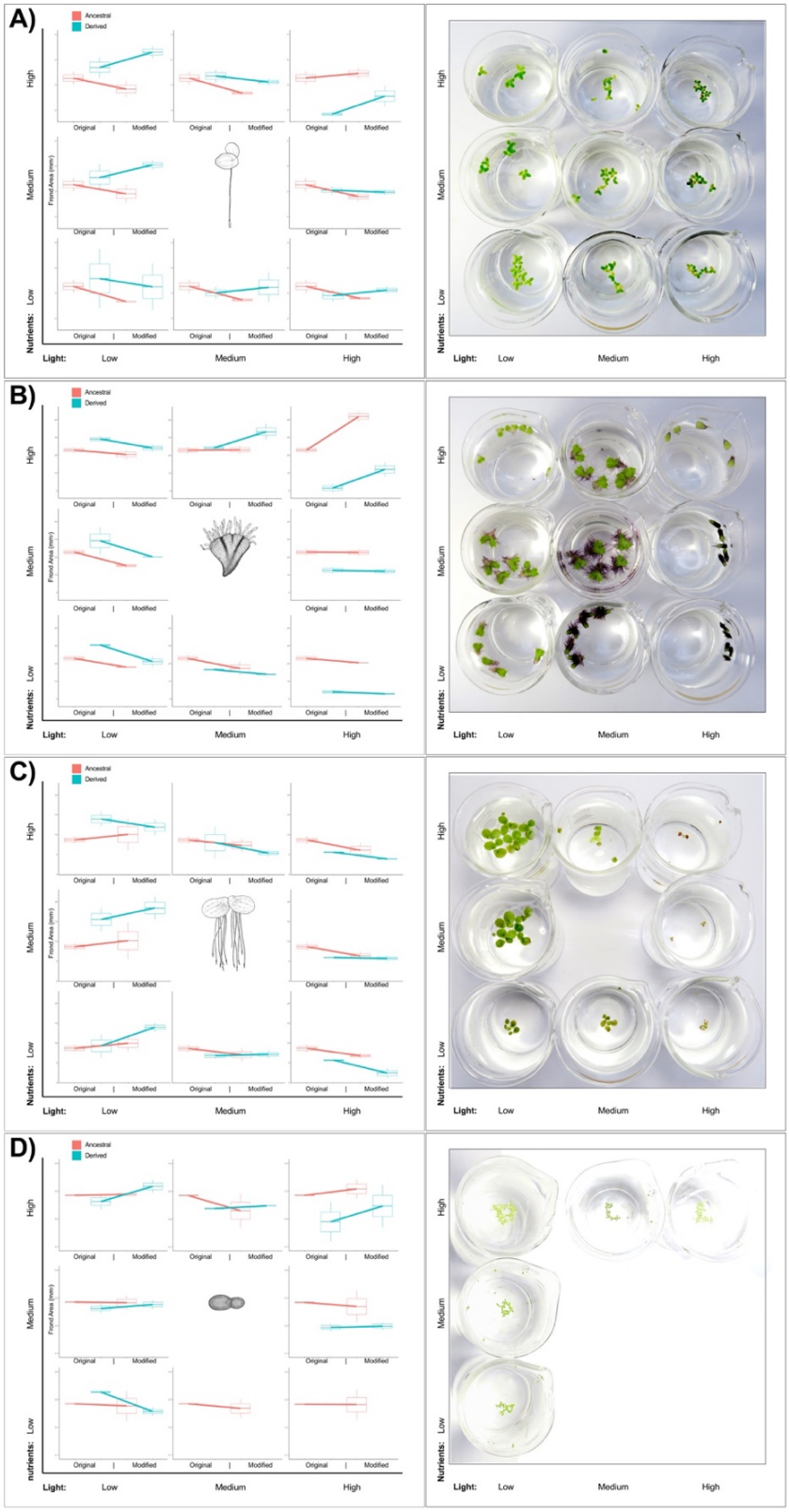

Fig. S1. Phenotypic consequences of 12 weeks of growth in modified environments (Phase 1), assessed with a reciprocal transplant experiment for A) *Lemna minor* , B) *Ricciocarpous natans,* C)*Spirodela polyrhiza* , and D) *Wolffia columbiana* . Community type can be either Ancestral or Derived, assay environment can be either Original or Modified. The Original environment is characterised by the medium light – medium nutrients combination. Each small panel is a reciprocal transplant for a single Ancestral-Derived pair, one for each of the eight unique Derived communities. Each of these is the result of 16 culture tub assays, (two replicate assay tubs × two replicate mesocosms per community × four community-environment combinations). Box plot means are the result of 10 individual plants per culture tub, × two replicate culture tubs, × two replicate mesocosms = 40 measurements. Box plots whiskers represent the variation among the two independent replicate mesocosms. Since the reciprocal transplant was done with the entire intact community, and not with each species separately, the four large panels are not independent. Difference in frond area between assay environments indicates a plastic response whereas differences between community type indicates evolution. Difference in slope between community types indicates evolved differences in the plastic response. The absence of data indicates local extinction of that species in the community. Photographs were taken of individuals from the derived community in the modified environment at the end of the reciprocal transplant.

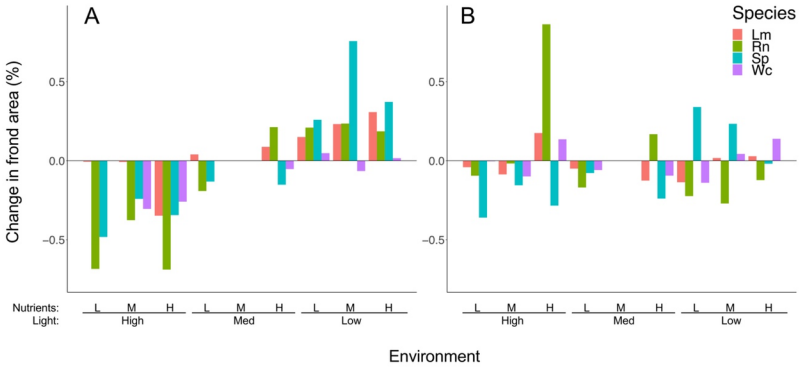

Fig. S2. – Components of intra-specific trait change revealed by the reciprocal transplant. A) Change in frond area due to adaptation. B) Change in frond area due to plasticity. Change in frond area is quantified separately for each species in each ancestral-derived pair (for a single modified environment). Change in frond area due to adaptation is calculated as the difference among mean frond area of the derived and ancestral populations across both assay environments, and standardised by dividing by that of the ancestral population, ((derived – ancestral)/ ancestral). Change in frond area due to plasticity is calculated as the difference among mean frond area of populations assayed in the original and modified assay environments across ancestral and derived populations, and standardised by dividing by that in the original assay environment, [(modified – original) / original].

Table S1 – Partition of Variance in community mean frond area for the reciprocal transplant and the In situ time series. Negative variance components are set to 0.

Reciprocal Transplant Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	Replicate mesocosm: 2	Replicate mesocosm: 2	Replicate mesocosm: 2	Replicate mesocosm: 2	Replicate mesocosm: 2	Replicate mesocosm: 2	Repl meso cosm 2
Source	**df**	**df**	**SS**	**MS**	**MS**	**Variance Component**	**df**	**df**	**SS**	**SS**	**MS**	**MS**	**Vari Com po- nent**
Species	*3*	*3*	*6761*	*2254*	*2254*	*4.02*	*3*	*3*	*4272*	*4272*	*1424*	*1424*	*2.53*
Community	*1*	*1*	*54*	*54*	*54*	*0*	*1*	*1*	*227*	*227*	*227*	*227*	*0*
Ecology			*101*	*101*	*101*	*0.48*			*17*	*17*	*17*	*17*	*0.06*
Evolution			*261*	*261*	*261*	*1.28*			*339*	*339*	*339*	*339*	*1.67*
Eco x Evo			*308*	*308*	*308*	*0*			*129*	*129*	*129*	*129*	*0*
Environment	*1*	*1*	*47*	*47*	*47*	*0*	*1*	*1*	*27*	*27*	*27*	*27*	
Spe x Com	*3*	*3*	*2502*	*719*	*719*	*5.12*	*3*	*3*	*3166*	*3166*	*753*	*753*	*5.34*
Spe x Env	*3*	*3*	*167*	*56*	*56*	*0.36*	*3*	*3*	*139*	*139*	*46*	*46*	*0.31*
Com x Env	*1*	*1*	*15*	*15*	*15*	*0*	*1*	*1*	*49*	*49*	*49*	*49*	*0*
Spe x Com x Env	*3*	*3*	*169*	*56*	*56*	*0.37*	*3*	*3*	*172*	*172*	*57*	*57*	*0.38*
Error	*384*	*384*	*1739*	*5*	*5*	*4.53*	*384*	*384*	*1337*	*1337*	*3*	*3*	*3.48*
Total	*399*	*399*	*11453*				*399*	*399*	*9389*	*9389*			

Reciprocal Transplant Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	Replicate mesocosm: 2	Replicate mesocosm: 2	Replicate mesocosm: 2	Replicate mesocosm: 2	Replicate mesocosm: 2	Replicate mesocosm: 2	Replicate mesocosm: 2
Reciprocal Transplant Environment: 2, High Light – Medium Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 2, High Light – Medium Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 2, High Light – Medium Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 2, High Light – Medium Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 2, High Light – Medium Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 2, High Light – Medium Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 2, High Light – Medium Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 2, High Light – Medium Nutrients Replicate mesocosm: 1	**Replicate mesocosm: 2**	**Replicate mesocosm: 2**	**Replicate mesocosm: 2**	**Replicate mesocosm: 2**	**Replicate mesocosm: 2**	**Replicate mesocosm: 2**
Source	**df**	**SS**	**SS**	**MS**	**Variance Component**	**Variance Component**	**Variance Component**	**df**	**df**	**SS**	**SS**	**MS**	**MS**
Species	*3*	*9653*	*9653*	*3218*	*6.47*	*6.47*	*6.47*	*3*	*3*	*10910*	*10910*	*3637*	*3637*
Community	*1*	*171*	*171*	*171*	*0*	*0*	*0*	*1*	*1*	*11*	*11*	*11*	*11*
Ecology		*39*	*39*	*39*	*0.17*	*0.17*	*0.17*			*56*	*56*	*56*	*56*
Evolution		*56*	*56*	*56*	*0.25*	*0.25*	*0.25*			*65*	*65*	*65*	*65*
Eco x Evo		*77*	*77*	*77*	*0.13*	*0.13*	*0.13*			*-110*	*-110*	*-110*	*-110*
Environment	*1*	*31*	*31*	*31*	*0*	*0*	*0*	*1*	*1*	*25*	*25*	*25*	*25*
Spe x Com	*3*	*609*	*609*	*181*	*1.44*	*1.44*	*1.44*	*3*	*3*	*948*	*948*	*236*	*236*

Reciprocal Transplant Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 1, High Light – Low Nutrients Replicate mesocosm: 2	Replicate mesocosm: 2	Replicate mesocosm: 2	Replicate mesocosm: 2	Replicate mesocosm: 2	Replicate mesocosm: 2	Repl meso cosm 2
Spe x Env	*3*	*228*	*228*	*76*	*0.58*	*0.58*	*0.58*	*3*	*3*	*230*	*230*	*77*	*77*
Com x Env	*1*	*48*	*48*	*48*	*0.01*	*0.01*	*0.01*	*1*	*1*	*15*	*15*	*15*	*15*
Spe x Com x Env	*3*	*124*	*124*	*41*	*0.30*	*0.30*	*0.30*	*3*	*3*	*75*	*75*	*25*	*25*
Error	*384*	*1671*	*1671*	*4*	*4.35*	*4.35*	*4.35*	*384*	*384*	*1938*	*1938*	*5*	*5*
Total	*399*	*12535*	*12535*					*399*	*399*	*14152*	*14152*		

Reciprocal Transplant Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	Replicate mesocosm: 2	Replicate mesocosm: 2	Replicate mesocosm: 2	Replica mesocos 2
Source	**df**	**SS**	**MS**	**Variance Component**	**df**	**SS**	**MS**	**Varian Compo nent**
Species	*3*	*13081*	*4360*	*7.97*	*3*	*11868*	*3956*	*7.03*
Community	*1*	*282*	*282*	*0*	*1*	*434*	*434*	*0*
Ecology		*1*	*1*	*0*		*9*	*9*	*0*
Evolution		*314*	*314*	*1.51*		*320*	*320*	*1.54*
Eco x Evo		*-33*	*-33*	*0*		*105*	*105*	*0.26*

Reciprocal Transplant Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	Replicate mesocosm: 2	Replicate mesocosm: 2	Replicate mesocosm: 2	Replica mesocos 2
Environment	*1*	*112*	*112*	*0*	*1*	*81*	*81*	*0*
Spe x Com	*3*	*4155*	*1419*	*10.35*	*3*	*2921*	*967*	*6.76*
Spe x Env	*3*	*2084*	*695*	*5.05*	*3*	*1409*	*470*	*3.30*
Com x Env	*1*	*20*	*20*	*0*	*1*	*51*	*51*	*0*
Spe x Com x Env	*3*	*142*	*47*	*0.30*	*3*	*588*	*196*	*1.35*
Error	*384*	*2175*	*6*	*5.66*	*384*	*2519*	*7*	*6.56*
Total	*399*	*22051*			*399*	*19871*		
Reciprocal Transplant Environment: 4, Medium Light – Low Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 4, Medium Light – Low Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 4, Medium Light – Low Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 4, Medium Light – Low Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 4, Medium Light – Low Nutrients Replicate mesocosm: 1	**Replicate mesocosm: 2**	**Replicate mesocosm: 2**	**Replicate mesocosm: 2**	**Replic mesocosm: 2**
Source	**df**	**SS**	**MS**	**Variance Component**	**df**	**SS**	**MS**	**Varian Compo nent**
Species	*3*	*10920*	*3640*	*7.32*	*3*	*9606*	*3202*	*6.27*
Community	*1*	*64*	*64*	*0*	*1*	*82*	*82*	*0.06*
Ecology		*12*	*12*	*0.04*		*86*	*86*	*0.41*
Evolution		*25*	*25*	*0.10*		*14*	*14*	*0.05*
Eco x Evo		*28*	*28*	*0.11*		*-18*	*-18*	*0.02*
Environment	*1*	*22*	*22*	*0*	*1*	*29*	*29*	*0*
Spe x Com	*3*	*491*	*279*	*2.23*	*3*	*58*	*6*	*0.02*
Spe x Env	*3*	*199*	*66*	*0.51*	*3*	*204*	*68*	*0.51*
Com x Env	*1*	*25*	*25*	*0*	*1*	*13*	*13*	*0*

Reciprocal Transplant Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	Replicate mesocosm: 2	Replicate mesocosm: 2	Replicate mesocosm: 2	Replica mesocos 2
Spe x Com x Env	*3*	*140*	*47*	*0.35*	*3*	*56*	*19*	*0.12*
Error	*384*	*1331*	*3*	*3.47*	*384*	*1165*	*3*	*3.03*
Total	*399*	*13193*			*399*	*11212*		
Reciprocal Transplant Environment: 6, Medium Light – High Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 6, Medium Light – High Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 6, Medium Light – High Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 6, Medium Light – High Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 6, Medium Light – High Nutrients Replicate mesocosm: 1	**Replicate mesocosm: 2**	**Replicate mesocosm: 2**	**Replicate mesocosm: 2**	**Replic meso cosm: 2**
Source	**df**	**SS**	**MS**	**Variance Component**	**df**	**SS**	**MS**	**Varian Com ponent**
Species	*3*	*16118*	*5373*	*11.24*	*3*	*12124*	*4041*	*8.17*
Community	*1*	*150*	*150*	*0.02*	*1*	*219*	*219*	*0.13*
Ecology		*223*	*223*	*1.09*		*428*	*428*	*2.11*
Evolution		*25*	*25*	*0.10*		*81*	*81*	*0.38*
Eco x Evo		*-98*	*-98*	*0*		*-289*	*-289*	*0.15*
Environment	*1*	*8*	*8*	*0*	*1*	*13*	*13*	*0*
Spe x Com	*3*	*405*	*176*	*1.46*	*3*	*280*	*31*	*0.23*
Spe x Env	*3*	*320*	*107*	*0.86*	*3*	*152*	*51*	*0.38*
Com x Env	*1*	*17*	*17*	*0*	*1*	*13*	*13*	*0*
Spe x Com x Env	*3*	*197*	*66*	*0.51*	*3*	*180*	*60*	*0.45*
Error	*384*	*1642*	*4*	*4.28*	*384*	*1462*	*4*	*3.81*
Total	*399*	*18856*			*399*	*14444*		

Reciprocal Transplant Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	Replicate mesocosm: 2	Replicate mesocosm: 2	Replicate mesocosm: 2	Replica mesocos 2
Reciprocal Transplant Environment: 7, Low Light – Low Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 7, Low Light – Low Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 7, Low Light – Low Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 7, Low Light – Low Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 7, Low Light – Low Nutrients Replicate mesocosm: 1	**Replicate mesocosm: 2**	**Replicate mesocosm: 2**	**Replicate mesocosm: 2**	**Replic mesocosm: 2**
Source	**df**	**SS**	**MS**	**Variance Component**	**df**	**SS**	**MS**	**Varian Component**
Species	*3*	*13499*	*4500*	*8.70*	*3*	*11836*	*3945*	*7.16*
Community	*1*	*9*	*9*	*0*	*1*	*81*	*81*	*0.00*
Ecology		*50*	*50*	*0.21*		*77*	*77*	*0.35*
Evolution		*44*	*44*	*0.18*		*42*	*42*	*0.18*
Eco x Evo		*-85*	*-85*	*0*		*-38*	*-38*	*0*
Environment	*1*	*8*	*8*	*0*	*1*	*25*	*25*	*0*
Spe x Com	*3*	*263*	*142*	*1.02*	*3*	*432*	*196*	*1.39*
Spe x Env	*3*	*398*	*133*	*0.99*	*3*	*181*	*60*	*0.40*
Com x Env	*1*	*61*	*61*	*0*	*1*	*53*	*53*	*0*
Spe x Com x Env	*3*	*540*	*180*	*1.36*	*3*	*272*	*91*	*0.62*
Error	*384*	*1759*	*5*	*4.58*	*384*	*2019*	*5*	*5.26*
Total	*399*	*16537*			*399*	*14900*		
Reciprocal Transplant Environment: 8, Low Light – Medium Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 8, Low Light – Medium Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 8, Low Light – Medium Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 8, Low Light – Medium Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 8, Low Light – Medium Nutrients Replicate mesocosm: 1	**Replicate mesocosm: 2**	**Replicate mesocosm: 2**	**Replicate mesocosm: 2**	**Replic mesocosm: 2**

Reciprocal Transplant Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	Replicate mesocosm: 2	Replicate mesocosm: 2	Replicate mesocosm: 2	Replica mesocos 2
Source	**df**	**SS**	**MS**	**Variance Component**	**df**	**SS**	**MS**	**Varian Com-ponent**
Species	*3*	*12156*	*4052*	*7.67*	*3*	*14921*	*4974*	*8.79*
Community	*1*	*11*	*11*	*0*	*1*	*84*	*84*	*0*
Ecology		*103*	*103*	*0.48*		*44*	*44*	*0.15*
Evolution		*94*	*94*	*0.44*		*119*	*119*	*0.52*
Eco x Evo		*-185*	*-185*	*0*		*-79*	*-79*	*0*
Environment	*1*	*21*	*21*	*0*	*1*	*72*	*72*	*0*
Spe x Com	*3*	*585*	*145*	*1.07*	*3*	*814*	*454*	*3.17*
Spe x Env	*3*	*222*	*74*	*0.53*	*3*	*674*	*225*	*1.52*
Com x Env	*1*	*44*	*44*	*0*	*1*	*177*	*177*	*0*
Spe x Com x Env	*3*	*232*	*77*	*0.55*	*3*	*849*	*283*	*1.93*
Error	*384*	*1725*	*4*	*4.49*	*384*	*4013*	*10*	*10.45*
Total	*399*	*14996*			*399*	*21604*		

Reciprocal Transplant Environment: 9, Low Light – High Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 9, Low Light – High Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 9, Low Light – High Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 9, Low Light – High Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 9, Low Light – High Nutrients Replicate mesocosm: 1	**Replicate mesocosm: 2**	**Replicate mesocosm: 2**	**Replicate mesocosm: 2**	**Replic mesocosm: 2**
Source	**df**	**SS**	**MS**	**Variance Component**	**df**	**SS**	**MS**	**Varian Com-ponent**
Species	*3*	*15036*	*5012*	*9.01*	*3*	*12712*	*4237*	*7.44*
Community	*1*	*27*	*27*	*0*	*1*	*129*	*129*	*0*
Ecology		*46*	*46*	*0.20*		*247*	*247*	*1.20*
Evolution		*121*	*121*	*0.57*		*48*	*48*	*0.21*
Eco x Evo		*-140*	*-140*	*0*		*-167*	*-167*	*0*
Environment	*1*	*38*	*38*	*0*	*1*	*14*	*14*	*0*

Reciprocal Transplant Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	Reciprocal Transplant Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	Replicate mesocosm: 2	Replicate mesocosm: 2	Replicate mesocosm: 2	Replica mesocos 2
Spe x Com	*3*	*781*	*278*	*1.98*	*3*	*475*	*421*	*2.94*
Spe x Env	*3*	*213*	*71*	*0.47*	*3*	*153*	*51*	*0.33*
Com x Env	*1*	*14*	*14*	*0*	*1*	*100*	*100*	*0*
Spe x Com x Env	*3*	*227*	*76*	*0.50*	*3*	*582*	*194*	*1.33*
Error	*384*	*2182*	*6*	*5.68*	*384*	*1566*	*4*	*4.08*
Total	*399*	*18518*			*399*	*15731*		

In situ time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	Replicate mesocosm: 2	Replicate mesocosm: 2	Repl meso cosm 2
Source	Source	**df**	**df**	**df**	**SS**	**SS**	**MS**	**MS**	**Variance Component**	**Variance Component**	**df**	**df**	**SS**
Species*	Species*	*2*	*2*	*2*	*506*	*506*	*253*	*253*	*0.45*	*0.45*	*2*	*2*	*586*
Community	Community	*1*	*1*	*1*	*18*	*18*	*18*	*18*	*0*	*0*	*1*	*1*	*35*
Ecology	Ecology				*7*	*7*	*7*	*7*	*0.02*	*0.02*			*3*
Evolution	Evolution				*29*	*29*	*29*	*29*	*0.13*	*0.13*			*50*

In situ time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	Replicate mesocosm: 2	Replicate mesocosm: 2	Repl meso cosm 2
Eco x Evo	Eco x Evo				*-18*	*-18*	*-18*	*-18*	*0*	*0*			*-18*
Environment	Environment	*1*	*1*	*1*	*65*	*65*	*65*	*65*	*0*	*0*	*1*	*1*	*163*
Spe x Com	Spe x Com	*3*	*3*	*3*	*321*	*321*	*211*	*211*	*1.51*	*1.51*	*3*	*3*	*765*
Spe x Env	Spe x Env	*3*	*3*	*3*	*194*	*194*	*97*	*97*	*0.68*	*0.68*	*3*	*3*	*113*
Com x Env	Com x Env	*1*	*1*	*1*	*62*	*62*	*62*	*62*	*0*	*0*	*1*	*1*	*61*
Spe x Com x Env	Spe x Com x Env	*3*	*3*	*3*	*144*	*144*	*72*	*72*	*0.50*	*0.50*	*3*	*3*	*395*
Error	Error	*384*	*384*	*384*	*978*	*978*	*3*	*3*	*2.52*	*2.52*	*384*	*384*	*857*
Total	Total	*399*	*399*	*399*	*2289*	*2289*					*399*	*399*	*2976*
**Local extinction of Wc, hence 2 df for Species*	**Local extinction of Wc, hence 2 df for Species*	**Local extinction of Wc, hence 2 df for Species*	**Local extinction of Wc, hence 2 df for Species*	**Local extinction of Wc, hence 2 df for Species*	**Local extinction of Wc, hence 2 df for Species*	**Local extinction of Wc, hence 2 df for Species*	**Local extinction of Wc, hence 2 df for Species*	**Local extinction of Wc, hence 2 df for Species*	**Local extinction of Wc, hence 2 df for Species*	**Local extinction of Wc, hence 2 df for Species*			

In situ time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	Replicate mesocosm: 2	Replicate mesocosm: 2	Repl meso cosm 2
In situ time series Environment: 2, High Light – Medium Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 2, High Light – Medium Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 2, High Light – Medium Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 2, High Light – Medium Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 2, High Light – Medium Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 2, High Light – Medium Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 2, High Light – Medium Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 2, High Light – Medium Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 2, High Light – Medium Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 2, High Light – Medium Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 2, High Light – Medium Nutrients Replicate mesocosm: 1	**Replicate mesocosm: 2**	**Replicate mesocosm: 2**	**Rep mes cosm 2**
Source	**df**	**df**	**SS**	**SS**	**SS**	**MS**	**MS**	**MS**	**Variance Component**	**Variance Component**	**df**	**df**	**SS**
Species	*3*	*3*	*1168*	*1168*	*1168*	*389*	*389*	*389*	*0.78*	*0.78*	*3*	*3*	*357*
Community	*1*	*1*	*7*	*7*	*7*	*7*	*7*	*7*	*0*	*0*	*1*	*1*	*20*
Ecology			*46*	*46*	*46*	*46*	*46*	*46*	*0.22*	*0.22*			*3*
Evolution			*75*	*75*	*75*	*75*	*75*	*75*	*0.37*	*0.37*			*16*
Eco x Evo			*-114*	*-114*	*-114*	*-114*	*-114*	*-114*	*0*	*0*			*1*
Environment	*1*	*1*	*6*	*6*	*6*	*6*	*6*	*6*	*0*	*0*	*1*	*1*	*24*

In situ time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	Replicate mesocosm: 2	Replicate mesocosm: 2	Repl meso cosm 2
Spe x Com	*3*	*3*	*265*	*265*	*265*	*88*	*88*	*88*	*0.71*	*0.71*	*3*	*3*	*878*
Spe x Env	*3*	*3*	*94*	*94*	*94*	*31*	*31*	*31*	*0.25*	*0.25*	*3*	*3*	*136*
Com x Env	*1*	*1*	*18*	*18*	*18*	*18*	*18*	*18*	*0.02*	*0.02*	*1*	*1*	*19*
Spe x Com x Env	*3*	*3*	*27*	*27*	*27*	*9*	*9*	*9*	*0.07*	*0.07*	*3*	*3*	*327*
Error	*384*	*384*	*242*	*242*	*242*	*1*	*1*	*1*	*0.63*	*0.63*	*384*	*384*	*392*
Total	*399*	*399*	*1827*	*1827*	*1827*						*399*	*399*	*2154*

In situ time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	Replicate mesocosm: 2	Replicate mesocosm: 2	Repl meso cosm 2
In situ time series Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 3, High Light – High Nutrients Replicate mesocosm: 1	**Replicate mesocosm: 2**	**Rep mes cosm 2**
Source	Source	**df**	**df**	**SS**	**SS**	**SS**	**SS**	**MS**	**MS**	**Variance Component**	**Variance Component**	**df**	**SS**
Species	Species	3	3	*1242*	*1242*	*1242*	*1242*	*414*	*414*	*0.76*	*0.76*	*3*	*2172*
Community	Community	1	1	*27*	*27*	*27*	*27*	*27*	*27*	*0*	*0*	*1*	*22*
Ecology	Ecology			*6*	*6*	*6*	*6*	*6*	*6*	*0.02*	*0.02*		*1*
Evolution	Evolution			*49*	*49*	*49*	*49*	*49*	*49*	*0.24*	*0.24*		*16*
Eco x Evo	Eco x Evo			*-28*	*-28*	*-28*	*-28*	*-28*	*-28*	*0*	*0*		*5*
Environment	Environment	1	1	*6*	*6*	*6*	*6*	*6*	*6*	*0*	*0*	*1*	*6*

In situ time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	Replicate mesocosm: 2	Replicate mesocosm: 2	Repl meso cosm 2
Spe x Com	Spe x Com	3	3	*514*	*514*	*514*	*514*	*177*	*177*	*1.29*	*1.29*	*3*	*59*
Spe x Env	Spe x Env	3	3	*54*	*54*	*54*	*54*	*18*	*18*	*0.12*	*0.12*	*3*	*76*
Com x Env	Com x Env	1	1	*13*	*13*	*13*	*13*	*13*	*13*	*0*	*0*	*1*	*23*
Spe x Com x Env	Spe x Com x Env	3	3	*108*	*108*	*108*	*108*	*36*	*36*	*0.25*	*0.25*	*3*	*316*
Error	Error	384	384	*482*	*482*	*482*	*482*	*1*	*1*	*1.25*	*1.25*	*384*	*445*
Total	Total	399	399	*2446*	*2446*	*2446*	*2446*					*399*	*3119*

In situ time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	Replicate mesocosm: 2	Replicate mesocosm: 2	Repl meso cosm 2
In situ time series Environment: 4, Medium Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 4, Medium Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 4, Medium Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 4, Medium Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 4, Medium Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 4, Medium Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 4, Medium Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 4, Medium Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 4, Medium Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 4, Medium Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 4, Medium Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 4, Medium Light – Low Nutrients Replicate mesocosm: 1	**Replicate meso-cosm: 2**	**Rep mes cosm 2**
Source	Source	**df**	**df**	**SS**	**SS**	**SS**	**SS**	**MS**	**MS**	**Variance Component**	**Variance Component**	**df**	**SS**
Species*	Species*	*3*	*3*	*4009*	*4009*	*4009*	*4009*	*2004*	*2004*	*4.06*	*4.06*	*3*	*3454*
Community	Community	*1*	*1*	*47*	*47*	*47*	*47*	*47*	*47*	*0*	*0*	*1*	*84*
Ecology	Ecology			*20*	*20*	*20*	*20*	*20*	*20*	*0.08*	*0.08*		*18*
Evolution	Evolution			*104*	*104*	*104*	*104*	*104*	*104*	*0.50*	*0.50*		*127*
Eco x Evo	Eco x Evo			*-77*	*-77*	*-77*	*-77*	*-77*	*-77*	*0*	*0*		*-61*
Environment	Environment	*1*	*1*	*37*	*37*	*37*	*37*	*37*	*37*	*0*	*0*	*1*	*246*
Spe x Com	Spe x Com	*3*	*3*	*369*	*369*	*369*	*369*	*327*	*327*	*2.64*	*2.64*	*3*	*425*

In situ time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	Replicate mesocosm: 2	Replicate mesocosm: 2	Repl meso cosm 2
Spe x Env	Spe x Env	*3*	*3*	*119*	*119*	*119*	*119*	*59*	*59*	*0.45*	*0.45*	*3*	*153*
Com x Env	Com x Env	*1*	*1*	*51*	*51*	*51*	*51*	*51*	*51*	*0.02*	*0.02*	*1*	*29*
Spe x Com x Env	Spe x Com x Env	*3*	*3*	*90*	*90*	*90*	*90*	*45*	*45*	*0.33*	*0.33*	*3*	*113*
Error	Error	*384*	*384*	*1449*	*1449*	*1449*	*1449*	*4*	*4*	*3.73*	*3.73*	*384*	*1674*
Total	Total	*399*	*399*	*6170*	*6170*	*6170*	*6170*					*399*	*6177*
**Local extinction of Wc, hence 2 df for Species*	**Local extinction of Wc, hence 2 df for Species*	**Local extinction of Wc, hence 2 df for Species*	**Local extinction of Wc, hence 2 df for Species*	**Local extinction of Wc, hence 2 df for Species*	**Local extinction of Wc, hence 2 df for Species*	**Local extinction of Wc, hence 2 df for Species*	**Local extinction of Wc, hence 2 df for Species*	**Local extinction of Wc, hence 2 df for Species*	**Local extinction of Wc, hence 2 df for Species*	**Local extinction of Wc, hence 2 df for Species*	**Local extinction of Wc, hence 2 df for Species*		

In situ time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	Replicate mesocosm: 2	Replicate mesocosm: 2	Repl meso cosm 2
In situ time series Environment: 6, Medium Light – High Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 6, Medium Light – High Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 6, Medium Light – High Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 6, Medium Light – High Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 6, Medium Light – High Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 6, Medium Light – High Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 6, Medium Light – High Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 6, Medium Light – High Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 6, Medium Light – High Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 6, Medium Light – High Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 6, Medium Light – High Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 6, Medium Light – High Nutrients Replicate mesocosm: 1	**Replicate mesocosm: 2**	**Rep mes cosm 2**
Source	Source	**df**	**df**	**SS**	**SS**	**SS**	**SS**	**MS**	**MS**	**Variance Component**	**Variance Component**	**df**	**SS**
Species	Species	*3*	*3*	*3627*	*3627*	*3627*	*3627*	*1209*	*1209*	*2.53*	*2.53*	*3*	*4997*
Community	Community	*1*	*1*	*9*	*9*	*9*	*9*	*9*	*9*	*0*	*0*	*1*	*11*
Ecology	Ecology			*215*	*215*	*215*	*215*	*215*	*215*	*1.06*	*1.06*		*395*
Evolution	Evolution			*235*	*235*	*235*	*235*	*235*	*235*	*1.16*	*1.16*		*387*
Eco x Evo	Eco x Evo			*-441*	*-441*	*-441*	*-441*	*-441*	*-441*	*0*	*0*		*-772*
Environment	Environment	*1*	*1*	*41*	*41*	*41*	*41*	*41*	*41*	*0.02*	*0.02*	*1*	*21*

In situ time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	Replicate mesocosm: 2	Replicate mesocosm: 2	Repl meso cosm 2
Spe x Com	Spe x Com	*3*	*3*	*596*	*596*	*596*	*596*	*150*	*150*	*1.25*	*1.25*	*3*	*592*
Spe x Env	Spe x Env	*3*	*3*	*62*	*62*	*62*	*62*	*21*	*21*	*0.16*	*0.16*	*3*	*132*
Com x Env	Com x Env	*1*	*1*	*6*	*6*	*6*	*6*	*6*	*6*	*0*	*0*	*1*	*9*
Spe x Com x Env	Spe x Com x Env	*3*	*3*	*134*	*134*	*134*	*134*	*45*	*45*	*0.36*	*0.36*	*3*	*101*
Error	Error	*384*	*384*	*562*	*562*	*562*	*562*	*1*	*1*	*1.46*	*1.46*	*384*	*794*
Total	Total	*399*	*399*	*5036*	*5036*	*5036*	*5036*					*399*	*6656*

In situ time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	Replicate mesocosm: 2	Replicate mesocosm: 2	Repl meso cosm 2
In situ time series Environment: 7, Low Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 7, Low Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 7, Low Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 7, Low Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 7, Low Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 7, Low Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 7, Low Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 7, Low Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 7, Low Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 7, Low Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 7, Low Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 7, Low Light – Low Nutrients Replicate mesocosm: 1	**Replicate mesocosm: 2**	**Rep mes cosm 2**
Source	Source	**df**	**df**	**SS**	**SS**	**SS**	**SS**	**MS**	**MS**	**Variance Component**	**Variance Component**	**df**	**SS**
Species	Species	*3*	*3*	*4813*	*4813*	*4813*	*4813*	*1604*	*1604*	*3.10*	*3.10*	*3*	*7088*
Community	Community	*1*	*1*	*4*	*4*	*4*	*4*	*4*	*4*	*0*	*0*	*1*	*7*
Ecology	Ecology			*56*	*56*	*56*	*56*	*56*	*56*	*0.26*	*0.26*		*72*
Evolution	Evolution			*57*	*57*	*57*	*57*	*57*	*57*	*0.27*	*0.27*		*64*
Eco x Evo	Eco x Evo			-*108*	-*108*	-*108*	-*108*	-*108*	-*108*	*0*	*0*		-*129*
Environment	Environment	*1*	*1*	*16*	*16*	*16*	*16*	*16*	*16*	*0*	*0*	*1*	*8*
Spe x Com	Spe x Com	*3*	*3*	*641*	*641*	*641*	*641*	*156*	*156*	*1.21*	*1.21*	*3*	*661*

In situ time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	Replicate mesocosm: 2	Replicate mesocosm: 2	Repl meso cosm: 2
Spe x Env	Spe x Env	*3*	*3*	*122*	*122*	*122*	*122*	*41*	*41*	*0.30*	*0.30*	*3*	*142*
Com x Env	Com x Env	*1*	*1*	*10*	*10*	*10*	*10*	*10*	*10*	*0*	*0*	*1*	*10*
Spe x Com x Env	Spe x Com x Env	*3*	*3*	*163*	*163*	*163*	*163*	*54*	*54*	*0.41*	*0.41*	*3*	*260*
Error	Error	*384*	*384*	*695*	*695*	*695*	*695*	*2*	*2*	*1.81*	*1.81*	*384*	*1181*
Total	Total	*399*	*399*	*6465*	*6465*	*6465*	*6465*					*399*	*9358*
In situ time series Environment: 8, Low Light – Medium Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 8, Low Light – Medium Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 8, Low Light – Medium Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 8, Low Light – Medium Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 8, Low Light – Medium Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 8, Low Light – Medium Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 8, Low Light – Medium Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 8, Low Light – Medium Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 8, Low Light – Medium Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 8, Low Light – Medium Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 8, Low Light – Medium Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 8, Low Light – Medium Nutrients Replicate mesocosm: 1	**Replicate mesocosm: 2**	**Rep mes cosm 2**

In situ time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	Replicate mesocosm: 2	Replicate mesocosm: 2	Repl meso cosm 2
Source	Source	**df**	**df**	**SS**	**SS**	**SS**	**SS**	**MS**	**MS**	**Variance Component**	**Variance Component**	**df**	**SS**
Species	Species	*3*	*3*	*7615*	*7615*	*7615*	*7615*	*2538*	*2538*	*4.80*	*4.80*	*3*	*6871*
Community	Community	*1*	*1*	*151*	*151*	*151*	*151*	*151*	*151*	*0*	*0*	*1*	*9*
Ecology	Ecology			*116*	*116*	*116*	*116*	*116*	*116*	*0.53*	*0.53*		*63*
Evolution	Evolution			*513*	*513*	*513*	*513*	*513*	*513*	*2.52*	*2.52*		*51*
Eco x Evo	Eco x Evo			*-479*	*-479*	*-479*	*-479*	*-479*	*-479*	*0*	*0*		*-105*
Environment	Environment	*1*	*1*	*22*	*22*	*22*	*22*	*22*	*22*	*0*	*0*	*1*	*17*
Spe x Com	Spe x Com	*3*	*3*	*2117*	*2117*	*2117*	*2117*	*791*	*791*	*5.94*	*5.94*	*3*	*514*
Spe x Env	Spe x Env	*3*	*3*	*634*	*634*	*634*	*634*	*211*	*211*	*1.55*	*1.55*	*3*	*141*
Com x Env	Com x Env	*1*	*1*	*75*	*75*	*75*	*75*	*75*	*75*	*0*	*0*	*1*	*9*
Spe x Com x Env	Spe x Com x Env	*3*	*3*	*525*	*525*	*525*	*525*	*175*	*175*	*1.27*	*1.27*	*3*	*123*
Error	Error	*384*	*384*	*2753*	*2753*	*2753*	*2753*	*7*	*7*	*7.17*	*7.17*	*384*	*1334*
Total	Total	*399*	*399*	*13892*	*13892*	*13892*	*13892*					*399*	*9018*

In situ time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	Replicate mesocosm: 2	Replicate mesocosm: 2	Repl meso cosm 2
In situ time series Environment: 9, Low Light – High Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 9, Low Light – High Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 9, Low Light – High Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 9, Low Light – High Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 9, Low Light – High Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 9, Low Light – High Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 9, Low Light – High Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 9, Low Light – High Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 9, Low Light – High Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 9, Low Light – High Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 9, Low Light – High Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 9, Low Light – High Nutrients Replicate mesocosm: 1	**Replicate mesocosm: 2**	**Rep mes cosm 2**
Source	Source	**df**	**df**	**SS**	**SS**	**SS**	**SS**	**MS**	**MS**	**Variance Component**	**Variance Component**	**df**	**SS**
Species	Species	*3*	*3*	*4506*	*4506*	*4506*	*4506*	*1502*	*1502*	*2.70*	*2.70*	*3*	*7719*
Community	Community	*1*	*1*	*15*	*15*	*15*	*15*	*15*	*15*	*0*	*0*	*1*	*25*
Ecology	Ecology			*119*	*119*	*119*	*119*	*119*	*119*	*0.58*	*0.58*		*190*
Evolution	Evolution			*80*	*80*	*80*	*80*	*80*	*80*	*0.38*	*0.38*		*110*
Eco x Evo	Eco x Evo			*-184*	*-184*	*-184*	*-184*	*-184*	*-184*	*0*	*0*		*-275*
Environment	Environment	*1*	*1*	*23*	*23*	*23*	*23*	*23*	*23*	*0*	*0*	*1*	*21*

In situ time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	*In situ* time series Environment: 1, High Light – Low Nutrients Replicate mesocosm: 1	Replicate mesocosm: 2	Replicate mesocosm: 2	Repl meso cosm 2
Spe x Com	Spe x Com	*3*	*3*	*606*	*606*	*606*	*606*	*202*	*202*	*1.44*	*1.44*	*3*	*785*
Spe x Env	Spe x Env	*3*	*3*	*346*	*346*	*346*	*346*	*115*	*115*	*0.82*	*0.82*	*3*	*178*
Com x Env	Com x Env	*1*	*1*	*18*	*18*	*18*	*18*	*18*	*18*	*0*	*0*	*1*	*17*
Spe x Com x Env	Spe x Com x Env	*3*	*3*	*75*	*75*	*75*	*75*	*25*	*25*	*0.17*	*0.17*	*3*	*209*
Error	Error	*384*	*384*	*629*	*629*	*629*	*629*	*2*	*2*	*1.64*	*1.64*	*384*	*1149*
Total	Total	*399*	*399*	*6218*	*6218*	*6218*	*6218*					*399*	*1010*