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Soil-mediated indirect impacts of an invasive predator on plant growth

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While several studies have shown that invasive plant effects on soil biota influence subsequent plant performance, corresponding studies on how invasive animals affect plants through influencing soil biota are lacking. This is despite the fact that invasive animals often indirectly alter the below-ground subsystem. We studied 18 offshore islands in northern New Zealand, half of which have been invaded by rats that are predators of seabirds and severely reduce their densities, and half of which remain non-invaded; invasion of rats thwarts seabird transfer of resources from ocean to land. We used soil from each island in a glasshouse experiment involving soil sterilization treatments to determine whether rat invasion indirectly influences plant growth through the abiotic pathway (by impairing seabird-driven inputs to soil) or the biotic pathway (by altering the soil community). Rat invasion greatly impaired plant growth but entirely through the abiotic pathway. Plant growth was unaffected by the soil community or its response to invasion, meaning that the responses of plants and soil biota to invasion are decoupled. Our results provide experimental evidence for the powerful indirect effects that predator-instigated cascades can exert on plant and ecosystem productivity, with implications for the restoration of island ecosystems by predator removal.

Keywords: invasive predator; soil community; trophic cascade

1. INTRODUCTION

Over the past decade, a growing number of studies have explored how invasive above-ground organisms influence the below-ground subsystem [1,2]. Most have focused on invasive plants, and several have shown that plant invasions can exert important effects on both the abiotic and biotic components of the soil environment [3]. However, a small but growing number of studies have also shown that invasive above-ground consumers can transform the below-ground subsystem when they feed upon organisms that themselves have a key ecological role [4]; examples include herbivorous insects [5] and deer [6], and predatory ants [7] and foxes [8]. Several studies have experimentally explored the mechanisms through

which the alteration of below-ground properties by invasive plants can in turn influence plant growth [1,9]. However, corresponding studies on how transformation of soils by the indirect impacts of invasive above-ground consumers are largely lacking.

Rat species (e.g. *Rattus rattus*, *Rattus norvegicus* and *Rattus exulans*) have been introduced to many coastal and island ecosystems worldwide, where they frequently serve as top predators by consuming eggs and chicks of seabirds, thereby severely reducing their populations [10]. When these predators are absent, seabirds serve as major ecosystem drivers in many coastal communities, in part, through transport of nutrients from the ocean to the land [11]. Invasion of these communities by predators of seabirds thwarts the sea-to-land transfer of nutrients, which can in turn lead to substantial reductions in soil fertility [8,12] and soil biota [12,13], and shifts in the community structure of plants [8] and invertebrates [13].

We investigated soils collected from each of 18 forested islands off the coast of northeastern New Zealand in order to explore mechanisms by which invasive rats could indirectly influence plant growth via changes in the soil. These include nine islands that have never been invaded by rats and have high seabird densities, and nine that have been invaded and have severely reduced seabird densities. Previous studies on these islands reveal that thwarting of seabird-driven nutrient inputs by rats causes reductions in soil nutrient availability [12], soil biota [12,13], decomposer processes [14], plant growth [12] and foliar nutrition [14]. Responses of plant growth to extirpation of seabirds by rats could conceivably occur through two mechanisms (figure 1). First, rat predation may reduce plant growth through reducing seabird fertilization effects, i.e. transport of nutrients from ocean to land (figure 1, abiotic pathway). Second, seabirds may stimulate soil biota through transferring resources from ocean to land [12] with the modified soil biota in turn influencing plant growth [2]; rat predation may alter plant growth through reversing seabird effects on soil biota (figure 1, biotic pathway). This mechanism is analogous to the ways that invasive plants influence subsequent plant growth through altering the soil community [9]. Here, we use a glasshouse experiment to explore how these two mechanisms contribute to indirect effects of rat invasion on plant growth via soil, and thus aim to better understand how cascading effects of invasive predators indirectly influence plant productivity.

2. METHODS

On each island, we collected approximately 30 l soil to 10 cm depth. Previous work on these islands reveals that rat invasion reduces densities of soil biota and amounts of soil nutrients in this depth layer (see the electronic supplementary material, table S1). The soil from each island was divided into four subsamples, which were then each subjected to different sterilization treatments to enable the assessment of soil biotic effects on plant growth [15]. These treatments were non-sterilization, sterilization by gamma-irradiation to kill all soil biota, re-inoculation of sterilized soil with non-sterilized soil from the same island and re-inoculation of sterilized soil with non-sterilized soil from a different island that differed in invasion status (i.e. sterilized soil from each invaded island was re-inoculated with non-sterile soil from a corresponding non-invaded island and vice versa). Each of the four soil subsamples was then placed in two pots and left to equilibrate; one each was planted with a seedling of the tree *Meliccytus ramiflorus* (Violaceae, hereafter *Meliccytus*) and the tree *Kunzea ericoides* (Myrtaceae, hereafter *Kunzea*). These species differ in key traits, with *Meliccytus* and *Kunzea* having traits

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2012.0201> or via <http://rsbl.royalsocietypublishing.org>.

Table 1. Results of ANOVA (F -values with p -values in parenthesis) for the effects of island invasion status, plant species and soil sterilization, on seedling properties 240 days after planting. (F -values that are significant at $p = 0.05$ are shown in bold. Degrees of freedom for $I = 1, 8$; for $P = 1, 16$; for $S = 3, 86$ and for $I \times P = 1, 16$. Interaction terms $I \times S$, $P \times S$ and $I \times P \times S$ were never significant at $p = 0.10$ (F - and p -values not presented).)

response variable	island invasion status (I)	plant species (P)	soil sterilization treatment (S)	$I \times P$ interaction
total leaf weight	26.6 (<0.001)	25.0 (<0.001)	0.2 (0.880)	6.6 (0.021)
total stem weight	14.2 (0.006)	3.6 (0.072)	0.5 (0.720)	3.7 (0.071)
total root weight	15.1 (0.005)	15.1 (0.003)	0.2 (0.931)	5.4 (0.034)
total plant weight	18.6 (0.003)	5.4 (0.034)	0.2 (0.929)	0.8 (0.391)
total leaf area	30.6 (<0.001)	41.5 (<0.001)	0.8 (0.525)	10.7 (0.005)
specific leaf area	1.0 (0.378)	37.7 (<0.001)	0.1 (0.941)	0.5 (0.485)
leaf to leaf + stem ratio	4.8 (0.061)	206.4 (<0.001)	2.2 (0.090)	10.4 (0.006)
root to root + shoot ratio	0.8 (0.407)	5.4 (0.034)	0.2 (0.929)	0.8 (0.391)

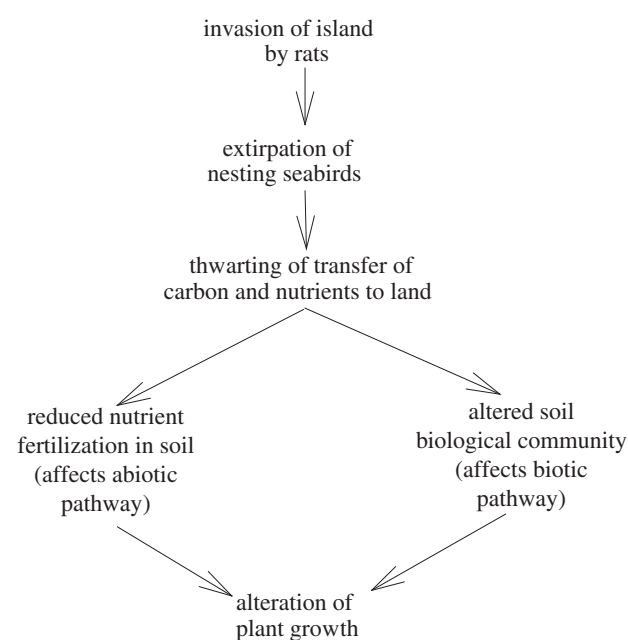


Figure 1. Mechanisms through which cascading effects of invasive rats may indirectly affect plant growth via abiotic and biotic pathways.

associated with resource acquisition and conservation, respectively (see the electronic supplementary material, table S2). After 240 days, the pots were harvested, and biomass and leaf area characteristics of each seedling were measured. Data were analysed by a split-plot ANOVA test for the effects of island invasion status, tree seedling species and soil sterilization treatment; pairs of islands served as the units of replication. A detailed methodology is outlined in the electronic supplementary material.

3. RESULTS

Total plant weight, weight of each of the three plant tissue types (roots, stems and leaves) and total leaf area were reduced by rat invasion (table 1 and figure 2). There was also an interactive effect between island invasion status and plant species on total leaf weight, root weight and leaf area (table 1); the latter two of these variables were significantly reduced by rat invasion for *Melicytus* but not for *Kunzea* (figure 2). Specific leaf area and the root-to-shoot ratio were unaffected by invasion status and by the interaction of invasion status with species, but the leaf to leaf + stem mass ratio was influenced by the invasion status \times species interaction (table 1) as it was promoted by rat invasion only for *Kunzea* (figure 2).

There was no significant effect of soil sterilization treatment, or any interactive effect of sterilization treatment with any other factor, on any response variable (table 1).

4. DISCUSSION

Rat invasion reduces the productivity of woody plants common on the islands through altering the below-ground environment [12], and the present study reveals that this occurs entirely through rat invasion affecting abiotic, but not biotic, soil properties (figure 1). This most likely stems from rat invasion greatly reducing the levels of carbon and available nutrients present in the soil [12]. For some growth variables (total root weight and total leaf area), *Melicytus* showed a statistically significant response to invasion, whereas *Kunzea* did not, despite it showing a greater percentage reduction of these variables owing to invasion. *Melicytus* has traits more associated with rapid nutrient acquisition (see the electronic supplementary material, table S1) and is therefore expected to be more responsive to altered soil fertility [16]. Rat invasion generally did not affect plant allocation to different tissues, and the root-to-shoot ratio for both species was unresponsive to reduced soil fertility caused by rat invasion, despite this ratio often being promoted by soil infertility elsewhere [16]. However, for *Kunzea*, rat invasion did cause plants to allocate more to leaf than to stem tissue, consistent with smaller plants allocating a lower proportion of resources to structural tissues [17].

Despite rat invasion greatly reducing soil biota [12], and several studies pointing to soil biota as a driver of plant growth [4], our soil sterilization treatments revealed that rat effects on soil biota had no effects on plants. Several studies have pointed to the influence of invasive plant species on soil biota in turn altering plant growth [1,18], but no comparable studies have been performed on above-ground invasive animals despite their capacity to transform the below-ground environment [2,4]. Our results suggest that, for a widespread invasive animal, whatever effects it has on the soil community are independent of its effects on plant growth. This reveals a decoupled response of plants and soil biota to the cascading effects of rat invasion. The lack of soil biotic effects on plant growth in our study presumably arose because of the overriding importance of abiotic factors (e.g. high concentrations of

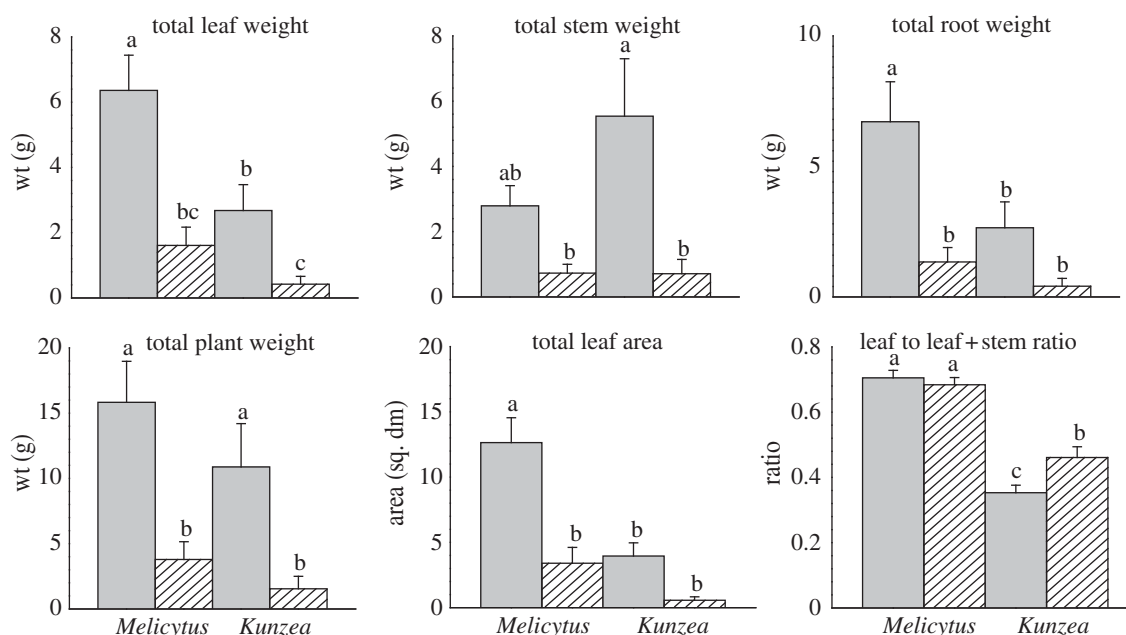


Figure 2. Mean values for seedling properties 240 days after planting for invaded (bars with lines) and uninvaded (filled bars) islands for both *Melicytus* and *Kunzea*. Error bars are mean within-treatment standard errors ($n = 9$), and within each panel bars topped with the same letter do not differ at $p = 0.05$ (Tukey's test following ANOVA; table 1).

mineral soil nutrients) in determining growth; such abiotic factors may operate as important determinants of the occurrence and strength of plant–soil feedbacks [19].

There is growing recent recognition that trophic cascades instigated by top predators may affect not only the abundance of organisms in lower trophic levels, but also the ecosystem processes that those organisms drive [20,21]. Our results highlight the fact that even though invasive predatory rats indirectly influence soil biota and plants independently of one another, rat-induced cascades nevertheless profoundly impair plant growth through changes in soil properties. Rat invasion and predation of seabirds is a widespread problem in many coastal and island systems worldwide [10,11]. Our results provide evidence that restoration of ecosystems that have been subjected to rat invasion requires not only the removal of the invader, but also the active return of seabird populations in order to restore soil fertility, and therefore, plant and ecosystem productivity [22].

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