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Linking vegetation change, carbon sequestration and biodiversity: insights from island ecosystems in a long-term natural experiment

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Running Headline: Islands and Ecosystem Processes

Summary

1. Despite recent interest in linkages between above- and belowground communities and their consequences for ecosystem processes, much remains unknown about their responses to long-term ecosystem change. We synthesize multiple lines of evidence from a long-term ‘natural experiment’ to illustrate how ecosystem retrogression (the decline in ecosystem processes due to long-term absence of major disturbance) drives vegetation change, and thus aboveground and belowground carbon (C) sequestration, and communities of consumer biota.

2. Our study system involves 30 islands in Swedish boreal forest that form a 5000 year fire-driven retrogressive chronosequence. Here, retrogression leads to lower plant productivity and slower decomposition, and a community shift from plants with traits associated with resource acquisition to those linked with resource conservation.

3. We present consistent evidence that aboveground ecosystem C sequestration declines, while belowground and total C storage increases linearly for at least 5000 years following fire absence. This increase is driven primarily by changes in vegetation characteristics, impairment of decomposer organisms and absence of humus combustion.

4. Data from contrasting trophic groups show that during retrogression, biomass or abundance of plants and decomposer biota decreases, while that of aboveground invertebrates and birds increases, due to different organisms accessing resources via distinct energy channels. Meanwhile, diversity measures of vascular plants and aboveground (but not belowground) consumers respond positively to retrogression.

5. We show that taxonomic richness of plants and aboveground consumers are positively correlated with total ecosystem C storage, suggesting that conserving old growth forests simultaneously maximizes biodiversity and C sequestration. However, we find little observational or experimental evidence that plant diversity is a major driver of ecosystem C storage on the islands relative to other biotic and abiotic factors.

6. *Synthesis.* Our study reveals that across contrasting islands differing in exposure to a key extrinsic driver (historical disturbance regime and resulting retrogression), there are coordinated responses of soil fertility, vegetation, consumer communities, and ecosystem C sequestration, which all feed back to one another. It also highlights the value of well replicated natural experiments for tackling questions about aboveground-belowground linkages over temporal and spatial scales that are otherwise unachievable.

Key-words: aboveground; belowground; biodiversity; carbon sequestration; chronosequence; island ecology; natural experiment; retrogression; succession

Introduction

All terrestrial communities consist of a producer subsystem that regulates ecosystem carbon (C) input, and a decomposer subsystem that regulates C output. While the ecological importance of linkages between the two components has been long recognized (Müller 1884; Handley 1961), the past decade has witnessed a substantial research effort in this area. A rapidly growing number of studies have explored how plant community attributes affect the soil biotic community (e.g., Wardle et al. 1999, Porazinska et al. 2003), and how the soil biota in turn affects the plant community, leading to feedbacks between the plant and soil subsystems (e.g., De Deyn *et al*. 2004; Kardol *et al*. 2006). Several studies have also explored how the diversity of plants and soil biota may be linked, and how these associations drive community diversity both above- and belowground (Porazinska *et al.* 2003; Scherber *et al*. 2010). A key emerging trend is that there is a greater level of specificity between the plant and associated soil communities than has historically been assumed (Wardle *et al.* 2004a; Bezemer *et al*. 2010; Eisenhauer *et al.* 2010). Another expanding area of activity explores how plant and soil communities interact to influence ecosystem processes such as C and nutrient cycling, and the capacity of ecosystems to sequester and store C (De Deyn *et al*. 2008). An improved understanding of the ways in which plant and soil communities interact to influence ecosystem C fluxes is increasingly recognized as critical for understanding feedbacks involving terrestrial ecosystems and global change phenomena such as atmospheric CO_2 enrichment and climate change (Bardgett & Wardle 2010; Singh *et al*. 2010).

Most studies that have explored linkages and/or feedbacks between above- and belowground subsystems (and in particular between above- and belowground diversity) have used controlled experimental approaches and fast-growing herbaceous plant species. However, there is increasing recognition that observational approaches and 'natural experiments' (in which sites are selected across which one or more factors vary with all others being constant) have considerable potential for answering ecological questions over much greater spatial and temporal scales (e.g., Croll *et al*. 2005., Vitousek 2004) than can be achieved with conventional experiments (Fukami & Wardle 2005; Sagarin & Pauchard 2010). Among the most potentially powerful natural experiments for addressing how ecological phenomena change over the long-term are chronosequences, which involve 'space for time substitution'. Despite some criticisms of the approach (e.g., Johnson & Miyanishi 2008), and problems that can arise when they are used inappropriately (Walker *et al.* 2010), there are many instances of chronosequences enabling the study of long-term phenomena both above- and belowground in a manner that would otherwise be impossible (Vitousek 2004; Wardle *et al*. 2004b; Peltzer *et al.* 2010). As such, chronosequence studies have often demonstrated how the long-term absence of major disturbances leads to declines in nutrient availability, decomposer processes and plant productivity. This impairment has been demonstrated in several locations globally, and is termed 'ecosystem retrogression' (Walker *et al.* 2001; Vitousek 2004; Wardle *et al.* 2004; for a more detailed explanation of retrogression see Peltzer *et al.* 2010). Although some recent studies have used long-term chronosequences to understand linkages between above- and belowground biota over long periods (e.g., Williamson *et al.* 2005; Doblas-Miranda *et al.* 2008), their use for this purpose has remained limited.

In this paper, we focus on insights derived from a fire-driven retrogressive chronosequence, involving 30 islands in the boreal forest zone of northern Sweden, which spans around 5000 years (Wardle *et al.* 1997; 2003a). Specifically, we synthesize and analyze the results of previously published and unpublished data collected from this system over the past 15 years to provide an understanding of the linkages between the above- and belowground subsystems, and more specifically to explore whether vegetation properties, biodiversity across multiple trophic levels, and ecosystem C sequestration show coordinated responses to retrogression. First, we provide an overview of the study system, and explain how retrogression affects vegetation composition and soil fertility. Second, we explore variation among the islands in ecosystem C inputs, outputs and thus C sequestration. Third, we focus on how community properties (abundances, community composition and diversity) of above- and belowground consumer groups change along the chronosequence, and how these are linked to plant community properties. Fourth, we consider how C sequestration and community properties may be linked across the chronosequence. We also use this study to highlight how natural experiments that substitute space for time provide opportunities for exploring the extrinsic drivers of community and ecosystem properties in real ecosystems that are not available with other approaches.

Characterizing the study system

The study system involves 30 forested islands in lakes Hornavan and Uddjaure in the boreal zone of northern Sweden (65°55’ – 66°09’N, 17°43’ – 17°55’E). The mean annual precipitation is 750 mm, and the mean temperature is 13°C in July and -14°C in January. All islands were formed from unconsolidated granite boulders deposited by glacial eskers following the retreat of land ice about 9000 yr ago. The only major extrinsic factor that differs among islands is the history of lightning ignited wildfire, with larger islands having burned more frequently than smaller islands because of their larger area to intercept lightning (Wardle *et al*. 1997, 2003a); this has been confirmed both by ^{14}C dating of charcoal and by measurement of fire scars on trees (Table 1). The islands range from those that last burned 60 years ago to those that last burned 5350 years ago, and thus form a post-fire chronosequence with increasing time since fire as island size decreases. The larger, most recently burned islands experience a fire regime comparable to that occurring naturally in the surrounding mainland forest (Zackrisson 1977), while the smaller islands represent the situation that is often expected with long-term fire suppression (Wardle *et al.* 2003a). For this paper, we classify these 30 islands into three size classes with 10 islands each: large (>1.0 ha), medium (0.1 – 1.0 ha) and small (<0.1 ha) (Table 1).

The vegetation on the islands undergoes a distinct succession with increasing time since fire. Over 99.8% of the tree biomass is made up of *Pinus sylvestris*, *Betula pubescens*, and *Picea abies*. Of these, the abundance of *P. sylvestris* peaks on the large (mostly recently burnt) islands while that of *P. abies* peaks on the small islands; *B. pubescens* peaks on the medium islands but contributes a high proportion of the total tree biomass across all size classes (Wardle *et al*. 1997). Over 98% of the understorey shrub layer consists of the three dwarf shrub species *Vaccinium myrtillus*, *Vaccinium vitis-idaea* and *Empetrum hermaphroditum,* which have their greatest biomass on large, medium and small islands respectively (Wardle *et al.* 2003a). The ground layer vegetation consists of the feather mosses *Pleurozium schreberi* and *Hylocomium splendens*, whose biomasses increase slightly with decreasing island size (Lagerström *et al*. 2007). Detailed analysis of pollen core data from full-depth humus cores on two of the study islands also confirms that as time since fire increases over a time span of 1500 years there is a strong transition from forest domination by *P. sylvestris* and *B. pubescens* to domination by *P. abies* and *B. pubescens* (Hörnberg *et al.* 2004). The vascular plant species that dominate on the small islands (and in the long-term absence of fire), namely *P. abies* and *E. hermaphroditum*, are also well known for being adapted to nutrient-poor conditions, relative to those that dominate on medium and large islands. As such, both produce well-defended foliage and litter with morphological and chemical characteristics (Gallet & Lebreton 1995; Nilsson & Wardle 2005) that reduce biological activity and nitrogen (N) availability (Northup *et al.* 1995). Consistent with this, humus on small islands has higher concentrations of polyphenolics than that on large islands (Wardle *et al.* 1997) (Table 1).

As island size diminishes and time since last fire increases, the islands move along a pathway of increasing ecosystem retrogression, during which availability of major nutrients, notably N and phosphorus (P), decreases (Table 1). Although total N concentration in the humus increases and total P concentration stays constant, there is a decline in the most plant-available forms of both elements. The concentrations of both mineral N and dissolved organic N (DON) decrease from medium to small islands, as does the ratio of mineral N to DON (Wardle & Zackrisson 2005). Further, decomposition rates of plant litter and the release rate of N from decomposing standardized litter is least on the smallest islands (Wardle *et al*. 1997, 2003a). The chemical composition of the soil P pool is increasingly recognized as of ecological importance (Turner et al. 2008); in this system NaOH-extractable P (which is recalcitrant) increases with decreasing island size, while membrane-extractable P (which has high biological availability) decreases (Lagerström *et al*. 2009). The lower availability of N and P on the small islands is linked to reduced activity and biomass of the microbes that break down plant litter, as well as the quality of litter entering the soil, as we discuss later. Further, the higher concentrations of polyphenolics in the humus of the smaller islands that occur with increasing dominance of *E. hermaphroditum* and *P. abies* is likely to lead to greater binding of N and reduced N mineralization (Hättenschwiler & Vitousek 2000; Schimel & Bennett 2004), thus explaining both the higher total N and lower labile N concentrations on the small islands.

The decline in nutrient availability is reflected in vegetation characteristics. For instance, leaf traits of *B. pubescens*, a dominant tree species that occurs across the entire island gradient, changes in ways consistent with reduced nutrient availability as island size declines, including declining foliar N concentration, specific leaf area, and both gross and net photosynthesis (Fig. 1). There is also evidence of greater allocation by *B. pubescens* to secondary defence compounds such as polyphenolics with decreasing island size; some compounds such as gallic acid and ellagic acid show especially large increases (Crutsinger *et al*. 2008). Further, there is greater investment by leaves into structural material such as foliar fibre and cellulose, resulting in greater leaf toughness and dry matter content (Fig. 1). Therefore, the decline in soil nutrient availability that occurs with ecosystem retrogression resulting from long-term fire absence not only causes changes in plant species composition, but also induces within-species shifts towards greater resource conservation rather than resource acquisition. This is consistent with what has been observed for some species during ecosystem retrogression in temperate and subtropical regions (Cordell *et al.* 2001; Richardson *et al*. 2005).

The build-up of N stocks in the humus layer and increase in the humus N:P ratio as retrogression proceeds is, in part, due to significant N inputs from biological N fixation. A major biological input of N to boreal forests in northern Sweden is N fixation by cyanobacteria that live within the leaves of feather mosses (De Luca *et al.* 2002). Studies on the island system have revealed that the rate of biological N fixation associated with the mosses *P. schreberi* and *H. splendens* is much larger on the small islands (mean ± SE fixation rate 2.02 ± 0.38 kg N ha^{-1} yr^{-1}) than on the medium and small islands (0.82 ± 0.14 and 0.52 ± 0.14 kg N ha^{-1} yr^{-1} respectively) (Lagerström *et al*. 2007). In comparison, the N input from atmospheric deposition is less than 2 kg N ha^{-1} yr^{-1}. Greater N fixation on the small islands may be due to greater soil moisture resulting from deeper humus, less mineral N present (given that high N availability reduces N fixation; Zackrisson *et al*. 2004), or shifts in interactions between mosses and other vegetation components. In support of the latter explanation, plant removal experiments have shown that shrubs and tree roots have positive effects on N fixation by mosses on small but not large islands (Gundale *et al.* 2010). However, it appears that this biological N input to the small islands is not readily available to other plants, given their lower available soil and foliar N. It is possible that the fixed N is instead locked up by recalcitrant humus generated from decomposing bryophyte material, or by polyphenols in the soil, and contributes to the net accumulation of ecosystem N stocks as retrogression proceeds which in the absence of fire has occurred at an average rate of 1.8 kg ha^{-1} yr^{-1} over the past 5000 years (Lagerström *et al.* 2007).

Carbon storage and fluxes

The declining nutrient supply that occurs retrogression proceeds reduces net primary productivity (NPP) of both trees and dwarf shrubs, and thus C input to the ecosystem (Fig. 2). There are also shifts in the relative contributions from different floristic components to NPP and C input. At the plant functional group level, while most standing biomass is of trees, a substantial proportion of NPP is derived from understorey dwarf-shrubs and mosses (Fig. 3), which is a consequence of understorey plant biomass having a much more rapid turnover than tree biomass (Nilsson & Wardle 2005). Further, the contribution of trees to total NPP declines significantly as island size decreases while that of mosses increases; hence for the small islands, NPP of the understorey vegetation exceeds that of the trees (Fig. 3). Within functional groups, there are also shifts with island size in the relative contribution of different species to NPP in both the tree and dwarf shrub layers as described above. Diminishing inputs of organic matter from NPP with declining island size, and changes in the composition of these inputs, both between and within functional groups, have important implications for the decomposer subsystem and therefore for fluxes of C below ground.

Concomitant with the decline in NPP and thus C input with decreasing island size is a decline in C release through soil respiration (on a per soil mass basis) and plant litter decomposition rates (Fig. 2). A litter reciprocal transplant experiment, in which vascular plant litters collected from each of the three size classes were each decomposed on islands of all size classes, was used to show that at least three factors can explain the slower rates of litter decomposition on the small islands (Wardle *et al*. 2003a). First, litter from plant species that are most abundant on small islands (*P. abies* and *E. hermaphroditum*) decomposes more slowly than that from species which dominate on larger islands, regardless of which islands they are sourced from or placed on. Second, several of the species produce more slowly decomposing litter when present on smaller islands. Third, any given litter decomposes more slowly on small islands because those islands support inherently lower decomposer activity. Other factors may also contribute to slower rates of litter breakdown and C release on small islands. One is that as island size decreases, twigs make up a greater proportion of total litter input; twig litter decomposes much more slowly than leaf litter (Dearden *et al.* 2006). Another is that the contribution of feather mosses (*H. splendens* and *P. schreberi*) to total NPP increases with decreasing island size (Fig. 3); moss litter decomposes more slowly than that of vascular plants (Wardle *et al*. 2003b; Lang *et al*. 2009). However, this negative effect of mosses on ecosystem-level decomposition rates may be partially offset by the capacity of the moss layer to promote decomposition of vascular plant litters by improving moisture retention during the summer (Jackson *et al.* 2011).

The decline in NPP with decreasing island size leads to less C storage aboveground, while the corresponding decline in decomposition and soil respiration per soil mass leads to greater C storage belowground (Fig. 2). As decomposition is reduced before NPP during retrogression (Wardle *et al.* 2003), the net result is that total C storage increases with decreasing island size. This rate of C accumulation in the absence of fire is constant regardless of island size, so that during at least 5000 years in the absence of fire, total ecosystem C storage increases linearly at the rate of 0.45 kg m^{-2} every century. The fact that all island size classes accumulate C at the same rate irrespective of time since fire is also supported by the finding that net ecosystem exchange (NEE) measurements of the understorey (which contributes to around half of the total ecosystem C input) are unrelated to island size (Fig. 2). While gross photosynthesis of this layer is almost significantly greater on medium relative to small and large islands, this trend is largely offset by greater gross respiration, resulting in NEE being relatively constant across the gradient (Fig. 2). The NEE measures also point to the understorey as a weak net source of C for all island size classes, but this is specific only to the time of measurement. These results in combination highlight that in the long-term absence of fire, total ecosystem C sequestration rate is constant for at least several thousand years.

The use of structural equation modeling on the above- and belowground C storage data from the islands gives further insights into the drivers of C storage in this system (Jonsson & Wardle 2010) (Fig. 4). The decline in aboveground C storage during retrogression is driven primarily by shifts in plant community composition (represented by primary ordination axis of the plant community from Principal Component Analysis), from faster growing acquisitive species such as *P. sylvestris* and *V. myrtillus* to slower-growing conservative (and better defended) species such as *P. abies* and *E. hermaphroditum*. Meanwhile, the increase in both belowground and total ecosystem C storage is driven both by this shift in community composition and by the absence of humus combustion by fire. There is also a weak effect of plant species diversity on C storage, but this is probably unimportant compared to the overriding effect of community composition and abiotic factors (see below). In total, our data support the view that shifts in the functional composition of vegetation, and the underlying trait spectra, are important drivers of ecosystem C sequestration (Wardle *et al*. 2004b; De Deyn *et al*. 2008), both above- and belowground. These results also highlight that conservation of old growth forests dominated by conservative species is effective in promoting long-term ecosystem C storage, particularly belowground.

Composition and diversity across contrasting trophic levels

Concomitant with shifts in ecosystem-level properties across the island area gradient are changes at the community level, including consumer organisms. Retrogressive chronosequences are potentially powerful tools for evaluating the influence of plant-derived resource quantity and quality on both below- and aboveground trophic levels across large environmental gradients (Peltzer *et al.* 2010), although they have seldom been used for this purpose (Gruner 2007; Doblas Miranda *et al*. 2008). Studies on the island system have explored changes in biomass or density of several consumer groups spanning at least three trophic levels, including soil microbes, above- and belowground invertebrates and insectivorous birds (Fig. 5). Of these, only primary and secondary consumers in the decomposer food web (i.e. microbes and microbe-feeding nematodes respectively) decline in response to declining resource quality and quantity during retrogression. For the microbes, there is also an increase in the abundance of fungi relative to bacteria with declining island size (Fig. 5), which is indicative of both poorer quality litter inputs and more conservative nutrient cycling (Bardgett & Wardle 2010). Other soil faunal groups such as top predatory nematodes, and mites and springtails, are unresponsive to the gradient and therefore bottom-up control from the plant community (Jonsson *et al.,* 2009)

In contrast, densities of several aboveground invertebrate groups and insectivorous birds increased as island size decreased despite declining NPP and resource quality (Fig. 5). For the most abundant foliar herbivore in the system, the weevil *Depaurus betulae* that specializes on *B. pubescens* leaves, greater density on small islands is linked to a preference for leaves containing high levels of secondary metabolites (Fig. 1) (Crutsinger *et al*. 2008). The increase of insectivores such as predatory beetles, spiders and birds during retrogression appears to be due to greater inputs to the land (per unit area) of invertebrate prey such as chironomids from the surrounding water on smaller islands, which have a larger perimeter to area ratio. Consistent with this interpretation, densities of chironomids on the land surface are greater on small than large islands (Jonsson & Wardle 2009), and spiders on smaller islands have stable isotope ($\delta^{13}C$) values that are closer to those of chironomids (Hyodo & Wardle 2009). Structural equation modeling also points to invertebrate prey availability (notably spiders, beetles and chironomids) as the best predictor of insectivorous bird density across islands (Jonsson *et al*. 2011). As such, larger islands promote some soil-dwelling decomposer organisms because of a higher quantity and quality of resource input by plants, while smaller islands promote several aboveground consumer groups as a result of a greater contribution of productivity from the surrounding water.

Community composition has also been measured across the island gradient for several groups of organisms, including plants, soil biota, and aboveground consumers (Tables 2, 3). For plants, there is a significant increase during retrogression of both vascular plant species richness and the Shannon-Weiner diversity index (hereafter diversity index) (Wardle *et al.* 2008a), but no corresponding shifts in these measures for mosses (Table 2). The island system enables exploration of why vascular plant richness and diversity increases with decreasing soil fertility and productivity. It has been proposed that as soil fertility declines, diversity is promoted by greater spatial heterogeneity of limiting resources (Tilman 1982; Tilman & Pacala 1993). However, spatial heterogeneity of soil resource availability, as determined through measurements of each of five properties (NH_4^+, amino acid N, $PO_4^{3-,}$ litter decomposition and microbial biomass) across a spatial grid of 49 points on each island, was greater on larger islands with the lowest diversity (Gundale *et al.* 2011). This means that changes in vascular plant diversity across the gradient cannot be explained by changes in resource heterogeneity. An alternative explanation is that species with the highest growth rates that dominate on the most productive islands (*P. sylvestris* and *V. myrtillus*) exclude weaker competitors when resource availability is high (Grime 1979; Grace 1999), leading to lower diversity on large islands. Consistent with this, experimental studies have shown that on large islands, understorey shrubs are more competitive against each other (Wardle & Zackrisson 2005), and against colonization by other species (Wardle *et al.* 2008b). This suggests that declining productivity and competition intensity as island size decreases allows a greater number of vascular plant species to coexist. Conversely, neither bryophyte productivity nor biomass show a simple decline with decreasing island size, reducing the potential for competitive exclusion to vary across the gradient, and resulting in no net shift in bryophyte diversity.

We considered community properties of two key groups of belowground consumers that are each key components of the decomposer subsystem - microbes and nematodes (Tables 2, 3). Microbial community measures were determined from data for both microbial phospholipid fatty acids (PLFAs; different acids correspond to different subsets of the microbial community) and substrate utilization profiles (SUPs; functional community structure is assessed by the relative response of the soil community to different added substrates (Schipper *et al.* 2001). Soil nematode community analyses were performed using identifications at genus or family level (Jonsson *et al.* 2009). We found that community composition of only PLFAs was related to island size (mainly due to a greater fungal to bacterial ratio on small islands), and that richness and diversity index values were not responsive to island size for any group (Tables 2, 3). Further, across the islands, only the diversity index values of PLFAs were related to vascular plant diversity, and only nematode community composition was related to vascular plant composition (Table 4). This does not provide strong support for suggestions that plant communities drive decomposer communities (Hooper *et al*. 2000) as a consequence of specificity between decomposer biota and plant species (Bezemer *et al*. 2010; Eisenhauer 2010). It is also inconsistent with the results of some controlled experiments in which species richness has been experimentally varied (e.g. De Deyn *et al.* 2004; Scherber *et al*. 2010 but see Carney *et al.* 2004). In contrast to many studies exploring diversity linkages between plants and soil biota, the island system involves a naturally assembled gradient of plant diversity, composition and resource availability, and one which is dominated by longer lived woody rather than herbaceous plant species. We show that in this natural setting, the link between the plant community and soil community is weak, and that decomposer community properties can remain reasonably invariant across large gradients of soil resource availability, vegetation composition and plant diversity.

We have also determined community level measures for each of three aboveground consumer groups - spiders, beetles and insectivorous birds (Tables 2, 3). Species richness of both spiders and beetles was greatest on small islands and was related to plant species richness across islands (Table 4). This suggests that richness was driven by the heterogeneity of habitats provided by the plant community (which is greater on small islands) than by island size *per se* (Jonsson *et al.* 2009). This is consistent with experimental studies pointing to plant species richness as a driver of invertebrate species richness (Siemann *et al.* 1988; Scherber *et al.* 2010). In contrast, neither diversity nor composition of either invertebrate group was related to the corresponding measure for the plant community (Table 4). For birds, our measures of diversity are not directly comparable to those of the other groups since they were performed at the whole island scale rather than on plots or samples that were independent of island size. However, structural equation modeling enabled assessment of the role of factors other than island size *per se* on bird species richness, and showed that richness was also driven by NPP and the availability of invertebrate prey (Jonsson *et al.* 2011), as predicted by species energy theory (Hurlbert 2004). In contrast, bird species richness and diversity indices had no relationship with plant richness or diversity indices when the effects of island size *per se* were corrected for (Table 2). However, bird species composition was significantly correlated with plant community composition (Table 3), suggesting that island size effects on the plant community in turn drive the bird community, presumably through different plant species offering distinct niches (Urban & Smith 1989). In total, our data suggest that plant species diversity and composition can sometimes exert positive effects on comparable measures of consumer groups, but that these effects are not recurrent or consistent among different groups (Table 4).

Linking biodiversity and carbon storage

Thus far we have discussed the effects of island size and ecosystem retrogression on processes contributing to C sequestration and biodiversity. There has been considerable recent interest in attempting to link these two components, not least because of policy imperatives to maximize both biodiversity and C storage in forested ecosystems (Huston & Marland 2003; Midgley *et al*. 2010). However, there have been few empirical tests of whether biodiversity and C sequestration are driven by the same factors or whether management for one of these properties also maximizes the other (Huston & Marland 2003; Díaz *et al*. 2009). Through measurements of both C sequestration and community characteristics of each of several contrasting groups of biota, our data set allows explicit testing of this idea across spatially discrete ecosystems. We found that aboveground C storage was negatively correlated with plant species richness and diversity, and with bird diversity, but was unrelated to diversity of any other group (Table 5). However, belowground C storage was positively correlated with species richness of plants and all aboveground consumer groups; total ecosystem C storage was also positively correlated with richness of all but one of these groups (Table 5). This emerges because diminishing soil fertility during retrogression simultaneously promotes plant species richness (with knock-on effects for the richness of other aboveground groups), and causes C accumulation to occur at a constant rate due to reduced decomposer activity. Our results also show that in the boreal forest at least, both ecosystem C storage and biodiversity of plants and aboveground consumers can be simultaneously maximized by the maintenance and conservation of old-growth forests, while decomposer biodiversity remains unaffected. Further, it suggests that C storage and biodiversity would both be disadvantaged by large disturbances, including those associated with intensive forestry.

There has also been much recent interest in whether plant biodiversity impacts ecosystem C storage in its own right. Many experimental studies have shown that plant species richness promotes NPP and thus C input to the soil (Balvanera *et al.* 2006). Recent studies have also used such experiments to suggest that plant richness promotes ecosystem C sequestration (Fornara & Tilman 2008; Steinbass *et al.* 2008), including in forests (e.g. Ruiz-Jaen & Potvin 2011). However, such studies are recognized as having significant limitations for understanding the role of diversity on C storage in natural ecosystems, where species communities are assembled through successional processes and not at random (Lepš 2004; Wardle *et al*. 2011). Our study shows that aboveground standing biomass (and NPP and C sequestration) is negatively correlated with plant species richness (Fig. 6), meaning that any positive effect of plant richness on biomass accumulation is not detectable against the background of other factors that cause biomass to decline across the gradient. In contrast, plant species richness and diversity indices are both positively correlated with both belowground and total ecosystem C storage (Table 5), but this is primarily because of extrinsic factors that drive both C storage and species richness, rather than because species richness is itself directly driving C storage. As such, structural equation modeling (Jonsson & Wardle 2010) reveals that while plant diversity does have some direct effect on both belowground and total C storage, its effect is weak and probably unimportant relative to the much stronger effects of plant species composition and abiotic disturbances (Fig. 4). Instead, our results suggest that plant species composition, and the shift of the spectrum of plant species traits from those associated with resource acquisition to those linked to resource conservation, is the primary means through which plant communities drive C sequestration.

Experimental studies at the within-island scale also fail to provide strong evidence that plant species richness is a major driver of C storage. On each of 30 islands, a plant removal experiment was established in 1996 which is still ongoing, that includes manipulations at both the functional group and species levels. This includes plots on each island with each of the three main dwarf shrub species growing in monoculture and all possible combinations (Wardle & Zackrisson 2005; Wardle *et al.* 2008b). Measurements in 2010 showed that aboveground plant biomass and thus C storage was never significantly greater in the three species treatment than in any of the two species treatments or the best performing monoculture (Fig. 6). However, there were differences between monocultures for all island size classes, and between two species treatments for medium and large islands. These results suggest that any effects of increasing species richness on aboveground C storage saturates at two species, and that compositional effects (i.e. identities of species within any richness level) are more important than those of richness. They also show that these compositional effects are context-dependent and vary across island size classes, being stronger on medium and large islands (Fig. 6). Meanwhile in the soil, measurements performed in 2003 showed that the presence of particular species, notably either of the *Vaccinium* species, promoted loss of belowground C through greater microbial respiration and litter breakdown but only on medium and large islands, pointing to context-dependent effects of species composition on belowground C loss (Wardle & Zackrisson 2005). These results provide experimental evidence that while species diversity is not a major driver of ecosystem C gain or loss, species composition can have effects which become most important on medium and large islands. These effects result from particular species (notably *Vaccinium* spp.) on large islands both promoting aboveground C gain and belowground C loss, which matches the patterns of C storage on larger islands.

Conclusions and a way forward

The study of retrogressive chronosequences has significantly enhanced our understanding of the mechanisms through which soil fertility drives ecosystem processes in subtropical, temperate and boreal regions, and in both grassland and forest (Vitousek 2004; Wardle *et al.* 2004; Peltzer *et al*. 2010). The work we described on this island system reveals how above- and belowground community and ecosystem properties are linked across a strong environmental gradient driven by ecosystem retrogression and declining soil fertility. It highlights that as vegetation changes across the gradient from resource-acquisitive to resource conservative plant species, there are important shifts in both the above- and belowground drivers of the terrestrial C cycle, and in community characteristics across multiple trophic levels, especially aboveground. It also shows that ecosystem C gains and losses (and thus net ecosystem C sequestration), and biodiversity of plants and some groups of consumer organisms, shift in tandem across the gradient, but that there is little evidence of any direct causative relationship between biodiversity and C storage.

From this work, we suggest some ways to advance understanding of linkages between biodiversity, ecosystem C dynamics and vegetation change in real ecosystems. First, we emphasize that natural experiments under natural conditions have considerable untapped potential for understanding long-term ecological processes, despite being overlooked by many ecologists in favour of shorter-term controlled experiments or theoretical approaches (Sagarin & Pauchard 2010). While we recognize the substantial contribution of controlled experiments in significantly enhancing ecological understanding over the past few decades, we emphasize that studies involving comparisons of real ecosystems, combined with knowledge of the extrinsic drivers that vary between them, can yield insights about community and ecosystem processes over larger temporal and spatial scales than are possible with other approaches. This is especially true for forests, for which even a single generation of trees greatly exceeds the duration of any controlled experiment, and for which natural experiments that have run for hundreds or thousands of years therefore have particular advantages. As an example, much has been written about how forest tree biodiversity affects ecosystem C storage (Scherer-Lorenzen *et al*. 2005; Díaz *et al*. 2009), and considerable effort is being devoted to exploring this with formal experimental approaches. However, our understanding of the issue remains poor, and in our lifespan at least, significant insights are probably more likely to arise through the use of natural experiments in which diversity gradients have formed through real successional processes and over ecologically meaningful time scales. Further, concerns about confounding factors that co-vary with diversity across such gradients, and which are sometimes directed toward such studies, can frequently be addressed through an informed understanding of the study system, the judicious use of analytical techniques devised to cope with such issues (Grace *et al.* 2007; Jonsson & Wardle 2010) (Fig. 4), and manipulative experiments nested within natural experiments (Fig. 6).

Our work also suggests other issues that may merit further investigation in other systems. First, despite substantial recent interest in plant traits and their ecological effects, much remains unknown about how variation in plant traits either between or within species governs consumer trophic levels and their contribution to above- and belowground processes (De Bello *et al.* 2010). In our study system at least, such effects appear to be important. Second, despite many recent studies that have explored short term plant-soil feedbacks involving antagonistic and mutualistic soil biota (Kulmatiski *et al.* 2008), little attention has been given to longer term feedbacks involving the decomposer biota. We provide evidence that plants growing on nutrient-poor islands impair decomposer biota (e.g. through producing recalcitrant litter and secondary metabolites), thus reducing nutrient supply from the soil, and negatively feeding back to plant growth. Such mechanisms could be of widespread importance. Third, our data show that long-term fire history may have substantial impacts on ecosystem C dynamics. While most work has focused on the short term effects of fire on the C cycle, understanding these longer-term effects is essential for predicting how human-induced changes in natural fire cycles (e.g. by fire suppression or climate change) may alter this feedback of C between land and the atmosphere, and ultimately the Earth climate system. Fourth, despite much interest in whether the same factors promote both biodiversity and C storage in real ecosystems, and in whether ecosystem management can simultaneously promote both goals (Huston & Marland 2003; Midgley *et al*. 2010), there are surprisingly little convincing data available. There is therefore a pressing need for comparative studies between real ecosystems that simultaneously consider both C sequestration and biodiversity across multiple trophic levels. Ultimately, a greater emphasis by the research community on utilizing natural experiments will advance our understanding of these and other questions relating to the above- and belowground subsystems, over ecologically meaningful spatial and temporal scales, and in a manner that often cannot otherwise be achieved.

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Table 1. Changes in abiotic factors (disturbance regime and soil nutrient properties; mean values with standard errors) across the island size gradient. Data from Wardle *et al.* (1997, 2003a), Wardle & Zackrisson (2005), Lagerström *et al*. (2009) and Gundale *et al.* (2011). Within each row, numbers followed by the same letter are not statistically significant at *P* = 0.05 (Tukey's test following one-way ANOVA with 2,27 d.f.; *N* = 10 for each size class). *P*-values in bold are significant at *P* = 0.05.

Response variable	Large island (>1.0 ha)	Medium island (0.1 – 1.0 ha)	Small island (<0.1 ha)	*F* (*P*)
Disturbance regime				
Time since last major fire (^{14}C data) (yr)	585 (233) c	2180 (385) b	3250 (439) a	**13.4 (<0.001)**
Number of fire scars caused in past 250 yrs	0.667 (0.256) a	0.208 (0.085) b	0.143 (0.016) b	**3.5 (0.037)**
Humus properties (0-10 cm depth)				
Polyphenols (μg/g)	175 (6) b	204 (6) a	225 (8) a	**7.2 (0.002)**
pH	3.51 (0.029) a	3.42 (0.027) ab	3.38 (0.039) b	**3.4 (0.034)**
Total N (%)	1.28 (0.06) b	1.46 (0.04) a	1.59 (0.07) a	**8.7 (<0.001)**
Total P (%)	0.087 (0.005) a	0.097 (0.003) a	0.091 (0.003) a	1.5 (0.223)
Total C to N ratio	41.0 (1.7) a	35.3 (0.8) b	32.8 (1.2) b	**10.8 (<0.001)**
Total C to P ratio	600 (31) a	532 (16) a	556 (20) a	2.2 (0.127)
Total N to P ratio	14.7 (0.5) a	15.2 (0.5) a	17.5 (0.8) b	**5.7 (0.009)**
Mineral N (ammonium + nitrate) (MIN) (μg/g)	38.2 (14.4) b	58.1 (9.2) a	25.3 (8.0) b	**13.9 (<0.001)**
Dissolved organic N (DON) (μg/g)	39.1 (7.2) b	50.7 (5.5) a	40.3 (4.6) b	**3.6 (0.028)**
MIN/DON	0.49 (0.04) a	0.53 (0.05) a	0.39 (0.03) b	**5.7 (0.009)**
N release from decomposing litter (mg/g/yr)	5.8 (0.1) a	5.3 (0.1) b	5.1 (0.1) b	**4.0 (0.030)**
Phosphate (μg/g)	43.6 (4.9) a	37.7 (4.3) a	24.7 (2.3) b	**5.9 (0.007)**
NaOH-extractable P (μg/g)	103 (6) b	123 (4) a	119 (5) ab	**4.6 (0.019)**
Membrane-extractable P (μg/g)	87.4 (10.2) ab	97.1 (6.5) a	74.7 (5.3) b	**3.7 (0.039)**

Table 2. Taxonomic richness and Shannon-Weiner diversity index values (means and standard errors) for plants, microbes and animals, in response to island size. Vascular plant data from Wardle *et al*. (1997, 2008a), bryophyte data from Gundale et al (2011), SUP data from Schipper *et al.* (2001), soil nematode, beetle and spider data from Jonsson *et al.* (2009), and bird data from Jonsson *et al*. (2011). Previously unpublished data for PLFA are as described in the Supplementary Online Material. All richness measures are for fixed plot sizes (plants, beetles and spiders) or fixed soil weights (nematodes) irrespective of island size, except for birds for which whole island measures are used. Within each row, numbers for each measure followed by the same letter are not statistically significant at *P* = 0.05 (Tukey's test following one-way ANOVA with 2,27; d.f.; *N* = 10 for each size class). *P*-values in bold are significant at *P* = 0.05.

Organism group	Richness of taxa				Shannon-Weiner diversity index			
	Large islands (<1.0 ha)	Medium islands (0.1 – 1.0 ha)	Small islands (>1.0 ha)	*F* (*P*)	Large islands (<1.0 ha)	Medium islands (0.1 – 1.0 ha)	Small islands (>1.0 ha)	*F* (*P*)
Vascular plant species	6.6 (0.5) c	8.6 (0.4) b	10.6 (0.6) a	**16.6 (<0.001)**	0.62 (0.11) b	0.86 (0.06) ab	0.97 (0.06) a	**5.0 (0.014)**
Bryophyte species	3.6 (0.4)	3.8 (0.5)	4.8 (0.4)	0.9 (0.407)	0.82 (0.07)	0.79 (0.09)	0.91 (0.04)	0.6 (0.540)
Microbial PLFAs[1]	ND	ND	ND		1.94 (0.01)	1.96 (0.01)	1.94 (0.01)	3.3 (0.052)
Microbial SUPs[2]	ND	ND	ND		3.01 (0.02)	3.01 (0.01)	3.07 (0.04)	1.3 (0.301)
Soil nematode genera	12.5 (0.82)	12.2 (0.87)	12.8 (0.77)	0.1 (0.876)	1.56 (0.10)	1.51 (0.09)	1.62 (0.10)	0.1 (0.076)
Ground dwelling beetle species	4.3 (0.7) b	7.7 (0.9) a	8.5 (0.5) a	**9.1 (<0.001)**	0.90 (0.14) b	1.33 (0.14) a	1.30 (0.09) ab	**3.4 (0.047)**
Ground dwelling spider species	6.6 (1.2) b	8.2 (1.1) ab	10.8 (0.8) a	**3.9 (0.032)**	1.54 (0.19)	1.78 (0.17)	1.57 (0.16)	0.5 (0.583)
Insectivorous bird species	8.4 (0.4) a	4.5 (0.6) b	1.7 (0.3) c	**51.8 (<0.001)**	1.96 (0.04) c	1.30 (0.17) b	0.39 (0.10) a	**44.0 (<0.001)**

[1] phospholipid fatty acids; [2] substrate utilization profile; ND = not determined

Table 3. Results from ANOVA of the effects of island size class on principal component axis scores (PC1 and PC2) for plants, microbes and animals. Data shown are *F* values with *P* values in parentheses (following rank-transformation of ordination score values), and the percentage of total variation in the data set explained by the ordination axes. *P*-values in bold are significant at *P* = 0.05. All data are from the same sources as for Table 2.

Organism group	PC1		PC2	
	F (*P*)	% explained	*F* (*P*)	% explained
Vascular plant species	**36.3 (<0.001)**	47.8	**3.9 (0.032)**	20.4
Bryophyte species	0.3 (0.717)	24.9	1.1 (0.336)	17.9
Microbial PLFAs[1]	**5.4 (0.010)**	38.4	1.4 (0.256)	21.6
Microbial SUPs[2]	0.2 (0.789)	28.9	1.4 (0.285)	14.3
Soil nematode genera	0.5 (0.614)	20.6	2.3 (0.121)	13.2
Ground dwelling beetle species	1.6 (0.214)	12.6	1.8 (0.182)	9.6
Ground dwelling spider species	2.8 (0.077)	14.1	2.5 (0.100)	11.5
Insectivorous bird species	**30.3 (<0.001)**	18.6	**3.8 (0.034)**	12.6

[1] phospholipid fatty acids; [2] substrate utilization profile

Table 4. Pearson's correlation coefficients (*r*) between vascular plant and consumer taxonomic richness, Shannon-Weiner diversity index and community composition (rank-transformed primary ordination axis) across N=30 islands. For bird data, because diversity was measured on a whole island scale (rather than on a fixed area or soil mass independent of island size), *r*-values for richness and diversity indices are partial correlation coefficients correcting for the effect of island size. *, **, *** indicate that *r* is significant at *P* = 0.05, 0.01 and 0.001 respectively. All data are from the same sources as for Table 2.

Consumer group	Plant versus consumer taxonomic richness	Plant versus consumer diversity index	Plant versus consumer community composition
Microbial PLFAs[1]	ND	0.513**	0.216
Microbial SUPs[2]	ND	0.020	0.138
Soil nematode genera	0.176	-0.104	0.074
Ground dwelling beetle species	0.380*	0.100	0.141
Ground dwelling spider species	0.362*	0.043	0.192
Insectivorous bird species	-0.020	-0.098	0.594**

[1] phospholipid fatty acids; [2] substrate utilization profile; ND = not determined

Table 5. Pearson's correlation coefficients (*r*) between measures of ecosystem C storage (on a per area basis) and diversity of different organism groups across N=30 islands. For bird data, because diversity was measured on a whole island scale (rather than on a fixed area or soil mass independent of island size), *r*-values are partial correlation coefficients correcting for the effect of island size. *, **, *** indicate that *r* is significant at *P* = 0.05, 0.01 and 0.001 respectively. All data are from the same sources as for Table 2.

Measure	Organism group	Aboveground C storage	Belowground C storage	Total C storage
Richness of taxa	Vascular plant species	-0.453*	0.490**	0.461*
	Bryophyte species	-0.259	0.162	0.131
	Soil nematode genera	-0.191	0.042	0.016
	Ground dwelling beetle species	-0.306	0.422*	0.410*
	Ground dwelling spider species	-0.286	0.373*	0.358
	Insectivorous bird species	0.257	0.366*	0.379*
Shannon-Weiner diversity index	Vascular plant species	-0.439*	0.501**	0.477**
	Bryophyte species	-0.134	0.070	0.050
	Microbial PLFAs[1]	-0.139	0.314	0.320
	Microbial SUPs[2]	-0.287	0.248	0.239
	Soil nematode genera	-0.040	0.005	-0.001
	Ground dwelling beetle species	-0.144	0.272	0.276
	Ground dwelling spider species	0.128	0.053	0.076
	Insectivorous bird species	-0.388*	0.186	0.239

[1] phospholipid fatty acids; [2] substrate utilization profile

Figure legends

Fig. 1. Leaf characteristics (mean and standard error) of *Betula pubescens* on islands in different size classes (L = large, M = medium, S = small). SLA = specific leaf area; LDMC = leaf dry matter content; N = nitrogen. Data for panels (d) to (i) are derived from previously published data (Crutsinger *et al.* 2008). Methods for previously unpublished data (panels (a) to (c) and (j) to (l)) are given in the Supplementary Online Material, and for other panels are in the source publications. *F* values are derived from one way ANOVA with 2,27 degrees of freedom. NS, *, ** and *** indicates that effect of island size is non-significant or significant at *P* = 0.05, 0.01, 0.001 respectively. Within each panel, bars topped by the same letter are not significantly different according to Tukey's test at *P* = 0.05.

Fig. 2. Island carbon storage (a-c), and fluxes that influence C storage (d-i), on islands in different size classes (L = large, M = medium, S = small). Respn = respiration, NPP = Net Primary Productivity. Data from panels (a) to (f) are from Wardle et al. (1997, 2003a). Measures of NPP in panel (g) are the sum of tree and shrub NPP values from Wardle *et al.* (2003a) and previously unpublished moss NPP values; methods for determining moss NPP are given in the Supplementary Online Material. For previously unpublished data in panels (h) and (i), measures are made for the understorey vegetation only and the methods are given in the Supplementary Online Material. *F* values are derived from one way ANOVA with 2,27 degrees of freedom. NS, *, ** and *** indicates that effect of island size is non-significant or significant at *P* = 0.05, 0.01, 0.001 respectively. Within each panel, bars topped by the same letter are not significantly different according to Tukey's test at *P* = 0.05.

Fig. 3. Relative contribution of trees, shrubs and mosses to (a) total aboveground plant biomass and (b) total aboveground net primary productivity, across island size classes. Significance of differences in proportions of different components between the island size class groups were determined by one way ANOVA on arcsine-transformed data (with d.f. = 2, 27) as follows: (a): Trees: $F = 16.1$, $P < 0.001$; Shrubs: $F = 9.9$, $P < 0.001$; Mosses: $F = 14.6$, $P < 0.001$; (b): Trees: $F = 5.8$, $P = 0.008$; Shrubs: $F = 0.5$, $P = 0.619$; Mosses: $F = 13.6$; $P < 0.001$. Data for trees and shrubs are from Wardle *et al.* (2003a). Methods for previously unpublished moss data are given in the Supplementary Online Material.

Fig. 4. Results from Structural Equation Modeling on the drivers of (a) aboveground carbon, (b) belowground carbon, and (c) total carbon. Bold arrows indicate statistically significant paths at $P = 0.05$ (thick bold arrows indicate $P = 0.01$). Dashed arrows indicate non-significant paths that were necessary to include for obtaining the most parsimonious model. Signs (‘ + ’ or ‘- ’) indicate direction of relationships. From Jonsson & Wardle (2010).

Fig. 5. Biomass or density data for producers and consumer groups of multiple trophic levels across island size classes. SIR = substrate-induced respiration; bacterial to fungal ratios are for microbial phospholipid fatty acids. Densities of predatory beetles and ground dwelling spiders are total catches during two weeks of pitfall trapping; densities of web spiders are total catches from 20 sweeps using sweep-netting. Herbivorous weevil data are for the species *Depaurus betulae*. Data for panels (a) and (b) are from Wardle et al. (2003a), for panels (f), (g), (i), (j) and (k) are from Jonsson et al. (2009) (data from 2007 only), for panel (h) from Crutsinger et al. (2008) and from panel (l) from Jonsson et al. (2011). Methods for previously unpublished data in

panels (c) to (e) are given in the Supplementary Online Material and for other panels are in the source publications. *F* values are derived from one way ANOVA with 2,27 degrees of freedom (after log-transformation for the nematode and bird data). NS, *, ** and *** indicates that effect of island size is non- significant or significant at $P = 0.05, 0.01, 0.001$ respectively. Within each panel, bars topped by the same letter are not significantly different according to Tukey's test at $P = 0.05$.

Fig. 6. Relationship between vascular plant standing biomass and plant species richness. (a) Relationship at the among-island scale using 20m radius plots; each point represents a different island. (b) – (d). Relationship at the within-island scale, for understorey shrubs in plots in an ongoing removal experiment, 14 years after set-up in 1996. Species codes for species remaining in removal treatments (X-axis of panels b-d) are: M = *Vaccinium myrtillus*; V = *Vaccinium vitis-idaea*; E = *Empetrum hermaphroditum*. Split plot ANOVA results (with islands as main plots and removal treatments as split plots) for panels (b) – (d) are: Island size: $F_{2,18} = 1.09$ ($P = 0.356$); Removal treatment: $F_{6,162} = 13.6$ ($P < 0.001$); Island size × removal treatment interaction: $F_{12,162} = 5.9$ ($P < 0.001$). Within each panel bars topped by the same letter are not significantly different according to Tukey's test at $P = 0.05$. Data for panel (a) are from Wardle *et al.* (1997, 2008a), and that for panels (b) – (d) are from the ongoing experiment described by Wardle & Zackrisson (2005) but using previously unpublished data collected in August 2010.

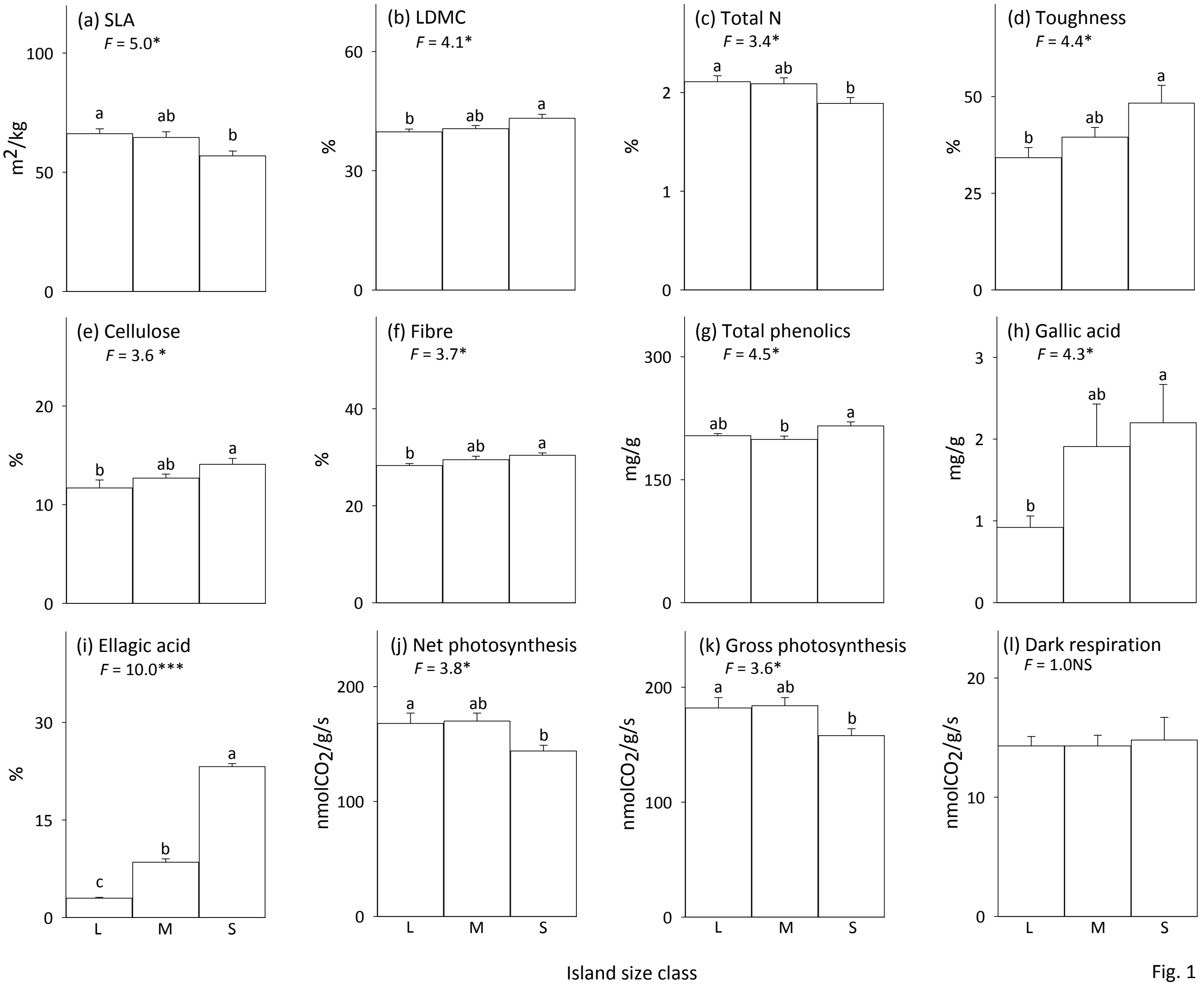

(a) SLA
F = 5.0*
m2/kg
100
50
0
a
ab
b
(b) LDMC
F = 4.1*
%
60
30
0
b
ab
a
(c) Total N
F = 3.4*
%
2
1
0
a
ab
b
(d) Toughness
F = 4.4*
%
50
25
0
b
ab
a
(e) Cellulose
F = 3.6 *
%
20
10
0
b
ab
a
(f) Fibre
F = 3.7*
%
40
20
0
b
ab
a
(g) Total phenolics
F = 4.5*
mg/g
300
150
0
ab
b
a
(h) Gallic acid
F = 4.3*
mg/g
3
2
1
0
b
ab
a
(i) Ellagic acid
F = 10.0***
%
30
15
0
c
b
a
(j) Net photosynthesis
F = 3.8*
nmolCO2/g/s
200
100
0
a
ab
b
(k) Gross photosynthesis
F = 3.6*
nmolCO2/g/s
200
100
0
a
ab
b
(l) Dark respiration
F = 1.0NS
nmolCO2/g/s
20
10
0
L
M
S
Island size class

Fig. 1

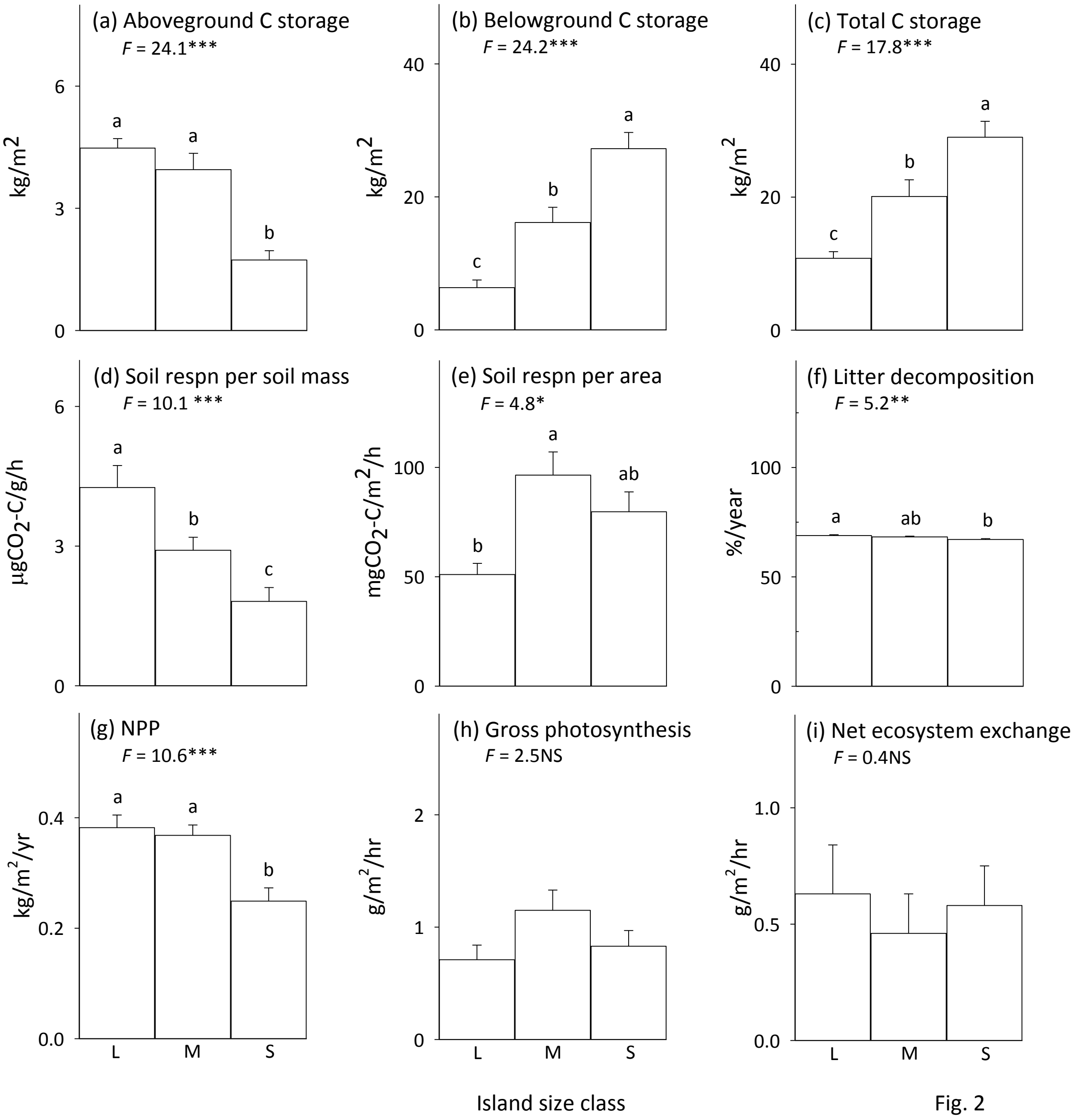
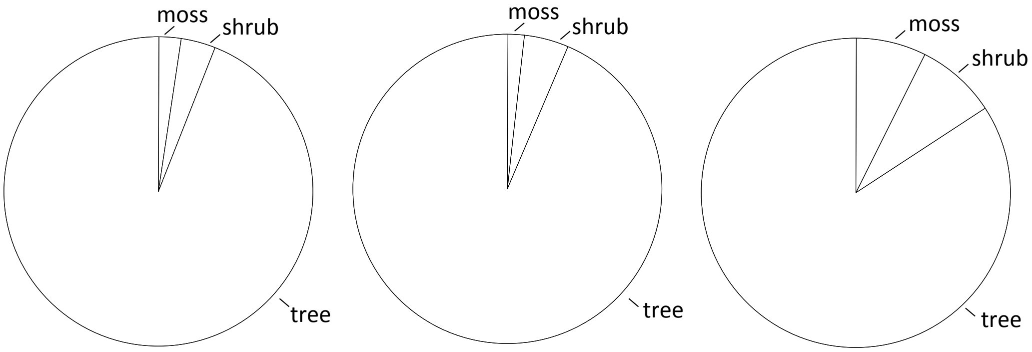

(a) Aboveground C storage
F = 24.1***
kg/m2
0
3
6
a
a
b
(b) Belowground C storage
F = 24.2***
kg/m2
0
20
40
c
b
a
(c) Total C storage
F = 17.8***
kg/m2
0
20
40
c
b
a
(d) Soil respn per soil mass
F = 10.1 ***
µgCO2-C/g/h
0
3
6
a
b
c
(e) Soil respn per area
F = 4.8*
mgCO2-C/m2/h
0
50
100
b
a
ab
(f) Litter decomposition
F = 5.2**
%/year
0
50
100
a
ab
b
(g) NPP
F = 10.6***
kg/m2/yr
0.0
0.2
0.4
a
a
b
(h) Gross photosynthesis
F = 2.5NS
g/m2/hr
0
1
2
(i) Net ecosystem exchange
F = 0.4NS
g/m2/hr
0.0
0.5
1.0
L
M
S
Island size class

Fig. 2

(a) Standing biomass



(b) Net primary productivity

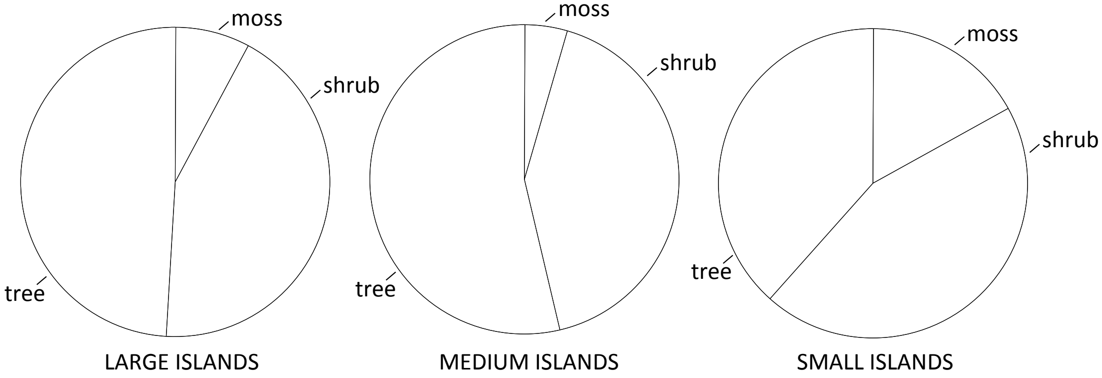


Fig. 3

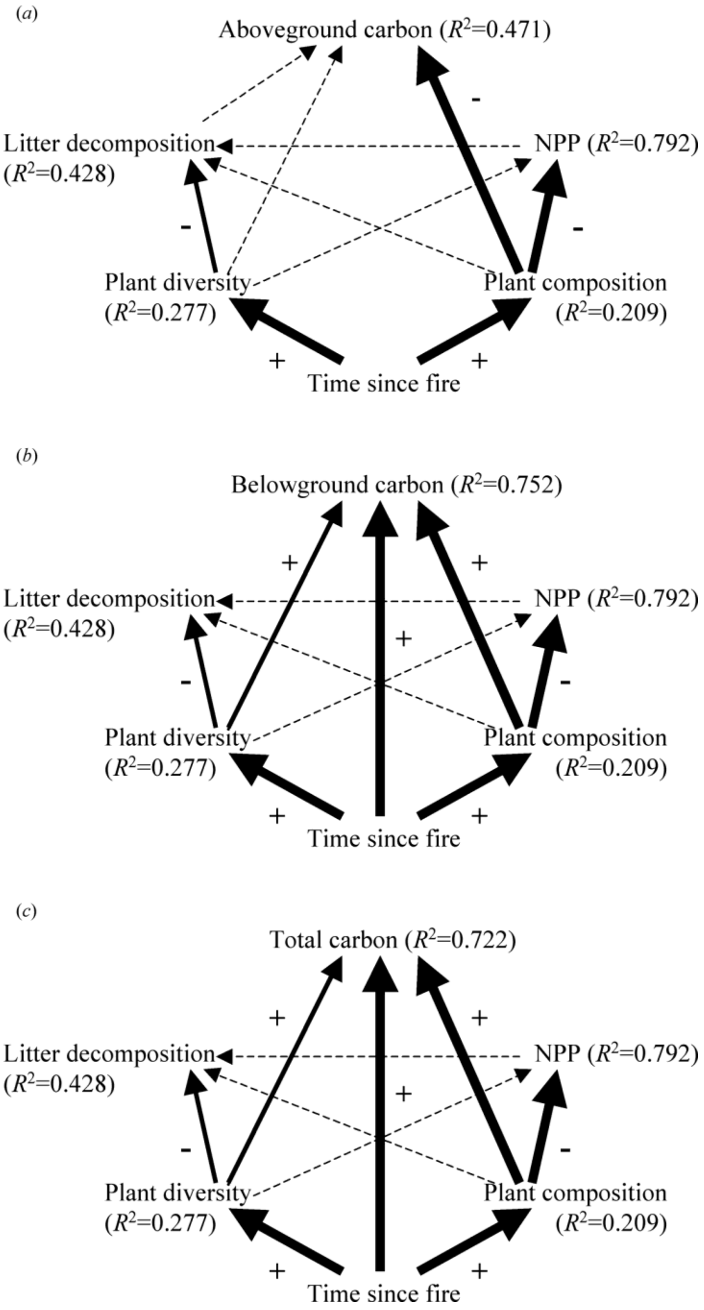

(a)
Aboveground carbon (R^2=0.471)
Litter decomposition (R^2=0.428)
NPP (R^2=0.792)
Plant diversity (R^2=0.277)
Plant composition (R^2=0.209)
Time since fire
-
-
-
+
+
(b)
Belowground carbon (R^2=0.752)
Litter decomposition (R^2=0.428)
NPP (R^2=0.792)
Plant diversity (R^2=0.277)
Plant composition (R^2=0.209)
Time since fire
+
+
+
-
-
+
+
(c)
Total carbon (R^2=0.722)
Litter decomposition (R^2=0.428)
NPP (R^2=0.792)
Plant diversity (R^2=0.277)
Plant composition (R^2=0.209)
Time since fire
+
+
+
-
-
+
+

Fig. 4

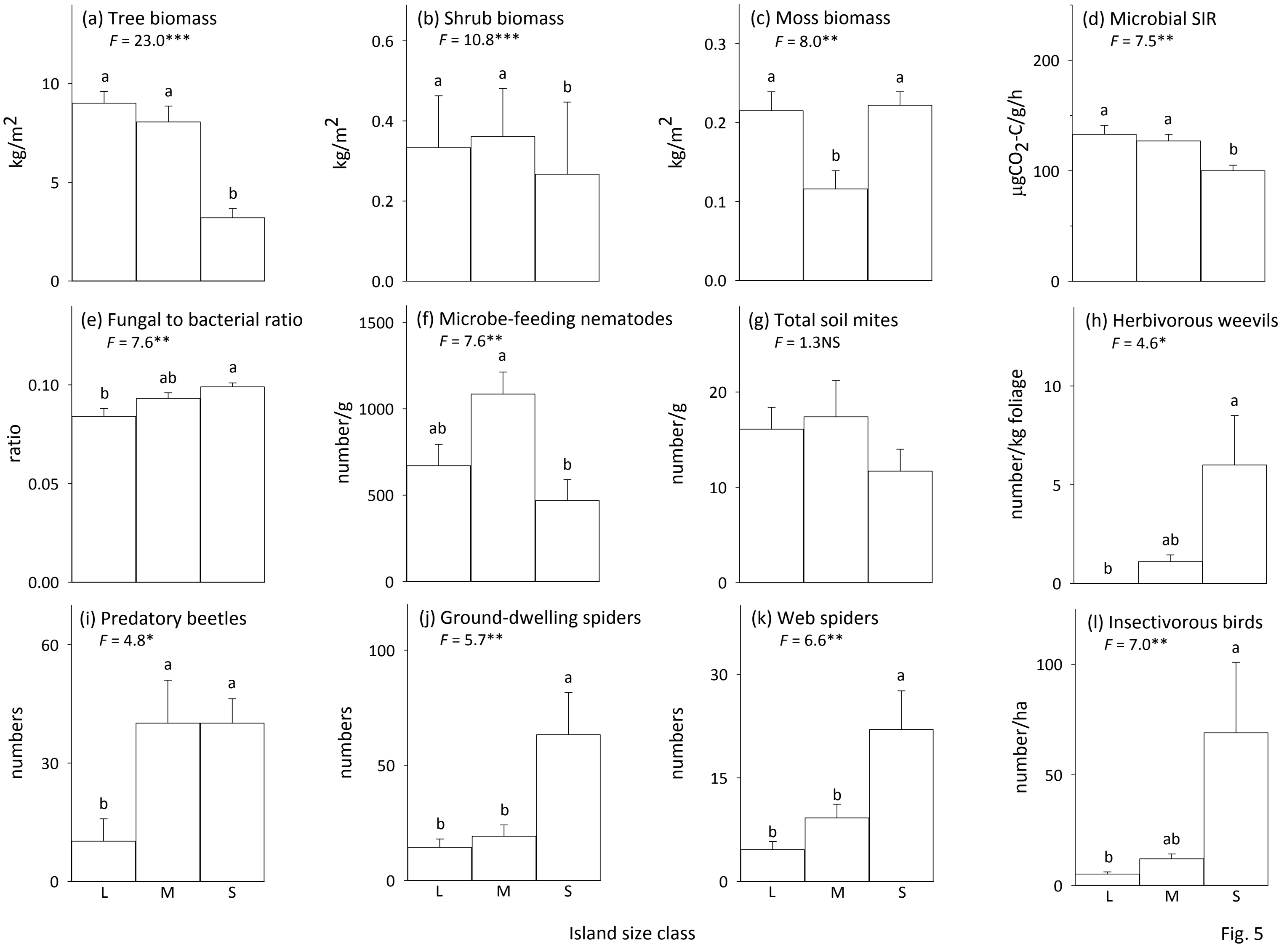

(a) Tree biomass
F = 23.0***
kg/m2
0
5
10
a
a
b
(b) Shrub biomass
F = 10.8***
kg/m2
0.0
0.2
0.4
0.6
a
a
b
(c) Moss biomass
F = 8.0**
kg/m2
0.0
0.1
0.2
0.3
a
b
a
(d) Microbial SIR
F = 7.5**
μgCO2-C/g/h
0
100
200
a
a
b
(e) Fungal to bacterial ratio
F = 7.6**
ratio
0.00
0.05
0.10
b
ab
a
(f) Microbe-feeding nematodes
F = 7.6**
number/g
0
500
1000
1500
ab
a
b
(g) Total soil mites
F = 1.3NS
number/g
0
10
20
(h) Herbivorous weevils
F = 4.6*
number/kg foliage
0
5
10
b
ab
a
(i) Predatory beetles
F = 4.8*
numbers
0
30
60
b
a
a
(j) Ground-dwelling spiders
F = 5.7**
numbers
0
50
100
b
b
a
(k) Web spiders
F = 6.6**
numbers
0
15
30
b
b
a
(l) Insectivorous birds
F = 7.0**
number/ha
0
50
100
b
ab
a
L
M
S
Island size class

Fig. 5

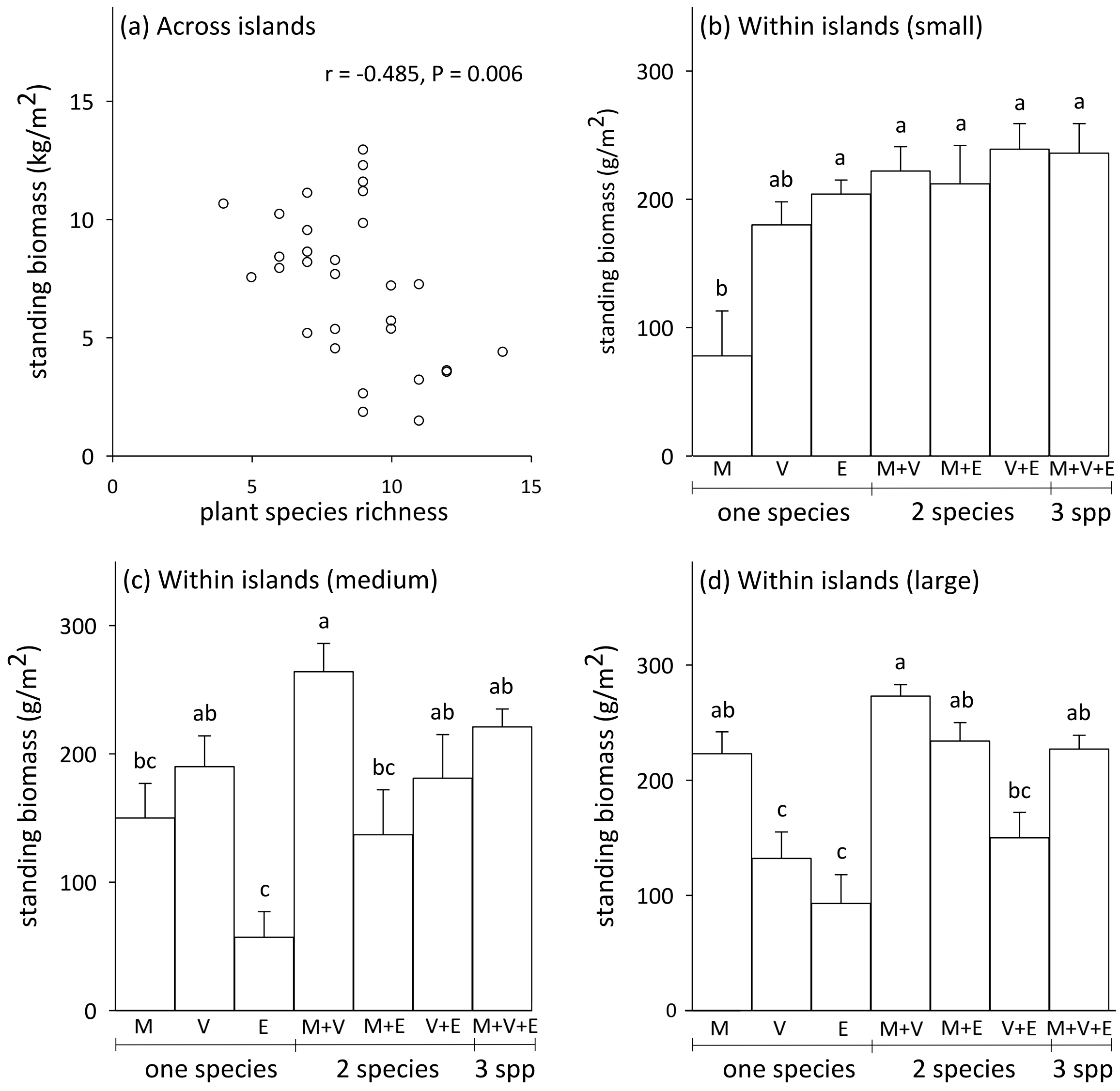

(a) Across islands
r = -0.485, P = 0.006
standing biomass (kg/m^2)
0
5
10
15
plant species richness
(b) Within islands (small)
standing biomass (g/m^2)
0
100
200
300
b
ab
a
a
a
a
a
M
V
E
M+V
M+E
V+E
M+V+E
one species
2 species
3 spp
(c) Within islands (medium)
standing biomass (g/m^2)
bc
ab
c
a
bc
ab
ab
M
V
E
M+V
M+E
V+E
M+V+E
one species
2 species
3 spp
(d) Within islands (large)
standing biomass (g/m^2)
ab
c
c
a
ab
bc
ab
M
V
E
M+V
M+E
V+E
M+V+E
one species
2 species
3 spp

Fig. 6