

LETTER

Negative soil feedbacks accumulate over time for non-native plant species

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Abstract

The enemy release hypothesis is a common explanation for species invasions, suggesting that introduced species benefit from leaving behind natural enemies in the native range. However, any such advantage may attenuate over time. In this study, we test a prediction of this more dynamic enemy release hypothesis: that non-native plant species that became established longer ago exhibit stronger negative feedbacks with the soil. Consistent with declining enemy release over time, we found increasingly negative soil feedbacks for species established longer ago in New Zealand. Negative soil feedbacks were also stronger for more widespread species, but weaker for more locally abundant species, suggesting that species accumulate negative interactions as they spread and can be locally regulated by these interactions. We also present data to support the common assumption that relatives have similar impacts on and responses to soil communities. Together, these data highlight the dynamic nature of novel interactions arising from species introductions.

Keywords

Enemy release hypothesis, invasive species, plant–soil feedbacks.

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INTRODUCTION

The enemy release hypothesis (ERH) is widely invoked and tested as an explanation for the success of non-native species, suggesting that introduced species benefit from leaving behind natural enemies that regulate their populations in the native range (Mitchell & Power 2003; Colautti *et al.* 2004). Nevertheless, any such advantage for introduced species might be expected to attenuate over time for several reasons (Hawkes 2007). First, as introduced species become widespread after introduction they have an increasing probability of encountering potential enemies already resident in the region that could impact their performance. Second, natural enemies from the home range may be subsequently introduced either intentionally or unintentionally, thus ‘catching-up’ with their hosts. Third, novel relationships between introduced species and the pathogens, herbivores, and mutualists in the new region may form through exposure and evolutionary adaptation (Cox 2004). Recent work has shown that both introduced plants (Prentis *et al.* 2008) and native enemies (Carroll *et al.* 2005) may evolve rapidly in response to novel biotic associations.

These mechanisms suggest a more dynamic ERH than that usually tested, in which any initial advantage of enemy release may decline over time as enemies accumulate post-establishment (Hawkes 2007). Anecdotal evidence suggests that such processes may be responsible for the boom and bust dynamics of certain non-native species (Williamson & Fitter 1996; Simberloff & Gibbons 2004), and a recent meta-analysis found support across study systems for a decline in enemy release post-introduction (Hawkes 2007). Other studies examining the accumulation of enemies on non-native plant species have focused on aboveground invertebrate herbivores and not found clear relationships over time (Strong *et al.* 1977; Andow & Imura 1994; Carpenter & Cappuccino 2005). However, none to our knowledge has examined changing effects on plant performance mediated by below-ground interactions, despite the strong influence of belowground organisms on plants (Klironomos 2002; van der Putten *et al.* 2007a).

In this study, we test a prediction of this more dynamic ERH: that introduced plant species with longer residence times in a new region should exhibit stronger negative soil feedbacks than species established more recently. We

focused on plant–soil interactions because strong evidence for the ERH comes from studies of plant–soil feedbacks (Reinhart *et al.* 2003; Callaway *et al.* 2004; van der Putten *et al.* 2007b). Plants grown in soil previously cultivated by individuals of the same species often show reduced performance, commonly attributed to the accumulation of soil biota that have an inhibitory effect on subsequent plant growth (negative soil feedback). Introduced plants have been shown to experience less negative soil feedbacks when grown in soil from their new region compared with soil from their home range (Callaway *et al.* 2004), and compared with native species from the new region (Agrawal *et al.* 2005).

We used plant–soil feedback experiments in a greenhouse to quantify soil feedbacks for 12 introduced plant species that established in the wild (i.e. ‘naturalized’) in New Zealand at various times over the last 210 years. Our choice of study species was designed to test two further predictions. First, we chose species found at a range of field abundances in our study region to test whether soil feedbacks were related to species’ abundances across the region, as found in previous work (Klironomos 2002). Second, we used three congeneric pairs to test whether soil feedbacks were stronger among more closely related species. Phylogenetically related species are hypothesized to exhibit similar effects on, and responses to, the soil due to shared physiology and traits (Agrawal & Kotanen 2003). Shared responses among relatives are often assumed in phylogenetically controlled experiments and would have important

implications for community-level patterns of species invasions.

MATERIAL AND METHODS

We selected 11 introduced plant species (Fig. 1) that were present on Banks Peninsula, Canterbury, New Zealand, and that spanned a range of dates of first establishment in New Zealand [using a database of dates of first recorded establishment in the wild for introduced plant species updated from Webb *et al.* (1988) by Gatehouse (2008)]. A 12th species that had not been recorded as established in the area, *Cerastium alpinum*, was included as a completely novel species to this community (zero years of establishment). Six of these 12 species were also chosen to provide congeneric pairs for comparison (*C. alpinum* and *C. glomeratum*, *Dianthus armeria* and *D. deltoides*, *Sisymbrium erysimoides* and *S. officinale*). We obtained seeds from native western-European populations for each species (B&T World Seeds, Aigues-Vives, France). Seeds were surface sterilized and germinated 3 weeks prior to planting. Soils were collected from 18 locations distributed across Banks Peninsula, chosen based on field surveys (described below) to maximize the probability that soil was sampled from sites where all study species were locally present. Soil was sieved with a 10 mm screen, homogenized, mixed 1 : 1 with sterile pumice and divided among 240 1 L pots. By sampling widely and homogenizing the soil before the experiment, it was assumed that each pot began with a similarly realistic suite of soil biota.

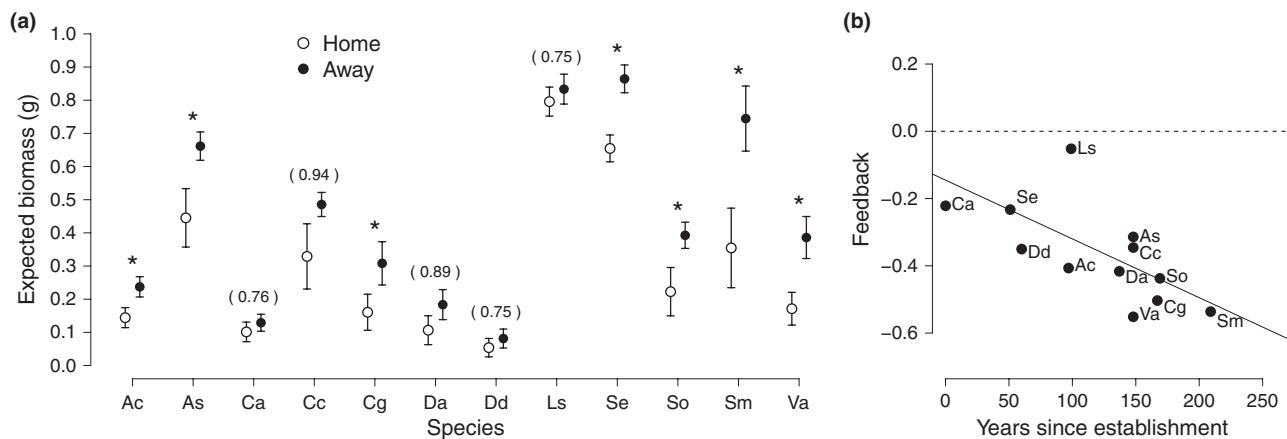


Figure 1 (a) Expected above-ground biomass of species when grown in soil conditioned by individuals of their own species (Home) and individuals of eight of the other species (Away). Expected biomass = $\text{Pr}(\text{growing to adult size}) \times (\text{biomass}/\text{adult}) + \text{Pr}(\text{remaining seedling size}) \times (\text{biomass}/\text{seedling})$ (see Methods). Asterisks indicate species for which there is ≥ 0.95 probability that the Away response was greater than the Home response; probabilities less than this are given in parentheses. (b) Soil feedback responses as a function of the number of years since establishing in New Zealand (linear regression, $P = 0.012$, $R^2 = 0.49$). Feedback was calculated as: $(\text{home biomass} - \text{away biomass}) / \text{maximum}(\text{away biomass}, \text{home biomass})$. Species codes: *Ac* – *Anthriscus caucalis* M.Bieb., *As* – *Arenaria serpyllifolia* L., *Ca* – *Cerastium alpinum* L., *Cc* – *Crepis capillaries* (L.) Wallr., *Cg* – *Cerastium glomeratum* Thuill., *Da* – *Dianthus armeria* L., *Dd* – *Dianthus deltoides* L., *Ls* – *Lactuca serriola* L., *Se* – *Sisymbrium erysimoides* Desf., *So* – *Sisymbrium officinale* (L.) Scop., *Sm* – *Stellaria media* (L.) Vill., *Va* – *Veronica arvensis* L.

Soil feedbacks were assessed by growing each species in eight pots planted previously with the same species (home soil) and in eight pots planted with a different study species that was not a congener (away soil). The experiment consisted of three stages in which different seedlings were grown in succession in each pot for 12 weeks per stage and harvested at the end of each stage. Seedlings were replaced if they died within the first 3 weeks. The first two stages consisted of the same species in any given pot. For the third stage, half of the pots were designated home and half were designated away treatments. In the home treatment pots, the third stage consisted of a new seedling of the same species being planted back into that pot; the away treatment had a seedling of another species that was not a congener planted. The same nine species were used to cultivate the away soils for all species (*Anthriscus caucalis*, *Arenaria serpyllifolia*, *Cerastium glomeratum*, *Crepis capillaris*, *Dianthus armeria*, *Lactuca serriola*, *Sisymbrium erylisimoides*, *Stellaria media*, *Veronica arvensis*, *Veronica arvensis*). An additional congener treatment was established for the six species with congeners by planting them in pots previously occupied by their congener. At the end of each stage, the above-ground biomass was removed, with roots and soil left undisturbed, and a new seedling was planted as close to the center of the pot as possible. This protocol was designed to maximize realism by not disrupting soil, rhizosphere organisms, or fungal hyphae, but has the disadvantage of not permitting chemical (including soil fertility) and biological effects to be separated. Above-ground biomass was dried at 60 °C for 48 h and weighed (diagram of experimental design in Figure S2).

Field abundance of each species was derived from floristic surveys of Banks Peninsula (conducted by Hugh Wilson; data available by request at Landcare Research's online National Vegetation Survey database: <http://nvs.landcareresearch.co.nz>, and used with permission of H. Wilson). These surveys, conducted between 1983 and 1988, recorded the abundance of all vascular plant species found in 1340 36 m² plots systematically located across the 100 500 ha area of Banks Peninsula. We used the number of plots in which each species was present as a measure of how widespread they were in the study region. The local abundance of each species in each plot was recorded in five ordinal categories: Occasional, Occasional–Common, Common, Common–Abundant, and Abundant, and subsequently scored numerically as 1, 1.5, 2, 2.5, and 3, respectively. We calculated species' mean local abundance as the average of these scores across all plots where the species was present. Having not been found established in the area, *C. alpinum* was excluded from analyses of abundance relationships. Two additional species (*Dianthus deltooides*, and *Sisymbrium erylisimoides*) were omitted from local abundance analyses because they were not found in the field survey plots although they are known to be in the area.

Final biomass data for some species were observed to be bimodal, with some individuals not growing past seedling size (although remaining alive) and others growing to adult size (raw data plots in Figure S1). Because we expected that these different responses represented different processes, and because the bimodal distribution would violate normality assumptions of standard analysis of variance, a two-part process model was used for data analysis. We modeled the expected biomass of each species in each treatment as the sum of two products: (1) the product of the probability of growing to adult size and the biomass given that it grew to adult size; and (2) the product of the probability of staying seedling size and the biomass given that it remained seedling size. This can be written symbolically as: Expected Biomass = Pr(growing to adult size) × (biomass/adult) + Pr(remaining seedling size) × (biomass/seedling). The probability of growing to adult size was modeled using a binomial distribution, where growth to the adult stage for each individual was a binary success or failure. The final biomasses of adults and stunted plants were modeled as normally distributed with mean and variance specific to each species-treatment combination. Models were fit in a Bayesian framework using OPENBUGS v2.10 (Thomas *et al.* 2006) called using the BRugs package of R version 2.9.0 (R Development Core Team 2008). Treatment effects were calculated as the difference in expected biomass between the treatments for each species, yielding probabilities that the responses were different among treatments.

The strength of feedback effects were calculated for each species from mean expected biomass estimates as: (home biomass – away biomass)/maximum(away biomass, home biomass). The maximum biomass is used on the denominator to avoid a potential bias toward negative values (Markham & Chanway 1996). Phylogenetic generalized least squares (Freckleton *et al.* 2002) was used to test for relationships between mean strength of feedback and both time since establishment and field abundance while controlling for phylogenetic relatedness among species. We used a phylogeny constructed using the online Phylomatic tool (Webb & Donoghue 2005), using the angiosperm consensus tree (Davies *et al.* 2004) and relationships among the six species in the Caryophyllaceae updated with a recent molecular phylogeny (Fior *et al.* 2006). The phylogenetic analysis estimated phylogenetic correlation (λ in the notation of Freckleton *et al.* 2002) to be zero, signifying no phylogenetic signal in these data, so ordinary least squares was used for all regressions.

RESULTS

All 12 study species grew more slowly in their home soil compared with away soils (Fig. 1a). For seven species, the probability that growth was reduced in the home soil

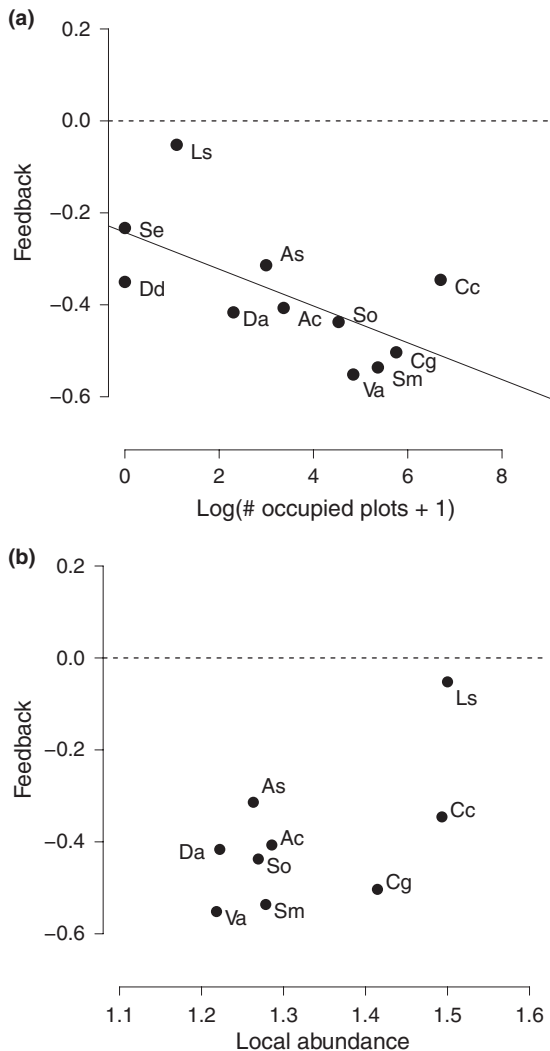


Figure 2 Feedback effects were (a) negatively correlated with species distributions (linear regression, $P = 0.005$, $R^2 = 0.56$) and (b) the opposite trend with mean local abundance within plots (linear regression, $P = 0.072$, $R^2 = 0.39$). Measures of distribution and abundance were based on field surveys of 1340 36 m^2 plots systematically located across the 100 500 ha Banks Peninsula. Local abundance was calculated as the mean abundance within plots in which the species was present. Two species (*Dianthus deltooides* and *Sisymbrium erylisimoides*) were included in (a) because they are known to be in the area but omitted from (b) because they were not found in the field survey plots. Feedback was calculated as: (home biomass – away biomass)/maximum(away biomass, home biomass).

compared with away soils was ≥ 0.95 , whereas the others showed a similar trend (Fig. 1a). Soil feedbacks, calculated as (home biomass – away biomass)/away biomass, were negatively correlated with time since establishment in New Zealand (Fig 1b; $P = 0.012$, $R^2 = 0.49$). Species' time since establishment in New Zealand was positively correlated with

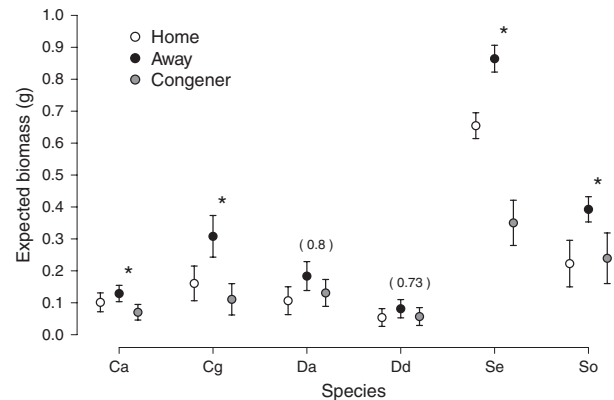


Figure 3 Expected above-ground biomass of species when grown in soil conditioned by individuals of their own species (Home), individuals of eight of the other species (Away), and individuals of their congener (Congener). Asterisks (*) indicate species for which there is ≥ 0.95 probability that the Away response was greater than the Congener response; probabilities less than this are given in parentheses.

the number of occupied survey plots across our study region and soil feedbacks as a result declined with the number of occupied plots (Fig. 2a; $P = 0.005$, $R^2 = 0.56$). In contrast, soil feedback exhibited a positive trend as a function of species' mean local abundance in the study area, but this relationship was not statistically significant (Fig. 2b; $P = 0.072$, $R^2 = 0.39$). Feedbacks showed no significant relationship with the total biomass of plants in the first two generations of the experiment ($P = 0.52$).

The three congeneric pairs exhibited similar growth in their congener's soil as in their home soil (Fig. 3). The probability that growth was reduced in the congener soil compared with away soils was ≥ 0.95 for four of the species, and showed a similar trend for the other two (Fig. 3). The only species for which biomass in the congener treatment was significantly less than the home treatment ($P > 0.95$) was *S. erylisimoides*.

DISCUSSION

The reduced growth in their home soil compared with away soils for all 12 species (Fig. 1a) demonstrates that these species alter local soil conditions in ways that negatively affect their subsequent growth. This pattern is broadly consistent with the predominance of negative soil feedbacks seen in previous plant-soil feedback studies (for review, see Reinhart & Callaway 2006), but in no case showed the positive feedbacks sometimes seen with introduced species (Callaway *et al.* 2004; Kulmatiski *et al.* 2008).

The stronger negative soil feedbacks experienced by non-native species that have been established in New Zealand for longer (Fig. 1b) supported our main prediction. This

outcome is consistent with an accumulating effect of below-ground enemies over time, whereby the soil biota cultivated by species established in New Zealand for longer had a greater inhibitory effect on their subsequent growth. These below-ground enemies may include a variety of microorganisms including pathogenic fungi (Mills & Bever 1998; Reinhart *et al.* 2005) and bacteria (Zeller *et al.* 2007), as well as soil invertebrates (De Deyn *et al.* 2003).

Nevertheless, other interpretations for reduced growth in home soil are possible, including decreased responsiveness to soil mutualists over time (Seifert *et al.* 2009) and chemical alterations to the soil (Casper *et al.* 2008). Soil feedbacks represent the net effect of a variety of potentially negative and positive interactions with the soil ecosystem (Bever *et al.* 1997; Wardle 2002; Reynolds *et al.* 2003). However, the entirely negative net feedbacks in this study point to an influential role of antagonistic soil pathogens and herbivores. Species-specific chemical alterations to the soil, including allelopathic effects and species-specific nutrient depletions, may also contribute to the overall pattern of reduced growth in home vs. away soils (Fig. 1a), but it is unlikely that such effects would change the strength of feedbacks over time (Fig. 1b). Also, the lack of a negative relationship between feedback and the total biomass of plants in the first two generations of the experiment suggests that negative feedbacks are not driven by plant nutrient demand. Further experiments that manipulate biotic and chemical variables would help tease apart the relative impact of these factors (Casper *et al.* 2008).

Abundance relationships

Although we cannot yet identify the specific mechanism underlying this relationship, the correlations between soil feedbacks and species abundance help to identify potential underlying processes. Species that established longer ago in New Zealand occupied more survey plots across our study region, with soil feedbacks becoming more negative with the number of occupied plots (Fig. 2a). The stronger negative soil feedback for more widespread species is consistent with the view that species accumulate negative interactions as they spread across the novel landscape. These negative interactions may either accrue through new encounters with pests and pathogens in the landscape, or through adaptation to the new plant species over time. This relationship could also arise due to a 'sampling effect' in which the soil organisms associated with more localized species were less likely to be present in the homogenized soil, although we tried to minimize this effect by sampling soil from wide variety of sites at which most species were present.

This negative relationship between species distribution and soil feedbacks is opposite to a previous study showing plant species abundance positively correlated with soil

feedback (Klironomos 2002), but we hypothesized that such patterns were likely to depend on the scale at which abundance is measured. Although some theoretical work has explored the implications of frequency-dependent interactions at different spatial scales (Molofsky *et al.* 2002), little empirical data exists to develop expectations for feedback–abundance relationships across scales. Here, soil feedbacks were positively correlated with species' mean local abundance within the 36 m² plots (Fig. 2b), in contrast to the negative relationship with the number of occupied plots across the 100 500 ha Banks Peninsula. This local measure of abundance is therefore more consistent with Klironomos (2002), which measured abundance as the percentage of 100 1 m² plots that were occupied within a *c.* 2 ha meadow. Thus the spread of non-native species across the region following introduction appears to increase their chance of developing negative soil feedbacks over time, and these negative feedbacks may in turn act to limit their local abundance.

Although this study provides unique experimental evidence that soil feedbacks become more negative over time for non-native species, there are several extensions that would provide additional insight into invasive species dynamics. First, by sourcing the seeds for this experiment from the native range, we isolated any effects of evolutionary change in the soil community from that of the plants. Ongoing evolutionary changes in plant traits, affecting competitive interactions or defense of natural enemies, will further affect the long-term dynamics of invasion (Lankau *et al.* 2009). Comparisons between seeds from the native range and introduced range could help tease apart these processes. Second, determining whether the observed negative feedbacks are less than experienced in the native range, and thus represent a release from natural enemy control (i.e. satisfy ERH), requires additional feedback experiments in the species' native ranges. The net effects of feedbacks on species abundance will depend also on soil-mediated interactions with coexisting species (Bever *et al.* 1997). Although theoretical work suggests a limited ability for plant–soil feedbacks to affect spread rates (Levine *et al.* 2006), a window of reduced enemy effects for non-native species may contribute to population growth and spread, as is the case for range-expanding species (Engelkes *et al.* 2008).

Congeners

The six species with congeners exhibited remarkably similar growth in their congener's soil as in their home soil (Fig. 3), suggesting that relatives have similar effects on soils and soil communities and respond to these below-ground conditions in similar ways. These similarities are most likely driven by shared physiology or other below-ground traits that shape

interactions with soil communities. Previous observations that the host ranges of plant pathogens tend to be phylogenetically clustered provide a potential mechanism for such effects (Parker & Gilbert 2004). Similar taxonomic patterns have also been seen in rates of aboveground herbivory (Dawson *et al.* 2009; Hill & Kotanen 2009; but see Cappuccino and Carpenter 2005). Other studies that use congeners as controls are thus likely to be conservative tests of enemy release, as is sometimes acknowledged (e.g. Agrawal *et al.* 2005). Nonetheless, congeneric pairs responded differently from each other to away soils, yielding differences in the relative feedback effects of home vs. away soils (as seen in Fig. 1b).

The mechanisms behind species' different responses to away soils are not clear but may depend on the specific host–pathogen and host–herbivore recognition systems involved (Verhoeven *et al.* 2009). Novel interactions may initially benefit the plant when defenses are unrecognized by native enemies, while plants may suffer if they lack receptors to identify novel enemies. The degree of virulence and resistance is also likely to vary more continuously and is likely to change through evolutionary dynamics (Parker & Gilbert 2004). Thus, although relatives may share similar responses to some enemies, soil feedbacks reflect the complex net effects of a combination of belowground interactions, all of which may evolve over time depending on species- or population-specific exposure.

Overall, the patterns of feedback seen in this study lend empirical support to a dynamic model of species invasions whereby initially novel interactions post-introduction change over time. Although the current, unprecedented rates of species movements around the globe (Hulme 2009) sometimes create advantages for introduced species, the adage may still apply: you can run but you cannot hide.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Raw above-ground biomass data plotted for each of the 12 species in the Home treatment (light grey) and Away treatment (darker grey).

Figure S2 Diagram of experimental methods. Each treatment consisted of eight replicates for each species (whereas only one is shown in the diagram).

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