A MULTI-SCALE INVESTIGATION OF SPECIES RICHNESS, PRODUCTIVITY AND NUTRIENT RELATIONSHIPS IN HERBACEOUS PLANT COMMUNITIES OF THE GRASSLANDS OF SOUTHERN INTERIOR BRITISH COLUMBIA

by

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ABSTRACT

Philip Grime's humped-back model predicts that species richness reaches a maximum at intermediate productivity and drops off at low and high productivities. Soil nutrient availability is known to influence primary productivity and plant species richness. In general, productivity increases with increasing soil nutrient availability, and experiments that increase soil nutrients often show increases in biomass with corresponding decreases in species richness; as such, certain patterns in soil nutrients are expected to coincide with the humped-back model. Scale is also an important factor, as the relationship between species richness and productivity may vary with scale. Objectives of this work were (1) to test the explicit humped-back model prediction that the relationship between species richness and productivity is unimodal; (2) to test implicit humped-back model predictions that species richness is related to nutrients that are tightly associated with productivity, such as carbon and nitrogen, by a unimodal relationship and identify patterns between soil nutrients, leaf nutrients, productivity and species richness; and (3) to evaluate the influence of increasing scales from 1 m^2 to 64 m^2 on relationships found between species richness, productivity and nutrients. This was done using biomass and litter collections and species richness counts from 14 multi-scale grids (8 m × 8 m grids containing 64, 1 m^2 plots), soil samples from a subset of four of the 14 multi-scale grids, and leaf samples from a subset of nine adjacent plots in each of the four multi-scale grids that were sampled for soil nutrients. Total carbon and nitrogen contents in soil and leaf samples were analyzed with a CE-440 Elemental Analyzer. Total aluminum, boron, calcium, copper, iron, magnesium, manganese, sodium, phosphorus, potassium, sulphur, and zinc were quantified in soil samples prepared by very high-pressure closed vessel microwave acid digestion in a Milestone “Ultrawave” single reaction chamber followed by analysis with a Teledyne/Leeman Labs “Prodigy” dual view inductively coupled plasma-optical emission spectrometer. In principal component analyses of soil nutrient data, the first and second principal components appeared to represent productivity and species richness, respectively; and carbon, nitrogen, phosphorus, potassium, boron, iron, magnesium and manganese were identified as important soil nutrients. Bivariate

regressions of the first principal component with total biomass (R^2 = 0.76) and the second principal component with species richness (R^2 = 0.35) returned strong R^2 values. Species richness was related to total biomass (R^2 = 0.11), soil carbon (R^2 = 0.15), soil nitrogen (R^2 = 0.14) and iron (R^2 = 0.29) by concave down relationships, to boron (R^2 = 0.17) and magnesium (R^2 = 0.49) by concave up relationships, to phosphorus (R^2 = 0.27) and manganese (R^2 = 0.25) by positive linear relationships and to potassium (R^2 = 0.14) by a negative linear relationship. Scaling results were inconclusive but suggested that patterns in the literature may be partly due to sample size. Results generally support the humped-back model and that nutrient availability is an important factor correlated with herbaceous plant productivity and species richness. Nutrient availability is likely an important driver of plant productivity and herbaceous plant diversity.

Keywords: carbon, humped-back model, nitrogen, phosphorus, potassium, productivity-diversity relationship, soil nutrients

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LIST OF ABBREVIATIONS

Al = aluminum

ADP = adenosine diphosphate

AMP = adenosine monophosphate

a.s.l = above sea level

ATP = adenosine triphosphate

B = boron

BC = British Columbia

$B(OH)_3$ = boric acid

Ca = calcium

CAR = conditional autoregressive model

Cu = copper

DNA = deoxyribonucleic acid

Fe = iron

GLM = generalized linear model

GLMM = generalized linear mixed model

GLS = generalized least squares

$H_2PO_4^-$ = dihydrogen phosphate

HPO_4^{2-} = hydrogen phosphate

HBM = humped-back model

ICP-OES = inductively coupled plasma-optical emission spectrometer

i.i.d = independently and identically distributed errors

K = potassium

LRMP = land and resource management plan

Mg = magnesium

Mn = manganese

Na = sodium

NH_4^+ = ammonium

NO_3^- = nitrate

P = phosphorus

PCA = principal component analysis

RNA = ribonucleic acid

S = sulphur

SAR = simultaneous autoregressive model

VHP = very high pressure

Zn = zinc

NOMENCLATURE

Plant species were identified according to the Illustrated Flora of British Columbia, all eight volumes of which are currently available at URL http://www.for.gov.bc.ca/hfd/pubs/docs/Mr/MR_IllustratedFlora.htm.

CHAPTER 1: INTRODUCTION

Recent trends of declining biodiversity have emphasized the relevance of the factors that control species richness. Consider planet-wide losses of diversity that have led to major species conservation initiatives in natural communities (Pimm et al. 1995); or eutrophication caused by centuries of fertilizer use to increase soil nutrient availability and boost the productivity of a given area of land while driving species numbers down (Vitousek 1994). The notion of a causal relationship between productivity and species richness has endured since at least Darwin's days (Darwin 1859). Fertilization is known to increase yield and reduce species richness; these responses are well documented in terrestrial and hydrological systems and highlight the important role that nutrients play as drivers of the productivity and diversity of ecosystems (Huston 1979, DiTommaso and Aarssen 1989, Goldberg and Miller 1990, Correll 1998). Dependence on scale has also emerged as an important consideration in understanding patterns of biodiversity, productivity and nutrients (Gross et al. 2000). It is important to strive for a more complete understanding of productivity, species richness and soil nutrient relationships not only because of their implications for the field of ecology but also in order to better direct management, conservation and restoration efforts towards sustainable use of the lands and waters.

The unimodal curve

There is general consensus that productivity can influence species richness, but despite extensive research, there is controversy on the form of the relationship, and on the underlying mechanisms that drive it. One recent review notes six common processes responsible for unimodal species richness curves including disturbance, predation and herbivory, productivity, environmental gradients, time, and latitude (Graham and Duda 2011). Of these, perhaps the most well-known pattern relates to productivity; in this case species richness is low at low productivity, rises to a maximum at intermediate productivity, and drops off again as productivity increases to high levels (Currie 1991, Rosenzweig and Abramsky 1993, Tilman and Pacala 1993, Grace 1999). This unimodal relationship was observed by Grime and termed the ‘humped-back model’ (HBM) (Grime 1973a, 1973b, 1979, Al-Mufti et al. 1977). Although originally developed to describe the species richness-productivity

relationship in herbaceous plant communities, the HBM has since been generalized to many other types of plant (Al-Mufti et al. 1977, Wheeler and Giller 1982, Walker and Peet 1983, Day et al. 1988, Moore and Keddy 1989, Puerto et al. 1990) and animal (Leibold 1999, Dodson et al. 2000, Reed et al. 2006) communities. While there is a range of empirical evidence that supports the HBM there are also studies that do not (see following section for references); after nearly four decades of investigation the debate has not been resolved. Questions that remain are as basic as whether the HBM can be applied to all herbaceous plant communities, to how the scale of measurement influences the relationship between species richness and plant productivity.

The humped-back model

Theory

Grime's humped-back model states that maximum species richness occurs at intermediate standing crop (Al-Mufti et al. 1977, Grime 1979). The unimodal curve of the model delineates the upper boundary of possible species richness-productivity values that may be found in nature (Safford et al. 2001). In other words, productivity is thought to set a limit for species richness, rather than control it strictly (Cornwell and Grubb 2003); so, values should not occur above the line of the curve but may occur below it, in which case the full potential productivity has not been realized. It is thought that at low levels of biomass (proxy for productivity) species richness is limited by high levels of stress or disturbance allowing only species with specific adaptations for those conditions to survive. These plant species tend to be small in stature, slow growing and long lived (Grime 1979). Even if limiting nutrients become abundant, these types of species continue to absorb nutrients slowly and maintain slow growth rates (Chapin 1980, Chapin and Shaver 1985). In high biomass environments, diversity is thought to be restricted by competitively dominant plant species which reduce community richness through interspecific competition; only a few competitively superior species will persist. These species of plants are usually large in stature, grow quickly and can rapidly acquire nutrients if they suddenly become more available. At intermediate levels of biomass there is some release from the constraints of stress, disturbance and competition allowing for the highest levels of species richness (Al-Mufti et al. 1977, Grime 1979). Grime described this medium level of productivity as a "corridor of species richness" which in

English herbs occurred between 350 - 750 g/m^2 of live biomass + standing crop (Grime 1979).

Debate

The HBM has been widely debated ever since its proposal four decades ago (Guo and Berry 1998, Waide et al. 1999, Safford et al. 2001). Although there is a large body of empirical evidence that supports the model (e.g. Al-Mufti et al. 1977, Wheeler and Giller 1982, Walker and Peet 1983, Tilman 1986, Austin 1987, Day et al. 1988, Wilson and Shay 1990, Shipley et al. 1991, Wheeler and Shaw 1991), including a study with belowground root biomass included in productivity estimates (Liira and Zobel 2000), there are also studies that do not (e.g. Moore and Keddy 1989, Gough et al. 1994, Adler et al. 2011).

Three meta-analyses have also been published looking at the comparative frequency of different species richness-productivity patterns in the literature (Mittelbach et al. 2001, Gillman and Wright 2006, Pärtel et al. 2007) but there is uncertainty in the utility of such studies due to complications involved in classifying datasets into categories and inconsistent scales of analysis (Whittaker and Heegaard 2003, Whittaker 2010). In a recent study by Adler et al. (2011) featuring sites in 48 herbaceous plant communities on five continents, it was concluded that there was no clear relationship between productivity and species richness as predicted by the HBM; however, their study has been criticized because litter was not collected for inclusion in estimates of productivity, high productivity sites were underrepresented, and anthropogenically influenced sites were excluded from the analysis (Fridley et al. 2012). In another recent study, Isbell et al. (2013) conclude that the relationship between species richness and productivity seems to "flatten" out over time and may eventually result in no relationship (as found in the Adler et al. 2011 study). They suggest that where there is a relationship it is simply a system in flux, and that it will flatten out with time (Isbell et al. 2013). Cornwell and Grubb (2003) also suggest that it is possible that positive correlations are simply a feature of "transient dynamics". As such, the debate concerning the validity of the HBM is ongoing.

The variety of methods available to estimate productivity (Sala and Austin 2000) has led to further ambiguity in what relationship emerges between productivity and species richness (Cardinale et al. 2009b). The original study leading to the proposal of the HBM measured standing biomass plus litter (Al-Mufti et al. 1977) hence researchers assessing the model since then typically follow suit (Fridley et al. 2012). The leading determinants of biomass, and therefore of litter, are disturbance and productivity (Cornwell and Grubb 2003). In areas of high productivity, litter accumulation may reduce species richness through inhibition of species establishment by shading and physical obstruction of seedlings (Foster and Gross 1998); this in turn reduces competition and plant density resulting in better growing conditions for the plants that are able to establish (Fowler 1986, Carson and Peterson 1990). Litter can also be important in low productivity areas because it can help negate stressful conditions such as low soil moisture or high variability of soil temperature (Fowler 1986, Willms et al. 1986, Facelli and Pickett 1991). Similarly, litter removal has been shown to decrease productivity by reducing soil moisture (Heady 1956). Litter is imperative to estimates of productivity for testing the HBM because it has significant effects on the plant community, it provides an indicator of site history, and because including litter allows a more accurate comparison of the results with those of previous studies, including the original.

The opposite relationship

Lately, the reverse relationship, where species richness is treated as the explanatory variable and productivity is appointed as the response variable, has been receiving considerable attention (Chapin et al. 2000, Cardinale et al. 2009a, Isbell et al. 2013). There are over 150 studies indicating that species richness exerts some control over productivity (Cardinale et al. 2006, 2009a). One version of the theory suggests that fewer species leads to reduced efficiency in the use of soil nutrients and results in reduced plant biomass compared with more diverse communities (Tilman et al. 1996). Other authors insist that research focussed on the dependence of species richness on productivity has actually been investigating the limitation of productivity and species richness by resources, and the limitation of standing biomass by species richness (Cardinale et al. 2009a). In this view resource supply rate has a direct effect on standing biomass, as well as an indirect influence through its control of

species richness (Cardinale et al. 2009a). A study by Isbell et al. (2013) also discusses direct and indirect effects. These ideas are discussed further in reference to nitrogen later on.

Nutrients

Soil nutrient availability is known to influence primary productivity and plant species richness. At the very least, the presence and availability of nutrients may, or may not, meet the nutrient requirements of different species and therefore defines a species' potential to survive in a given area. Productivity generally increases with increasing nutrient availability and, as such, nutrients and rate of nutrient supply are commonly used as proxies for estimating productivity (Waide et al. 1999, Cardinale et al. 2009a). The availability of limiting resources determines the potential productivity of a site; this may differ from the realized productivity based on how efficiently occupant species convert available resources into biomass (Loreau et al. 2001, Schmid 2002, Cardinale et al. 2009b).

Nutrients can be used as proxies of productivity (Waide et al. 1999, Cardinale et al. 2009a); it follows that certain patterns of soil nutrient availability can be expected to coincide with the HBM. The increasing phase of the humped-back curve that occurs from low to intermediate productivity is thought to be caused by decreasing levels of stress and disturbance (Al-Mufti et al. 1977, Grime 1979). One type of stress is limited resource availability such as limited nutrient, water, or light availability. Species richness is low when nutrients are less available because few species are able to tolerate the resource poor conditions, but as nutrient availability increases the minimum nutrient requirements of more species will be satisfied resulting in increasing species richness. Eventually, at high productivity, high availability of nutrients allows competitively superior species to dominate, thus reducing species richness through competitive exclusion. High biomass tends to lead to intense competition for light (Grime 1979, Grace 1999, Aerts et al. 2003, Cornwell and Grubb 2003). Nutrient limitation and availability are partly responsible for driving the relationship observed between species richness and productivity.

Experiments that increase soil nutrients often show increases in biomass with corresponding decreases in species richness (Kirchner 1977, Goldberg and Miller 1990, Bobbink 1991, Wilson and Tilman 1993, Chapin et al. 1995, Wedin and Tilman 1996, Gough et al. 2000,

Baer et al. 2003, Cornwell and Grubb 2003, Crawley et al. 2005). This pattern is observed in the Park Grass experiment at Rothemsted in England, the longest running plant ecology experiment in the world (1856 to present), where enrichment of soils with nitrogen, phosphorus, potassium and organic manures, separately and in various combinations, resulted in increased productivity and reduced species richness (Crawley et al. 2005).

Shifts in diversity likely occur because of differences in the traits of individual species that cause the outcome of competition to change under nutrient enrichment. However, with controlled fertilizer additions the productivity of naturally low productivity sites has been noted to respond less than that of high productivity sites (DiTommaso and Aarssen 1989), and the magnitude of species diversity response has been found to be independent of initial community productivity (Gough et al. 2000). The immobilization of added nutrients to low productivity soils may contribute to this trend (Chapin et al. 1986). It is also possible that the disappearance of species as a result of fertilization of moderate to high productivity plots happens faster than the addition of species caused by fertilization of low to moderate productivity plots. Loss and gain of species are caused through different mechanisms. While the loss of species may result from increased competition resulting in competitive exclusion, the gain of species would depend on dispersal and colonization capacity and other traits of individual species in the regional species pool (Zobel 1997, Gough et al. 2000, Safford et al. 2001).

Gough et al. (2000) and Suding et al. (2005) suggest that species richness-productivity relationships on natural gradients behave differently than those in experimental manipulations; however, humped-shape relationships have been identified in one observational study between species richness and extractable phosphorus, extractable potassium and total nitrogen (Janssens et al. 1998). Cornwell and Grubb (2003) point out that there is a scarcity of information in the literature on species richness patterns and their relation to the resources that control productivity. This knowledge gap motivates further study of soil nutrient patterns to see if they align with what the HBM predicts should coincide at different levels of productivity and richness in nature.

Relationships between soil nutrients and plant health can be complex and have extensive effects on productivity and species richness (Chapin 1980, DiTommaso and Aarssen 1989, Brady and Weil 1996). The concentration of nutrients required for optimal growth of individual plant species is often different, consequently nutrient additions are likely to have varying effects between species. The level of one nutrient that results in toxicity or deficiency is often influenced by the availability in the soil, plant uptake, and plant tissue content of one or more other nutrients (Chapin 1980, DiTommaso and Aarssen 1989, Brady and Weil 1996). Along the same lines, symptoms of toxicity or deficiency of one nutrient can sometimes be treated by increasing or decreasing concentrations of others (Ward et al. 2008). The identity of the limiting resource may change over time, for example over a season (Farrior et al. 2013). In addition, the pH of soils is important to nutrient availability and can also be a good predictor of species diversity (Roem and Berendse 2000). In some cases, an adequate supply of a nutrient can result in luxury consumption and storage of the nutrient. The range of supply in which sufficient nutrients are available but are not at high enough levels to cause negative effects on growth is usually wide for macronutrients, but often much narrower for micronutrients (Brady and Weil 1996). Too little or too much will be detrimental to plant health; this results in a spectrum ranging from deficiency to toxicity and the location of an environment on this spectrum has consequences for both its productivity and species richness (Brady and Weil 1996). Richness tends to be greatest when nutrients are somewhat limiting but conditions are not extremely stressful (Grime 1979, Moore and Keddy 1989). In systems with significant remineralization and decomposition rates productivity can also feed back to influence the rate at which limiting nutrient resources become available (Cardinale et al. 2009a). What follows is a brief overview of key mineral nutrients for plant growth.

Carbon

As the most basic component of all organic matter, carbon plays a fundamental role for living organisms. Plants fix carbon from atmospheric carbon dioxide through the process of photosynthesis and some of this carbon eventually reaches the soil as litter or dead root material. In this way plants remove carbon dioxide from the atmosphere, and through humification it is stored in the soil. Alternatively, some carbon is re-released into the

atmosphere as carbon dioxide during decomposition by microorganisms and animals that consume the plant matter (Brady and Weil 1996). The sequestration of carbon in the soil by plants is of interest in recent years because carbon dioxide is a greenhouse gas implicated in climate change (Brady and Weil 1996) and soil is the largest terrestrial pool of organic carbon (Batjes 1996). The total carbon content of soils also includes inorganic carbon stored as carbonate and bicarbonates (Brady and Weil 1996).

Levels of soil organic matter are regulated by productivity. Soils with higher plant productivity tend to have higher organic matter content because more litter is generated (Batjes 1996). Soil organic matter content lends soil many properties that influence plant growth, for example the organic content of soil confers much of its water holding and ion exchange capacity (Brady and Weil 1996). Organic material also contains nitrogen and other mineral nutrients necessary for plant health which are released slowly over time (Brady and Weil 1996). Soils with higher soil organic carbon content are thus able to support higher levels of productivity (Brady and Weil 1996).

Nitrogen

Nitrogen is the most commonly lacking nutrient in soils and as such the productivity of most ecosystems is nitrogen limited (Salisbury and Ross 1978, White 1993, Brady and Weil 1996). The majority of nitrogen in the soil is held in organic matter which releases about 2-3% per year in plant available forms. Some plants are able to fix their own nitrogen with the help of symbiotic bacteria in the genera *Rhizobium* or *Bradyrhizobiam* (Brady and Weil 1996). Plants absorb nitrogen mainly as ammonium (NH_4^+) and nitrate (NO_3^-), but these forms of nitrogen are mobile and readily lost from the soil by leaching (Brady and Weil 1996). Attraction to negatively charged clay particles prevents leaching of ammonium to some extent but over time this affinity may cause it to become trapped in the crystal structure of the clay particles rendering it unavailable to plants (this also occurs with potassium ions) (Brady and Weil 1996). Biological nitrogen fixation by free-living soil micro-organisms is another source of plant available forms of nitrogen (Brady and Weil 1996).

Nitrogen is a central component of many essential compounds including amino acids, nucleic acids and chlorophyll (Brady and Weil 1996, Smith and Smith 2001). A good supply of nitrogen stimulates plant growth below and, especially, above ground; it also promotes absorption of other nutrients and gives leaves their deep green colour (Brady and Weil 1996). Symptoms of nitrogen deficiency include pale yellow leaves (chlorosis) affecting older leaves first, and slowed or arrested growth possibly resulting in early leaf senescence (Brady and Weil 1996). Some species may exhibit purplish coloration of the stems, petioles and undersides of the leaves when nitrogen is deficient (Salisbury and Ross 1978). Plants not acquiring enough nitrogen tend to mature more quickly and have lower shoot to root ratios than those that do (Brady and Weil 1996). With excess nitrogen, vegetation has been shown to develop a higher shoot to root ratio and very dark green foliage (Salisbury and Ross 1978, Brady and Weil 1996). Plants may become top heavy because of extreme but structurally weak above ground growth which may result in lodging (falling over) (Brady and Weil 1996); delayed maturity and increased susceptibility to disease are other common side effects (Brady and Weil 1996). Productivity is affected in cases of nitrogen toxicity as nitrogen assimilation, photosynthesis, biomass production (root and shoot), and starch accumulation in plants is hindered (Andreeva et al. 1998).

Experimental nutrient additions strongly influence both productivity and diversity. The majority of controlled fertilization studies manipulate nitrogen because it is such a common limitation to vegetative growth. A study by Cornwell and Grubb (2003) at regional scales, in biomes of central Europe, reported a humped-shape curve between nitrogen and species richness. Collins et al. (1998) showed that the dominance of grasses shifts with varying nitrogen availability and further that the productivity of the dominant grasses is inversely related to community diversity. More recently, a study by Isbell et al. (2013) reported that nitrogen additions had direct positive effects on productivity and direct negative effects on species richness; however, decreases in species richness were also noted to have indirect negative effects on productivity. In other words, although increased nitrogen availability initially boosted production, enrichment also had the effect of decreasing species richness which fed back to reduce the magnitude of productivity benefits over time. Interestingly, enrichment of atmospheric carbon dioxide gave different results in the same study. There

were similar direct effects on productivity but there was no drop in species richness and the magnitude of fertilization benefits to production did not diminish over time.

Carbon to nitrogen ratio

Climate and vegetation are major determinants of soil organic carbon and nitrogen content. The ratio of organic carbon to nitrogen in soils is important because it determines the decomposition rate of dead material, the total amount of organic matter present in the soil, and the amount of nitrogen available, all of which have bearing on productivity and species richness. Nitrogen availability depends highly on the rate of nitrogen mineralization by microbes which, in turn, depends on the supply rates of above and below ground litter, and soil moisture, aeration status, temperature, and texture (Brady and Weil 1996). The ratio of organic carbon to nitrogen in soils is fairly stable because of the rate-limiting effects of nitrogen availability on the activity of microorganisms (Brady and Weil 1996). Additionally, the rate of increase in soil carbon with increasing productivity is generally greater than that of soil nitrogen so that soil carbon to nitrogen ratio generally increases with increasing productivity. This occurs because in productive areas there is high nutrient turnover; proportionally more of the total nitrogen in soil is available to plants and is taken up and held in the vegetation because plants from high resource environments tend to have high nitrogen uptake potential, and corresponding high levels of tissue nitrogen (Chapin et al. 1993). The activity of soil microorganisms is limited by the relative availability of nitrogen; generally about 24 parts carbon are required for every part nitrogen used. If plant residues entering the soil have carbon to nitrogen ratios higher than ~25:1 then there will be very little nitrogen available to plants due to competition for nitrogen by microorganisms. This, in turn, reduces the rate of decomposition, makes the availability of nitrogen for plant uptake extremely low, and ultimately results in lower plant productivity. The addition of organic material with a carbon to nitrogen ratio lower than ~20:1 to the soil will typically supply enough nitrogen to soil microbes with excess available for plant use. Under these circumstances higher levels of plant productivity could be maintained (Brady and Weil 1996).

The concentration of nutrients in plant tissues does not necessarily reflect the total quantities of nutrients present in soil because plants regulate the uptake of different nutrients to varying

extents and because much of the nutrients present in soil may be in insoluble forms which are unavailable for plant absorption (Brady and Weil 1996). Plant species that typically grow in nutrient poor soils tend to have lower nutrient concentrations in their tissues than those that typically grow in more fertile areas (Chapin 1980, Poorter et al. 1990). The percentage dry weight of plants can range in carbon content from 45-58% and in nitrogen from less than 1% to over 6% (Brady and Weil 1996); however, changes in the carbon to nitrogen ratio of biomass (and therefore litter) of an area are usually brought about by species replacement rather than by shifts in nutrient contents within a species. Changes of carbon to nitrogen ratio within species are relatively small compared to differences brought about by species turnover (Wedin and Tilman 1990, 1996). Plant species from nutrient poor environments tend to have slow leaf turnover and invest more to maintain antiherbivore defences, usually carbon-based, while plants from fertile environments usually have more rapid leaf turnover and lower levels of defences, usually nitrogen-based compounds (Bryant et al. 1983, Coley et al. 1985). Coincident with shifts in species composition, biomass carbon to nitrogen ratios have been shown to decrease with increasing productivity (Wedin and Tilman 1996).

Phosphorus

Phosphorus is second to nitrogen as the most limiting soil nutrient and plays many important roles in plants. Phosphorus is absorbed mainly in the form of dihydrogen phosphate ($H_2PO_4^-$) and hydrogen phosphate (HPO_4^{2-}), the first being more readily available in acidic soils and the second being more available under alkaline conditions (Salisbury and Ross 1978). Phosphate tends to react with soil components making it unavailable for plant uptake; for example, insoluble precipitates form when iron and phosphate interact with each other thereby limiting the availability of both nutrients (Dalton et al. 1983). Generally, there is only about 0.001 mg of phosphorus per litre of soil in infertile soils, and up to about 1 mg phosphorus per litre of soil in heavily fertilized soils. Approximately 0.01% of the total phosphorus present in soils is actually available for plant absorption (Brady and Weil 1996) but root hairs and symbioses with root colonizing (mycorrhizal) fungi aide in its acquisition (Bolan 1991, Brady and Weil 1996). In fact, these associations offer the greatest benefit to plants in acquiring nutrients that diffuse slowly in soil such as phosphorus, ammonium, potassium, and nitrate (Chapin 1980).

In plants, phosphorus is used in phospholipids as part of cell membranes and in sugar phosphates which are fundamental components of deoxyribonucleic acids (DNA) and ribonucleic acids (RNA). It is also involved in energy metabolism as part of adenosine triphosphate (ATP), adenosine diphosphate (ADP), and adenosine monophosphate (AMP) and plays important roles in photosynthesis, respiration and many other metabolic processes (Salisbury and Ross 1978, Brady and Weil 1996). When phosphorus supplies are adequate plants tend to have higher root to shoot ratios; this is opposite to when nitrogen is abundant and plants tend to have lower root to shoot ratios (Salisbury and Ross 1978). Nitrogen and phosphorus balance also affects timing of plant maturity with abundant phosphorus bringing on earlier maturity and abundant nitrogen causing delays (Salisbury and Ross 1978). Deficiency of the macronutrient phosphorus also causes slowed or arrested growth, stunted roots and dark green foliage. Yellowing of leaves or purple or red coloration also occurs in some plants (Salisbury and Ross 1978, Brady and Weil 1996). For nitrogen fixing plants, low phosphorus levels can result in poor nodulation and inhibition of the biological nitrogen-fixation process (Brady and Weil 1996). High levels of phosphorus may lead to zinc and iron deficiencies (Parks et al. 2000) and toxicity results in decreased photosynthetic rates (Shane et al. 2004), inhibition of growth, development of chlorotic leaves, and early leaf senescence (Parks et al. 2000).

Higher levels of species richness are usually associated with lower levels of available phosphorus (Janssens et al. 1998, Venterink et al. 2001, 2003) and a negative relationship between phosphorus and species richness has been reported in several studies (Janssens et al. 1998, Venterink et al. 2001, Lambers et al. 2010). Janssens et al. (1998) reported a humped-back curve with soil extractable phosphorus. They found that the highest species richness always occurred at low phosphorus concentrations that were suboptimal for most plants. In their study there were never more than 20 species per 100 m^2 if there was greater than 5 mg of phosphorus per 100 g of soil. From the functions of phosphorus in plants, the effects of deficiency and toxicity, and studies investigating its role in directing species richness and productivity, it is clear that phosphorus availability plays an important role in community dynamics.

Other ratios

Plant productivity and species richness respond to the identity of the most limiting nutrient and ratio of available nutrients. The number of different forms of available nutrients may contribute to the species richness of systems, while the most limiting nutrient and nitrogen to phosphorus ratio correlate directly with the productivity of vegetation (Venterink 2011). Additionally, the species composition of communities can be very different depending on whether nitrogen or phosphorus is limiting (Honsova et al. 2007, Chytrý et al. 2009, Venterink 2011) and species richness may be higher under phosphorus limitation than under nitrogen limitation (Venterink 2011). Braakhekke and Hooftman (1999) proposed the 'resource balance hypothesis of plant species diversity', a hypothesis which predicts a humped curve between species richness and nitrogen to phosphorus, phosphorus to potassium, and potassium to nitrogen ratios such that the highest diversity is expected to occur at ratios that are balanced to best meet the requirements of the community on average. Several studies have found empirical evidence to support this theory (Braakhekke and Hooftman 1999, Roem and Berendse 2000, Daufresne et al. 2005, Güsewell et al. 2005, Wassen and Venterink 2005, Cardinale et al. 2009b). However, Aerts et al. (2003) tested this idea with experimentally manipulated nutrient levels and found that nitrogen addition in nitrogen poor grasslands (low nitrogen to phosphorus ratio) decreased richness and increased biomass. Phosphorus addition decreased species richness without evoking any change in productivity. Their work also indicated that a nitrogen to phosphorus ratio of ~6 is a strong indicator of nitrogen limited growth and ~16 indicates phosphorus limitation.

Potassium

Potassium is another macronutrient that can affect plant productivity and is the third most commonly limiting nutrient in soils next to nitrogen and phosphorus (Brady and Weil 1996). Although most soils contain an abundance of potassium the majority of it is insoluble and therefore unavailable to plants. In fact, only about 1-2% of total soil potassium is actually available for absorption (Brady and Weil 1996). Accessible potassium is even more easily leached than phosphorus, especially from acidic soils, but liming and the affinity of potassium to clay particles helps to reduce losses (Brady and Weil 1996, Janssens et al.

1998). Plants need almost as much potassium as they do nitrogen and can absorb and store excess when it is available (Brady and Weil 1996). Potassium activates many enzymes including those that form sugars, starches and proteins, and is essential for photosynthesis, respiration, osmotic balance, and (in legumes) nitrogen fixation (Brady and Weil 1996, Mäser et al. 2002). Potassium is also important in stress adaptations such as drought and salinity tolerance, winter hardiness, and resistance to fungal and insect pests (reviewed in Wang et al. 2013). High calcium and magnesium levels may reduce potassium uptake from the soil (Brady and Weil 1996) and low potassium availability has been linked to iron toxicity (Li et al. 2001). Potassium deficiency results in yellowing and necrosis of older leaves starting at the outer edges and in some species white necrotic spots form (Brady and Weil 1996). Plants without enough potassium are also more vulnerable to pathogens and pests. With excess potassium, reduced growth rate and chlorosis of leaves may result (Ingestad 1973) and Nam et al. (2006) reported increased risk of infection by pathogenic anthracnose in strawberries. The highest species richness was found to occur around 20 mg exchangeable potassium per 100 g of soil which is a level optimal for the majority of plants (Janssens et al. 1998). Although potassium typically has less control of diversity than phosphorus (because it is usually less limiting), the roles of potassium and the results of its deficiency or excess in plants make it an important potential contributor to the determination of productivity and species richness.

Boron

The essential micronutrient boron is involved in at least 15 functions in plants including roles in cell division, pollen germination, carbohydrate metabolism, and water metabolism (Smith and Smith 2001); it is also responsible for helping stabilize cell walls and regulating membrane pore size (Brown et al. 2002). Boron is one of the most commonly deficient micronutrients (Brady and Weil 1996) and deficient soils can be found worldwide (Shorrocks 1997). Soils are considered to be low in boron when they contain less than 10 ppm of soil and high in boron at levels greater than 10 ppm of soil (Power and Woods 1997). Plant available boron (mostly boric acid $B(OH)_3$) is released into soil through microbial mineralization and weathering of rocks (Brady and Weil 1996) and makes up about 10% of the total boron in soils (Woods 1994, Power and Woods 1997). Soil pH affects boron

availability such that in neutral to marginally acidic soils it is available for absorption but is also easily leached; as a result, boron deficiencies actually occur more often in acidic soils (Brady and Weil 1996, Goldberg 1997). Boron availability can have direct effects on productivity because plants without adequate boron supply show reduced leaf and root growth, yellowing of leaves (Smith and Smith 2001) and inhibited development of reproductive structures (Brown et al. 2002). For years, levels of soluble boron greater than 5 ppm of soil were thought to be detrimental to agronomics, but many species native to arid and semi-arid environments can handle higher levels (Nable et al. 1997). Boron toxicity may result in chlorosis or necrosis of the outer margins of older leaves, deformed fruits or stem die back and reductions in overall productivity (Brown and Hu 1996, Nable et al. 1997).

Iron

Of all the essential micronutrients, plants require iron in the greatest quantities (Kobayashi and Nishizawa 2012). It is involved in production of chlorophyll, helps activate and carry oxygen in mitochondria and chloroplasts and is involved in respiration and photosynthesis (Smith and Smith 2001, Kobayashi and Nishizawa 2012). To meet iron requirements but prevent toxicity, plants strictly regulate iron uptake, storage and use (Puig et al. 2007, Kobayashi and Nishizawa 2012). Plants that are deficient in iron exhibit extreme chlorosis and reduced growth (Märschner 2012). Although total iron content in soils is generally high, at neutral or higher pH levels iron and some other minerals precipitate as hydroxides and become unavailable to roots (Puig et al. 2007, Jeong and Guerinot 2009). To some extent iron and copper can be used in the same reactions in plants and therefore iron may be a suitable replacement for copper in copper deficient plants and vice versa (Puig et al. 2007). The relative levels of phosphorus and iron are also important to plant health and symptoms of phosphate deficiency may be improved by reducing the amount of iron available in soil (Ward et al. 2008). Iron and phosphate interact to form insoluble precipitates which can limit the availability of both nutrients (Dalton et al. 1983). Iron toxicity has been implicated in phosphorus deficiency and in reduced root growth in *Arabidopsis thaliana* (Ward et al. 2008), and iron toxicity in rice plants can be aided by increasing potassium levels (Li et al. 2001). Generally, excess iron (and copper) causes damage to cell membranes, proteins and nucleic acids (Halliwell and Gutteridge 1984).

Magnesium

Magnesium is an essential macronutrient that is almost never limiting to plant growth in natural soils but is sometimes added with calcium during liming to increase soil pH in agriculture (Brady and Weil 1996). It is taken up by plants as Mg^{2+} (Smith and Smith 2001) and is critical for the activation of enzymes involved in protein synthesis, synthesis of RNA and DNA, photosynthesis and respiration; it also allows many other reactions to take place by the transfer of phosphates converting ATP to ADP (Smith and Smith 2001). Magnesium is the central atom of the chlorophyll molecule (Shaul 2002) and is also an integral part of the middle lamella of plants (Smith and Smith 2001). Magnesium deficiency leads to chlorosis of older leaves and limited chlorophyll production; when magnesium is completely absent chlorophyll does not form at all (Salisbury and Ross 1978). Excess soil magnesium (or calcium) can lead to phosphorus and boron deficiencies due to high associated pH values. In this case, phosphorus may become bound in insoluble calcium and magnesium phosphates rendering it unavailable to plants (Brady and Weil 1996).

Manganese

Plants take up the essential micronutrient manganese primarily in its Mn^{2+} form which becomes most available in acidic conditions (Mukhopadhyay and Sharma 1991, Brady and Weil 1996). One of the primary reasons to limit soil acidity is to prevent manganese and aluminum toxicity; however, care must be taken as manganese deficiencies may result if soils are over-limed (Brady and Weil 1996). Absorption of manganese is affected by magnesium and calcium such that calcium stimulates uptake while magnesium hinders it. Present together, calcium and magnesium produce an even greater inhibitory effect on absorption (Maas et al. 1969). In plants, manganese is important for nitrogen metabolism and assimilation, photosynthesis, and activation of numerous enzymes; particularly for fatty acid synthesis (Salisbury and Ross 1978, Smith and Smith 2001). Manganese is thought to play a structural role in the chloroplast and, during photosynthesis, is involved in the transfer of electrons from water molecules to chlorophyll, splitting the water molecule and releasing oxygen (Livorness and Smith 1982). Deficiencies of manganese are uncommon but may result in necrotic lesions, interveinal chlorosis of leaves (Salisbury and Ross 1978), hindrance

of cell elongation, and reduced uptake of many other essential nutrients such as aluminum, calcium, copper, iron, potassium, magnesium, nitrogen, phosphorus, and silicon (Mukhopadhyay and Sharma 1991). Productivity, chlorophyll content and photosynthesis also suffer dramatically (Mukhopadhyay and Sharma 1991). How much manganese is required to cause toxicity depends on how much magnesium is co-occurring in the soil (Goss and Carvalho 1992) but generally plant homeostatic mechanisms are able to maintain optimal manganese concentrations (Clemens 2001). Similar to deficiency symptoms, the toxic effects of manganese include compromised photosynthesis, respiration, nitrogen and protein metabolism and reduced levels of chlorophyll (Foy et al. 1978, Mukhopadhyay and Sharma 1991, El-Jaoual and Cox 1998).

Scale

An important consideration in understanding patterns of biodiversity is recognizing their dependence on scale. It is suggested that much of the variation in the productivity-diversity patterns that are reported in the literature is due, at least in part, to investigations being done at different spatial scales (Waide et al. 1999, Mittelbach et al. 2001, Chase and Leibold 2002, Cardinale et al. 2009b). Specifically, there seems to be no relationship between species richness and plant biomass at local scales within a community type (Moore and Keddy 1989, Guo and Berry 1998, Adler et al. 2011), a unimodal relationship is often reported across community boundaries or if plots are done in multiple community types (Waide et al. 1999), and at regional or geographic scales the relationship is most often reported as a monotonically increasing relationship (Pianka 1966, Currie 1991). Chase and Leibold (2002) suggest that the relationship shifts from being unimodal at local scales, to monotonically increasing at regional scales and that a positive correlation between productivity and β-diversity explains this shift with increasing scale of investigation.

The majority of studies investigating the HBM have typically been done using small plot sizes – usually close to 1 m^2. Oksanen (1996) asserted that the unimodal curve could be an artefact arising from small plot size because fewer large individuals (and therefore fewer species) than small individuals can fit inside a small plot frame. This ‘no-interaction model’ overlooks many known biological processes and interactions between plants (Grime 1997).

Additionally, different mechanisms govern species diversity at different scales (Moore and Keddy 1989, Grime 1997) and the relationship between species richness and productivity has been shown to have varying forms of scale dependence (Waide et al. 1999, Scheiner and Jones 2002, Chase and Leibold 2002, Fridley et al. 2006). At geographical scales, species richness is probably determined by broadly operating factors, such as climate, whereas at regional and local scales interactions between individual plants or species are likely to play a much greater role in determining diversity (Currie 1991). Richness at varying scales is clearly connected because large-scale species pools are ultimately a summation of species richness at local scales (Taylor et al. 1990, Currie 1991, Zobel 1997); however, species pool size also directs richness at local scales (Pärtel et al. 1996, Huston 1999). It is important to determine how broadly the HBM can be applied because some models are useful over many levels of organization while others apply only at specific scales (Moore and Keddy 1989, Waide et al. 1999, Chase and Leibold 2002, Cardinale et al. 2009b). In moving forward it will be important for researchers to clarify the ecological context and scale they are working at so that the conditions that produce one pattern or another and the responsible mechanisms can be elucidated (Waide et al. 1999).

Thesis overview

Several areas requiring further research have been identified. After nearly 40 years of investigation the nature of the relationship between species richness and productivity remains uncertain. The influence of scale on the forms of relationship between productivity and species richness needs to be clarified to assess the generalization of the HBM or other patterns found. There is also the call for further study of soil nutrient patterns and their control of productivity and species richness using an observational approach in natural systems in addition to the manipulative experiments that have been done.

In Chapter 2, live-biomass and litter weights, species counts, and data from soil and leaf nutrient analysis are analyzed to determine patterns between productivity, species richness and soil nutrients. The influence of scale on these patterns and (in a subsample of plots) relationships between soil carbon and nitrogen content, and leaf carbon and nitrogen content are also assessed. The data to evaluate species richness and productivity was collected from

896 one square meter plots in fourteen grids, and nutrient data was collected in 256 one square meter plots in four of the fourteen grids. The grid design, where each grid contains side by side plots, facilitates the process of analyzing species richness, productivity and nutrient relationships at various scales increasing from 1 m^2 up to 64 m^2. In Chapter 3 of my thesis I put the results of Chapter 2 in a broader ecological context, discuss implications for management and suggest directions for future research.

CHAPTER 2: A MULTI-SCALE INVESTIGATION OF SPECIES RICHNESS, PRODUCTIVITY AND NUTRIENT RELATIONSHIPS IN HERBACEOUS PLANT COMMUNITIES OF THE GRASSLANDS OF SOUTHERN INTERIOR BRITISH COLUMBIA

INTRODUCTION

The relationship between species richness and productivity has spurred a great deal of investigative effort over the years (see Tilman and Pacala 1993 and Waide et al. 1999 for overview), and out of this research 'the humped-back model' (HBM) (Grime 1979) has gained support. Grime's HBM predicts that the greatest species richness occurs at intermediate productivity because of constraint by high stress and disturbance at low productivity and by intense competition and competitive exclusion at high productivity (Grime 1973a, 1973b, 1979, Al-Mufti et al. 1977). While there is considerable empirical evidence to support the HBM (e.g. Al-Mufti et al. 1977, Wheeler and Giller 1982, Walker and Peet 1983, Tilman 1986, Austin 1987, Day et al. 1988, Wilson and Shay 1990, Shipley et al. 1991, Wheeler and Shaw 1991), there are also studies that do not (e.g. Moore and Keddy 1989, Gough et al. 1994, Adler et al. 2011). In a recent study by Adler et al. (2011) that featured sites in 48 herbaceous plant communities on five continents, it was concluded that productivity is not related to species richness as predicted by the HBM. This study has been criticized because litter was not collected for inclusion in estimates of productivity, high productivity sites were underrepresented, and anthropogenically influenced sites were excluded (Fridley et al. 2012). After close to four decades of research, the debate concerning the validity of the HBM has not been resolved. Characterizing the nature of the relationship between species richness and productivity remains a critical gap in our understanding of plant communities.

One source of confusion may be variation in the spatial scale of investigation between studies. The mechanisms that govern species diversity are different at different scales (Moore and Keddy 1989, Grime 1997) and some studies show that the relationship between species richness and productivity changes at different scales (Waide et al. 1999, Scheiner and Jones 2002, Chase and Leibold 2002, Fridley et al. 2006). The spatial scale of investigation is therefore likely an important determinant of the form of relationship between species

richness and productivity. A unimodal relationship is often reported when samples are taken across community boundaries or when plots are from different community types (Waide et al. 1999). Oksanen (1996) asserted that the unimodal curve could be an artefact caused by the small plot sizes that are typical to vegetation sampling because fewer large individuals (and therefore fewer species) than small individuals can fit inside a small plot frame. Grime (1997) points out that this 'no-interaction model' overlooks many known biological processes and interactions between plants. Determining how scale influences relationships between productivity and species richness will be an important step to clarify what form or forms of relationship can be expected at specific scales and to identify scales of application for the HBM.

Decreases from high levels of stress and disturbance are thought to drive the increasing phase of the HBM. Limited resource availability, such as limited nutrient, water or light availability, is a form of stress and soil nutrient availability is known to influence both primary productivity and plant species richness. Because the nutrient requirements of a species determine what environments are suitable for it to live in, a gradient of nutrient availability ranges from being able to support zero species, when nutrients are absent, to being able to meet the minimum nutrient requirements of many species as well support greater biomass production when nutrients are abundant. However, as nutrients become less limiting to growth, the increased biomass typically leads to intense competition for light (Grime 1979, Grace 1999, Aerts et al. 2003, Cornwell and Grubb 2003).

Systems may be limited by different soil nutrients, but are most often limited by nitrogen (Salisbury and Ross 1978, White 1993, Brady and Weil 1996). The importance of a nutrient in determining species richness and productivity in the increasing phase of the curve depends on how limiting it is to growth compared to other nutrients (Braakhekke and Hooftman 1999); the more limiting a nutrient, the greater its potential role in structuring communities. In the decreasing phase of the curve nutrients are available in adequate supply and support high biomass, and intense competition becomes the mechanism by which species richness is determined. Because different species have varying nutrient requirements it is also possible that more than one, rather than just the most limiting, influence production, species richness and species composition in communities (Braakhekke and Hooftman 1999).

Many studies have investigated the effect of nutrient additions on species richness and productivity and seem to support Grime's HBM (Al-Mufti et al. 1977, Grime 1979). Productivity generally increases with increasing soil nutrient availability and experiments that add soil nutrients often show increases in biomass at the expense of species richness (Kirchner 1977, Goldberg and Miller 1990, Bobbink 1991, Wilson and Tilman 1993, Chapin et al. 1995, Wedin and Tilman 1996, Gough et al. 2000, Baer et al. 2003, Cornwell and Grubb 2003, Crawley et al. 2005). These findings and the HBM theory suggest that certain patterns of nutrients should coincide with the HBM in nature.

However, in nutrient addition experiments, productivity has been reported to respond less in sites that were initially unproductive compared to sites that started out at high productivity (DiTommaso and Aarssen 1989). Additionally the magnitude and sometimes the direction of species diversity response has been found to be independent of initial community productivity, contrary to the predictions of the HBM (Gough et al. 2000). These findings have been attributed to the immobilization of added nutrients in low productivity sites (Chapin et al. 1986), the easier loss than gain of species, and species pool effects (Zobel 1997, Gough et al. 2000, Safford et al. 2001). Additionally, Gough et al. (2000) and Suding et al. (2005) indicate that relationships between species richness and productivity in experimental manipulations respond differently than species richness-productivity relationships in natural systems. Gough et al. (2000) also state that even long term studies are poor predictors of the relationship between species richness and productivity because "they are relatively small-scale perturbations whereas the pattern of species richness over natural productivity gradients is influenced by long-term ecological and evolutionary processes".

There are relatively few publications on non-manipulative observational studies between species richness, productivity and soil nutrients. Janssens et al. (1998) evaluated relationships between species richness and extractable phosphorus, extractable potassium and total nitrogen and reported a unimodal relationship. Cornewll and Grubb (2003) also found a unimodal relationship between soil nutrient supply and species richness within biomes at the regional scale. García et al. (1993) reported a peak in species richness at intermediate productivity and a negative relationship between salinity and species richness in a salt marsh

of the Guadalquivir delta (SW Spain). Cornwell and Grubb point out that there is a paucity of work on species richness patterns and their relation to the resources that control productivity. This motivates further observational study of soil nutrient patterns to determine if they align with those patterns that would be expected to coincide with the HBM in nature.

The knowledge-gaps outlined above include the need to characterize the nature of the relationship between species richness and productivity, the need to determine how scale influences relationships between productivity and species richness to assess the generalization of the HBM, and the need for further study of soil nutrient patterns and their control of productivity and species richness. The objectives that follow are intended to contribute towards addressing these knowledge-gaps.

Objectives

1) Determine the form of the relationship between species richness and productivity in the study area.

2) Identify patterns, in relation to those expected to coincide with the HBM, between total soil aluminum, boron, carbon, calcium, copper, iron, magnesium, manganese, nitrogen, sodium, phosphorus, potassium, sulphur, zinc (Al, B, C, Ca, Cu, Fe, Mg, Mn, N, Na, P, K, S, and Zn, respectively), leaf nitrogen and carbon content, biomass weight (as a proxy for productivity) and species richness in unmanipulated natural plots. For some nutrients, prediction of expected patterns is not straightforward because of lack of previous research; in these cases the nature of my work will be exploratory rather than hypothesis driven.

3) Evaluate the influence of increasing scale from 1 m^2 to 64 m^2 on relationships found in the species richness, productivity and nutrient investigations stated in objectives 1 and 2.

Predictions

I expected that the relationship between species richness and total biomass would be unimodal as predicted by the HBM. Soil nutrients that commonly limit growth such as

nitrogen, phosphorus and potassium were expected to be positively correlated with productivity; and species richness was expected to increase to a maximum and then decrease with increasing soil concentrations of the most limiting nutrients in accordance with the HBM. Because carbon is the most basic constituent of all organic matter I predicted that it would also be positively correlated with productivity and that species richness would increase to a maximum and then decrease with increasing soil carbon concentrations in accordance with the HBM. Soil carbon and nitrogen were expected to be positively correlated with each other because they are known to be tightly connected in systems, a positive correlation between soil carbon to nitrogen ratio and productivity was expected because of higher turnover of nutrients combined with the plant-uptake of a greater proportion of total nitrogen in the form of available nitrogen in productive systems, and a unimodal relationship was expected between soil carbon to nitrogen ratio and species richness in accordance with the HBM. Relationships between species richness, productivity and other soil nutrients are not readily predictable.

Leaf carbon and nitrogen are expected to be highly positively correlated with each other, to be higher in plants living in high productivity areas on fertile soils and to vary positively with soil carbon and nitrogen content. Leaf carbon to nitrogen ratio is predicted to decrease with increasing productivity because of, increased soil nutrient availability, and species turnover. Based on this last prediction, it is expected that there will be a negative correlation between soil carbon to nitrogen ratio and leaf carbon to nitrogen ratio.

Increasing scale is expected to weaken, and may completely break, the unimodal relationship between species richness and biomass. It is thought that this will occur because the mechanisms (especially competition) operating between plants in close contact within a 1 m^2 plot may not be able to operate at larger scales where plants within a plot are not all in close range of each other. Because productivity is expected to increase with higher concentrations of limiting soil nutrients the same hypothesis, wherein increasing scale is predicted to result in a weakening or complete breakdown of the relationship, applies to the expected unimodal relationship between species richness and limiting soil nutrients (likely nitrogen, phosphorus and potassium) when plot size is scaled up. The study objectives will be carried out by sampling low and high productivity sites for species richness, live biomass, litter, total

biomass, leaf nutrients, and soil nutrients; and aggregating data from plots within grids to investigate scales from 1 m^2 - 64 m^2.

METHODS

Site description

This study took place in the semi-arid, bunchgrass, grasslands of Lac du Bois Provincial Park (Figure 2.1) and at a field site in Lac La Hache (Figure 2.2). Lac du Bois Provincial Park is located immediately northwest of Kamloops, British Columbia, Canada and the site at Lac la Hache is located at the southeast end of the lake approximately 25 km northwest of 100 Mile House, British Columbia, Canada.

In the park the elevation of the grasslands increases from ~350 m a.s.l. to ~1100 m a.s.l. over a distance of about 10 km. The elevation gradient is linked to changes in precipitation and temperature (van Ryswyk et al. 1966). The Kamloops region has an average annual precipitation of 279.0 mm and an annual average daily temperature of 8.9 °C with the warmest month being July, 21.0 °C, and the coldest being January, -4.2 °C (Environment Canada 2012). The differences in precipitation and temperature maintain a productivity gradient across the park such that productivity increases with altitude. The grasslands in the park have been classified into three vegetation types that relate to elevation: *Pseudoroegneria – Artemesia*, *Pseudoroegneria – Poa*, and *Pseudoroegneria – Festuca,* which dominate the lower, middle and upper grasslands, respectively (van Ryswyk et al. 1966). Work by van Ryswyk et al. (1966) in Lac du Bois documents that soils were brown chernozemic at low elevation (~520 m.a.s.l), dark brown chernozemic at medium elevation (~695 m.a.s.l) and black chernozemic at high elevation (~950 m.a.s.l) and that corresponding pH values were 7.3, 7.5, and 7.2, respectively. The grasslands are used for recreation and grazed by wildlife and cattle. In the 1930s the park area was severely overgrazed (van Ryswyk et al. 1966). Now, cattle-grazing occurs from April to November following a rest-rotation schedule as outlined by the Kamloops LRMP Policy for Domestic Livestock Grazing in Protected Areas (Ministry of Environment 2000).

The elevation of the Lac la Hache site is ~810 m a.s.l. (Erskine 1964). The 100 Mile House region has an average annual precipitation of 453.3 mm and an annual average daily temperature of 4.2 °C with the warmest month being July, 15.2 °C, and the coldest being January, -8.4 °C (Environment Canada 2012). The site is dominated by *Phalaris arundinacea*, *Carex utriculata, Poa pratensia* and an unknown species of borage, and is a privately owned field that is hayed once yearly in August. The field is grazed by cattle from approximately October to April.

Figure 2.1. Map of the Lac du Bois Grasslands Provincial park study site (Google Earth 2014). L1-5, U1-5, and P1-2 are codes to identify each grid and indicate grid locations on the map.

Figure 2.2. Map of the Lac la Hache study site (Google Earth 2014). P3 and P4 are codes to identify grids and indicate grid locations on the map.

Study design

Fourteen 8 m × 8 m grids, each containing 64, 1 m^2 plots, were located at a range of biomass levels: five grids at low (L1-5, ~50 – 300 g/m^2) and intermediate (U1-5, ~300 – 750 g/m^2) biomass levels and four at high biomass levels (P1-4, ~750 – 2000 g/m^2)(Table 2.1)(see Fraser et al. 2014). Grid columns were labelled A-H and rows were labelled 1-8. For two grids at each biomass level, four of the 1 m^2 plots (G1-2, and H1-2) had smaller nested 1/4 m^2 plots with columns labelled a-d and rows labelled i-iv. In four of the 1/4 m^2 plots (ci-ii, and di-ii) there were smaller nested 1/16 m^2 plots with columns labelled w-z and rows labelled 100, 200, 300 and 400 (Figure 2.3).

Table 2.1. Identification, elevation and GPS location (datum: NAD83) of the fourteen study grids. Soil sampling was done in grids marked "*".

Grid ID	Elevation at A1 (m a.s.l.)	GPS Location at A1 (Lat/Lon)	Total Biomass Range (g/m^2)
L1	753	N50 45.611 W120 26.092	74.13 – 270.65
L2	715	N50 45.160 W120 23.933	81.48 – 334.14
L3	688	N50 44.323 W120 26.284	54.56 – 301.43
L4*	522	N50 43.014 W120 24.800	50.64 – 190.70
L5*	687	N50 44.360 W120 26.171	55.62 – 335.92
U1	914	N50 47.349 W120 26.844	139.23 – 782.69
U2	914	N50 47.216 W120 27.009	133.92 – 387.28
U3	855	N50 47.684 W120 23.561	72.37 – 241.58
U4	781	N50 47.886 W120 24.792	166.39 – 498.44
U5	894	N50 47.445 W120 26.264	275.40 – 1337.81
P1*	775	N50 48.140 W120 24.386	791.53 – 1844.40
P2*	833	N50 46.811 W120 25.942	572.48 – 1226.63
P3	807	N51 47.565 W121 27.803	546.20 – 1380.84
P4	806	N51 47.450 W121 27.472	1022.42 – 1869.17

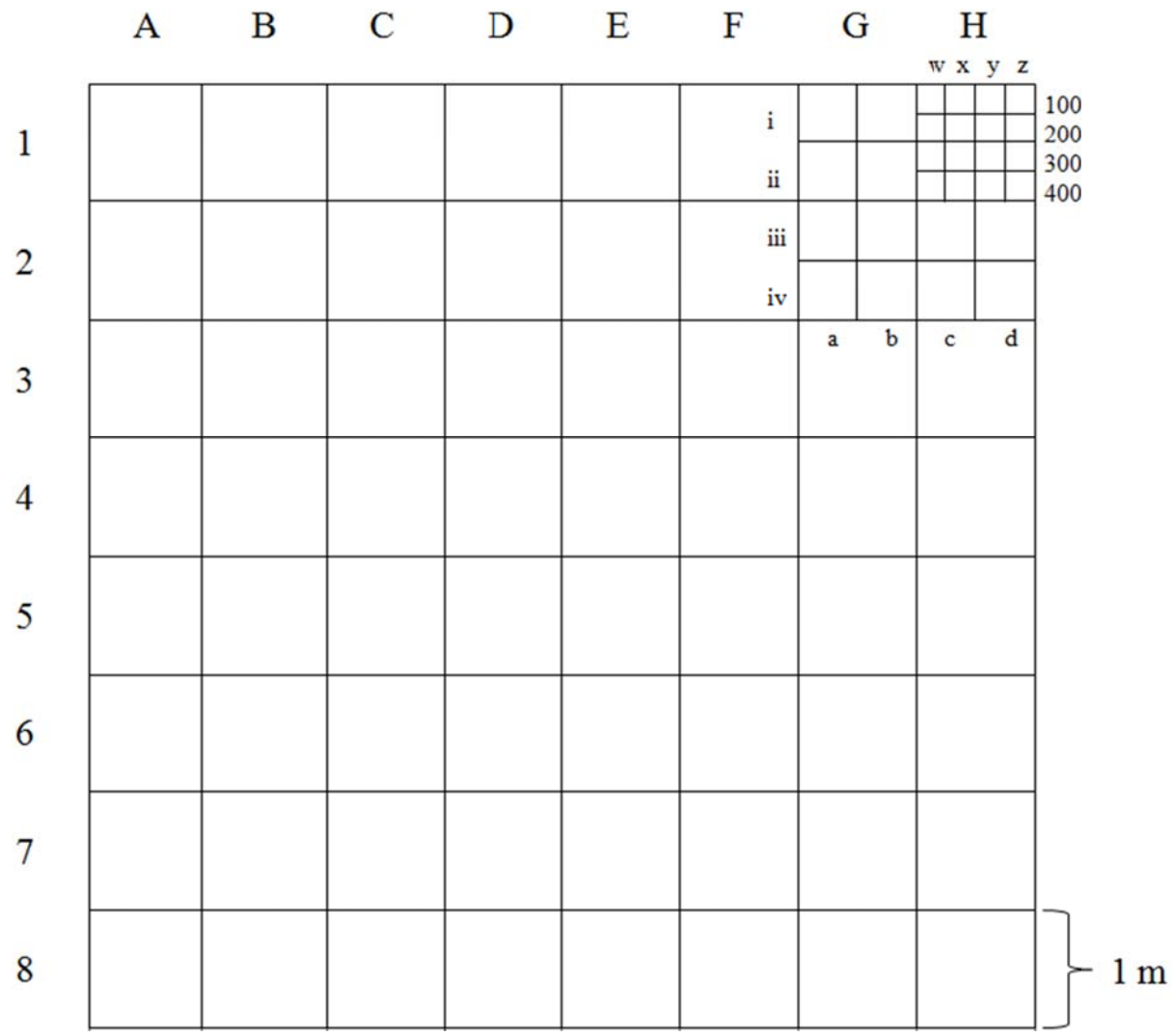

Figure 2.3. Diagram of grid layout showing smaller nested plots in the H1 corner.

Woody species were avoided as much as possible when selecting grid locations. Areas were not used if they were grazed during the three months before sampling because recent disturbance may be a confounding factor in the relationship between biomass and species richness and it may have been difficult to identify plants from recently grazed areas. Grids were placed to minimize visibility from roads in an effort to reduce the potential for vandalism or disturbance to the grids so that they may be used in future studies.

Marking grids

Once selected, grid areas were swept with a metal detector to check for background readings. Notes about the location of extra signals from the metal detector were taken as a guide for reference if the grids need to be located in the future. A measuring tape was used to lay out the grid by first measuring an 8 m line and then using Pythagorean Theorem to measure a square.

Each grid was marked using four buried 20.3 cm (8") nails, one of which had a circular wire antenna (~10 cm diameter). The purpose of the antenna was to make that nail easier to find so that it can be used as a starting point when searching for the grids in the future. If there were interfering background readings detected by the metal detector then copper wire antennas (~5cm diameter) were used instead. Copper induces a higher pitch from the metal detector which allows identification of the correct signals while searching for the points. The markers were buried ~15 cm deep, and the metal detector was used to verify detection. The locations of all four corners of the grids were recorded using GPS. The slope, aspect and orientation of the grid were measured. For reference, photos were taken of each grid and surrounding area before and after sampling. Notes about the site were taken such as about recent disturbance, appearance, grazing, and background metal readings.

Sampling was scheduled for late July and early August to capture the height of the growing season. In 2011, grids L1-3 and U1-3 were sampled; all other grids were sampled 2012. Plant sampling was conducted in each of the 1 m^2 plots in all 14 grids (Figure 2.4, Figure 2.5). In six grids (two each at low, intermediate and high productivity) plant sampling was done in smaller nested 1/4 m^2 and 1/16 m^2 plots, but I restricted my analysis of plant data to a scale no less than 1 m^2. Soil sampling involved only the 1 m^2 plots from four grids: two each at low (L4 and L5) and high (P1 and P2) productivity.

Figure 2.4. Grid P2, post-sampling. Holes are visible where soil samples were taken.

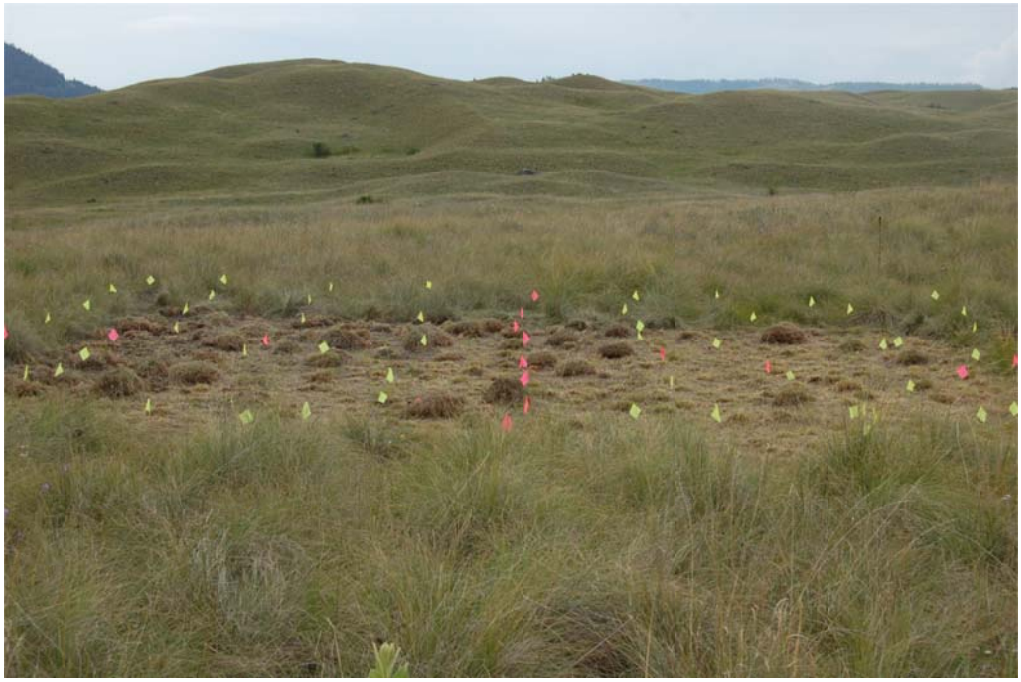

Figure 2.5. Grid U5, post-sampling. The pin-flags used for frame placement and hummocks left over from sampling large bunchgrasses are visible.

Plant sampling protocol

Plant sampling in each grid was done one plot at a time in two steps: species identification and harvesting. First, all plant species present in the plot were identified and recorded. A plant species was counted as being in a 1 m^2 plot if it was rooted in, or overhanging, the plot. Woody species in plots were noted and any plants that could not be identified in the field were collected for later identification and their weights were added to their corresponding biomass sample afterwards. Second, all live biomass and litter was separated in the field and collected. Live biomass was cut to ground level and included any material produced during the current year, but woody plants were not collected. Litter was raked up after live biomass was cut, and dead material was collected from bunchgrasses as much as possible; however, for large bunchgrasses hummocks were left to avoid collection of soil with the litter and for time efficiency (Figure 2.5). Samples were stored in a greenhouse until they could be dried in a Yamato oven (Model No. DKN812) at 80 ºC for 48 hours and weighed with an analytical balance (Fisher Scientific accuseries 4102).

Four of the grids were sampled for soil (see below). Of those four grids, samples of ~5 mg of mixed plant biomass from nine plots (A-C × 1-3) were analyzed separately for total carbon and nitrogen content using a CE-440 Elemental Analyzer.

Soil sampling protocol

Each 1 m^2 plot in four grids was sampled for soil, two at low (L4 and L5) and two at high (P1 and P2) productivity. After plant sampling a 10 cm × 10 cm × 10 cm soil core was taken from the center of each plot using a knife, four putty knives and a shovel. The top layer of organic matter (~3 cm) was removed from soil samples in the field with the knife. The soil was stored in open plastic zip lock bags in a greenhouse to air dry. The soil was sieved to <355 μm and total carbon and nitrogen content in subsamples of soil of ~10 mg was analyzed with a CE-440 Elemental Analyzer. Samples were also sent to the BC Ministry of Environment's Analytical Chemistry Laboratory (in Victoria, British Columbia) for soil nutrient analysis of total aluminum, boron, calcium, copper, iron, magnesium, manganese, sodium, phosphorus, potassium, sulphur, and zinc. Samples were prepared by very high-pressure (VHP) closed vessel microwave acid digestion. Sample extractions were done in

concentrated nitric acid (0.2 g soil per 4 ml acid) at 230 ºC and ~1500 psi in a Milestone "Ultrawave" single reaction chamber digester, then cooled and made up to 15 ml with 10% hydrochloric acid and analyzed using a Teledyne/Leeman Labs "Prodigy" dual view inductively coupled plasma-optical emission spectrometer (ICP-OES). Multiple sub-samples were oven-dried at 105 ºC to obtain the 'moisture factor' used to correct the analysis results to an oven-dry basis.

Data analysis

Data was managed in Excel worksheets. Statistical analyses were done using R version 2.15.2 (R Development Core Team 2012).

Outliers and missing values

One extreme litter value (originally over 2000 g/m^2) was corrected to 1000 g/m^2 to bring it in range with other high values from that grid. I think this value was high because it was the first plot with a large bunchgrass and we demolished every bit of it for collection. This methodology was not continued in other plots (Figure 2.5).

Two 1 m^2 plots had missing values for live biomass and, therefore, also for total biomass weights. One missing value was replaced with the average plot biomass for the grid it was in; this grid was not involved in soil sampling. The other plot that was missing a value was in one of the four grids involved in soil sampling and was a plot that was originally sampled in 16 parts; two of these samples were missing. In this case I had biomass measurements from 14 of the 16 subplots and simply averaged these to replace the two missing parts. These replacement weights for the plots were added to litter weights to calculate total biomass for the plots.

Principal component analyses

Only the soil nutrient data was included in the soil nutrient principal component analysis (PCA) while the soil and leaf nutrient PCA included all soil nutrients as well as soil carbon to nitrogen ratio and leaf carbon, nitrogen and carbon to nitrogen ratio. A soil and leaf carbon, nitrogen and carbon to nitrogen PCA, including only those nutrients, was also run. There

were no missing values but there were several potential outliers in the data. All PCAs were carried out on the correlation matrices (to standardize for very different ranges and quantities) of the nutrient variables to extract the major trends from the data and evaluate the relationship between nutrients, biomass variables, and species richness. The Kaiser–Guttman criterion and broken stick models were calculated to identify important axes (Borcard et al. 2011). Distance and correlation biplots of the important axes from the principal component analyses were made to visualize patterns in the data.

The circle in the distance biplots of the first two PCA axes is known as the 'circle of equilibrium contribution'. Its radius is equal to the number of axes represented in the biplot divided by the total number of PCA components. If the arrow of a variable extends exactly to the circle, it contributes equally to all dimensions of the PCA space. Those variables with arrows extending out past the circle contribute more than average and those with arrows that do not extend to the circle are not well represented by the first two axes and cannot be interpreted with confidence (Borcard et al. 2011). Distance and correlation biplots of the important axes were used to select the important soil nutrients for regression analyses.

Regression analyses

All of the regression analyses that were done were linear bivariate regressions. Quadratic models with both a linear and quadratic term were fit first; if the quadratic term was not significant (α=0.01) it was dropped to fit a linear model. If the linear term was not significant, a non-significant relationship was reported.

Regressions were run with species richness as the response variable and total biomass, live biomass, and litter as explanatory variables. This was done twice, once using data from all 14 grids and again using only the four grids involved in soil sampling. Regression analyses were used to evaluate the relationships between species richness, total biomass, live biomass, litter and the soil and leaf nutrients that were indicated as important by the PCA ordinations. Regressions were also done between the first, second and third axes of PCA ordinations and species richness, total biomass, live biomass, and litter. Data from adjacent plots within grids were summed for total biomass, live biomass and litter, aggregated for species richness and

averaged for soil nutrient measurements to analyze scale dependency relationships from plots at the 1 m^2, 2 m^2, 4 m^2, 16 m^2, and 64 m^2 scales.

Plots within a grid are side by side, so violation of the assumption of independently and identically distributed errors (i.i.d) required for basic regression analysis is extremely likely. This can elevate Type I error, the act of falsely rejecting the null hypothesis or in other words finding significance in tests when there actually is none. Moran's I statistic was calculated for each grid and, indeed, indicated significant spatial autocorrelation in many cases. Residuals from each of the nutrient regressions with species richness, total biomass, live biomass and litter were plotted in semi-variograms by grid and Dr. David Hill was consulted for help with their interpretation. They often had large nugget effects corresponding to local variation occurring at scales smaller than our sample plot size of 1 m^2. The patterns displayed in the rest of the semi-variograms (usually less than half of the semi-variogram if normalized) were shallow increases or erratic patterns suggesting that either the strength of spatial autocorrelation effects, if present, were probably weak to moderate, or that patterns were spurious. In addition, these plots indicate severe violation of the assumptions of spatial stationarity and isotropic spatial autocorrelation that should be met to proceed with the vast majority of spatial analyses routinely used to account for spatial autocorrelation. Examples of these approaches include generalized least squares (GLS), generalized linear models (GLM), spatial generalized linear mixed models (GLMM), and simultaneous and conditional autoregressive models (SAR and CAR). These and others are reviewed by Dormann et al. (2007) and Beale et al. (2010). In the interest of reducing the potential for committing a Type I error, I elected to adjust to an α of 0.01, an approach recommended as conservative by Dale and Fortin (2002). Correlograms of Moran's I statistics and semi-variograms of residuals from linear models are presented in APPENDIX A and APPENDIX B respectively. Semi-variograms of residuals for quadratic models looked nearly identical to those for linear models in the vast majority of cases, so they have not been included.

Species richness is not strictly normally distributed because it is count data, therefore regression models including this response variable were also fit using generalized linear modelling (non-spatial) with a Poisson distribution as it may be more suitable than standard linear regression (which assumes a Gaussian distribution). The Poisson regressions were

evaluated for over and underdispersion and because all had dispersion parameters close to 1 (0.5 - 1.5) no corrections were necessary (Zuur et al. 2009). Gaussian and Poisson regressions gave very similar results at the 1 m^2 scale and almost always returned the same form of significant model. Exceptions were regressions between species richness and PC2 from the soil nutrient PCA, species richness and phosphorus, species richness and manganese, and species richness and PC1 from the PCA of soil and leaf nutrients. Summary tables and plots of Poisson regressions are available in APPENDIX C. Influential points were identified with Cook's distance and leverage for all Poisson and Gaussian regressions at the 1 m^2 scale. Only two instances of influential points occurred however these points were not removed for the final analysis because removing them did not change the form of model selected (quadratic or linear) and only influenced multiple R^2 values by as much as 0.05; as well, removing points would have caused problems when combining plots to evaluate larger scales. Species richness was square root transformed and total biomass, live biomass and litter were log10 transformed to improve normality. Improvements by transforming nutrient variables were negligible, so they were not transformed. In nearly all cases models exhibited heterogeneity in residuals, which could be expected considering the presumed violation of the assumption of i.i.d, the fitting of non-optimal bivariate regression models and probable missing covariates.

RESULTS

Plots for all regressions included in the summary tables are available in APPENDIX D, APPENDIX F, and APPENDIX G; a small selection of these are also shown here, in Chapter 2. Biplots with PC3 axes are available in APPENDIX E. A list of the species that were identified is provided in APPENDIX H. For all regressions, the greatest difference between multiple R^2 values and adjusted R^2 values was 0.06, but most differences were less than 0.03. Multiple R^2 values were reported, rather than adjusted R^2 values, so that results could be expressed in terms of proportion of variation in the response variable explained by the explanatory variable.

Species richness and biomass regressions

With all 14 grids at the 1 m^2 scale, litter and total biomass explained 12% and 11% of the variation in species richness respectively and live biomass explained 1% of the variation. Where regressions were significant, the form of relationship between species richness with total biomass and litter was consistently concave down while with live biomass was consistently negative linear (Figure 2.6). For biomass and litter significant forms were comparable at the 1 m^2, 2 m^2, and 4 m^2 scales between the full 14-grid dataset (Table 2.2) and the dataset including only the four grids involved in soil sampling (Table 2.3); for live biomass significant forms occurred in both datasets only at the 1 m^2 scale.

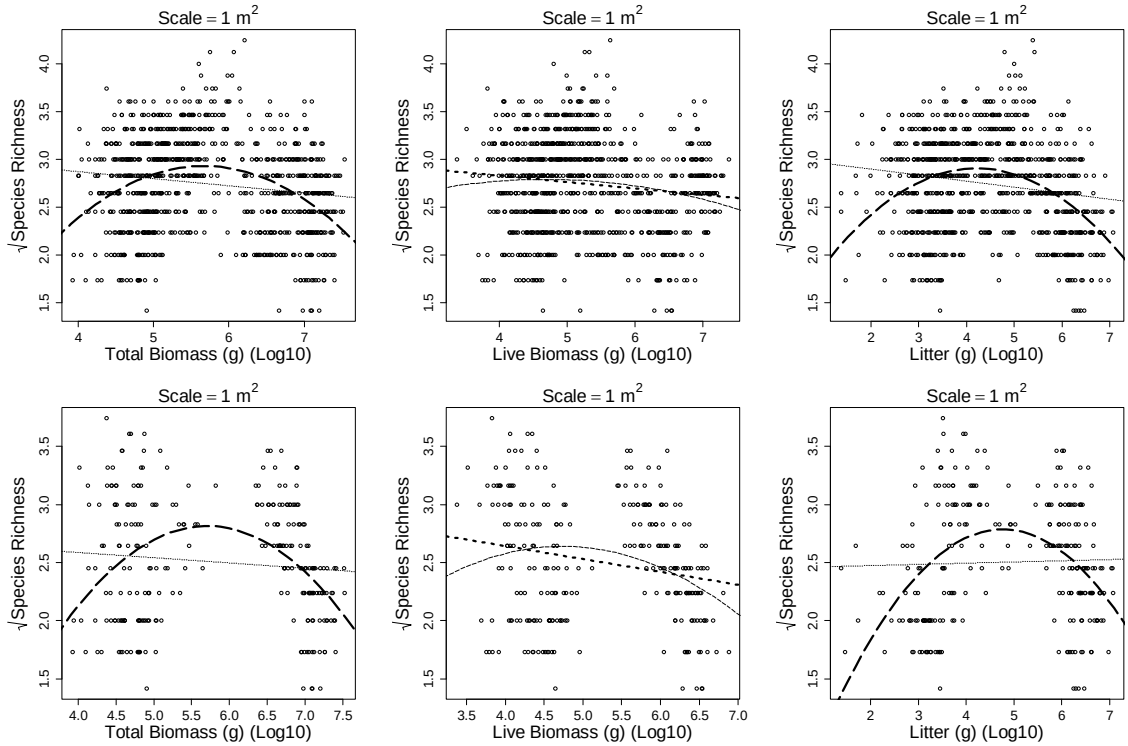

Figure 2.6. Square root transformed species richness with fitted curves from linear regression models at 1 m^2 having log transformed total biomass, log transformed live biomass and log transformed litter as the explanatory variables; this is shown for the 14-grid dataset (top panels) and the 4-grid dataset including only those grids involved in soil sampling (bottom panels). The dotted line is the fitted linear model and the dashed line is the fitted quadratic model. The significant model in each plot is shown in bold.

Table 2.2. Regressions using data from all 14 grids with square root transformed species richness as the response variable. Form codes are as follows: CD = concave down quadratic model, CU = concave up quadratic model, POS = positive linear model, and NEG = negative linear model. For quadratic models degrees of freedom are 2 on: 893 at 1 m^2, 445 at 2 m^2, 221 at 4 m^2, 53 at 16 m^2, 11 at 64 m^2; and for linear models are 1 on: 894 at 1 m^2, 446 at 2 m^2, 222 at 4 m^2, 54 at 16 m^2, and 12 at 64 m^2. Grey highlights show regressions at the 1 m^2 scale. Non-significant results are left blank.

Explanatory Variable	**Scale (m^2)**	**Form**	**Term 1**		**Term 2**		**Model**		
			t Statistic	*p* Value	*t* Statistic	*p* Value	*F* Statistic	*p* Value	Multiple R^2
Total Biomass (g) (log10)	1	CD	8.95	1.94E-18	-9.27	1.31E-19	53.91	7.86E-23	0.11
	2	CD	7.38	7.96E-13	-7.57	2.18E-13	34.16	1.58E-14	0.13
	4	CD	5.20	4.63E-07	-5.35	2.18E-07	19.50	1.59E-08	0.15
	16	CD	3.20	2.33E-03	-3.27	1.89E-03	7.20	1.71E-03	0.21
	64								
Live Biomass (g) (log10)	1	NEG	-3.69	2.39E-04			13.61	2.39E-04	0.01
	2	NEG	-2.81	5.18E-03			7.89	5.18E-03	0.02
	4	NEG	-2.82	5.21E-03			7.96	5.21E-03	0.03
	16								
	64								
Litter (g) (log10)	1	CD	9.14	4.20E-19	-9.92	4.66E-22	62.13	5.44E-26	0.12
	2	CD	7.96	1.48E-14	-8.35	8.92E-16	40.50	6.91E-17	0.15
	4	CD	5.23	3.89E-07	-5.52	9.47E-08	20.33	7.89E-09	0.16
	16								
	64								

Table 2.3. Regressions using data from only the four grids involved in soil sampling with square root transformed species richness as the response variable. Form codes are as follows: CD = concave down quadratic model, CU = concave up quadratic model, POS = positive linear model, and NEG = negative linear model. For quadratic models degrees of freedom are 2 on: 253 at 1 m^2, 125 at 2 m^2, 61 at 4 m^2, 13 at 16 m^2, 1 at 64 m^2; and for linear models are 1 on: 254 at 1 m^2, 126 at 2 m^2, 62 at 4 m^2, 14 at 16 m^2, and 2 at 64 m^2. Grey highlights show regressions at the 1 m^2 scale. Non-significant results are left blank.

Explanatory Variable	**Scale (m^2)**	**Form**	**Term 1**		**Term 2**		**Model**		
			t Statistic	*p* Value	*t* Statistic	*p* Value	*F* Statistic	*p* Value	Multiple R^2
Total Biomass (g) (log10)	1	CD	5.11	6.28E-07	-5.21	4.00E-07	14.92	7.49E-07	0.11
	2	CD	4.05	9.08E-05	-4.10	7.46E-05	9.04	2.15E-04	0.13
	4	CD	3.45	1.04E-03	-3.47	9.53E-04	6.29	3.28E-03	0.17
	16								
	64								
Live Biomass (g) (log10)	1	NEG	-3.31	1.06E-03			10.97	1.06E-03	0.04
	2								
	4								
	16								
	64								
Litter (g) (log10)	1	CD	6.75	1.03E-10	-6.73	1.12E-10	22.79	7.96E-10	0.15
	2	CD	6.79	4.01E-10	-6.77	4.58E-10	23.06	2.98E-09	0.27
	4	CD	5.97	1.29E-07	-5.94	1.47E-07	17.89	7.68E-07	0.37
	16	CD	4.20	1.03E-03	-4.17	1.10E-03	9.01	3.51E-03	0.58
	64								

Soil nutrient PCA and PCA regressions

The PCA of the soil nutrients indicated that the cumulative percentage of variation in the data accounted for by the first two axes is 76.5% and this rises to 84.4% if the third axis (PC3) is included. The first axis (PC1) alone explains 43.8% of the variation while the second axis (PC2) alone explains 32.6%. The percentage of variation in the data explained by the third axis alone is 8.0% (Table 2.4).

Table 2.4. Results for the first four axes from a PCA of the soil nutrient data collected from four 8 m × 8 m grids (L4, L5, P1 and P2).

	PC1	**PC2**	**PC3**	**PC4**
Eigenvalues	6.1376	4.5651	1.1139	0.6711
Proportion Explained	0.4384	0.3261	0.0796	0.0479
Cumulative Proportion	0.4384	0.7645	0.8440	0.8920

In the Kaiser-Guttman criterion for the PCA of the soil nutrients the first three axes were greater than the average eigenvalue. In the broken stick model only the first two axes were greater than the corresponding pieces of broken stick (APPENDIX E).

The distance biplot showing the first two axes of the soil nutrient PCA indicates that soil carbon, nitrogen, phosphorus, potassium, boron, magnesium, manganese and iron are variables that have contributed more than average to the ordination space (Figure 2.7). Soil carbon and nitrogen align in the opposite direction to soil iron and align slightly more with PC1 than with PC2. Soil magnesium and manganese also point in opposite directions from each other and align well with PC2.

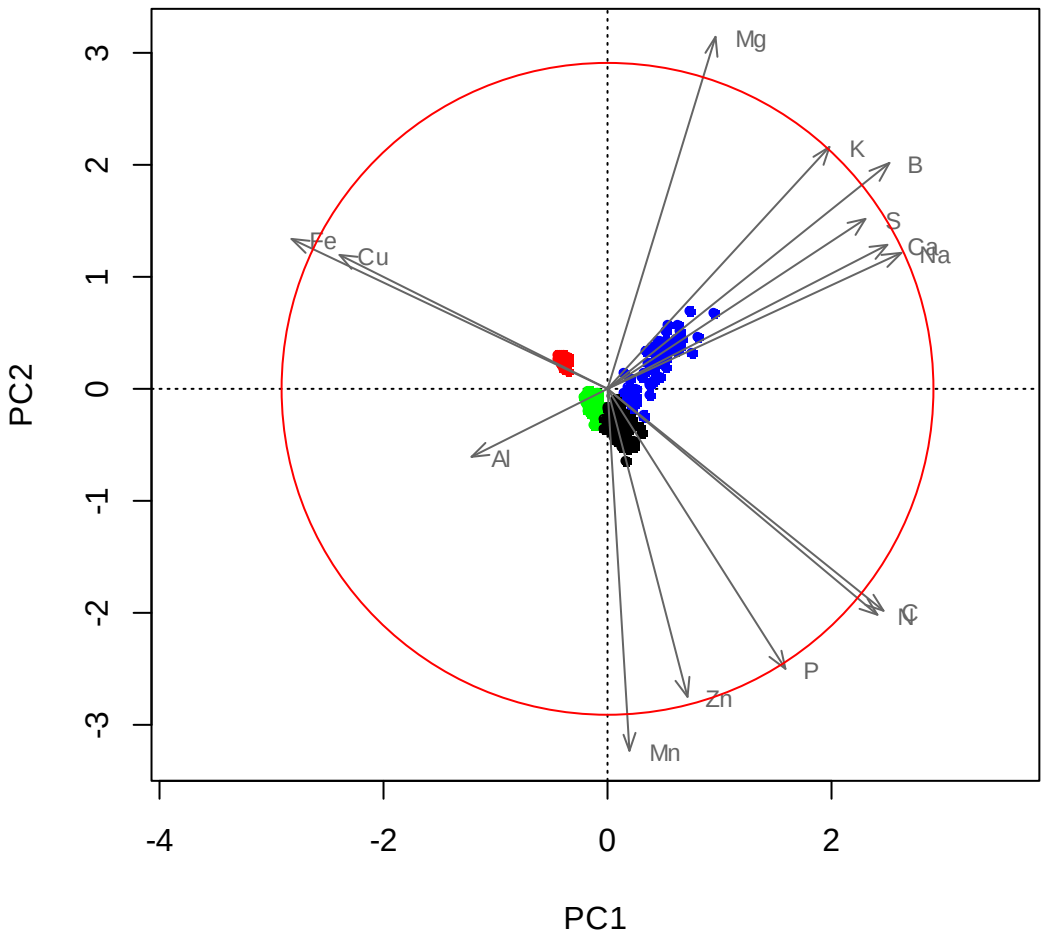

Figure 2.7. Distance biplot of the first two principal component axes of the PCA on the soil nutrient data. The red circle is the circle of equilibrium contribution. Each grid is indicated by points of a certain colour. The L4 (red points) and L5 (green points) grids were lower biomass grids while the P1 (blue points) and P2 (black points) grids were higher biomass grids.

Of the variables that contributed more than average to the ordination space in the distance biplot (Figure 2.7), the correlation biplot of PC1 and PC2 from the PCA of the soil nutrient data (Figure 2.8) shows that soil magnesium, potassium and boron are positively correlated, that soil carbon and nitrogen are tightly positively correlated, and that soil iron and manganese are not closely positively correlated with any of the other important nutrient variables. Instead, they are strongly negatively correlated with soil nitrogen and carbon, and

magnesium respectively. Soil iron is most tightly associated with the L4 grid and soil potassium and boron appear to be mostly associated with the P1 and P2 grids. Manganese is associated primarily with the P2 grid but about equally associated with the L5 grid while the P1 and P2 grids both seem about equally correlated to soil carbon and nitrogen. Soil aluminum is highly contributory to PC3 (APPENDIX E).

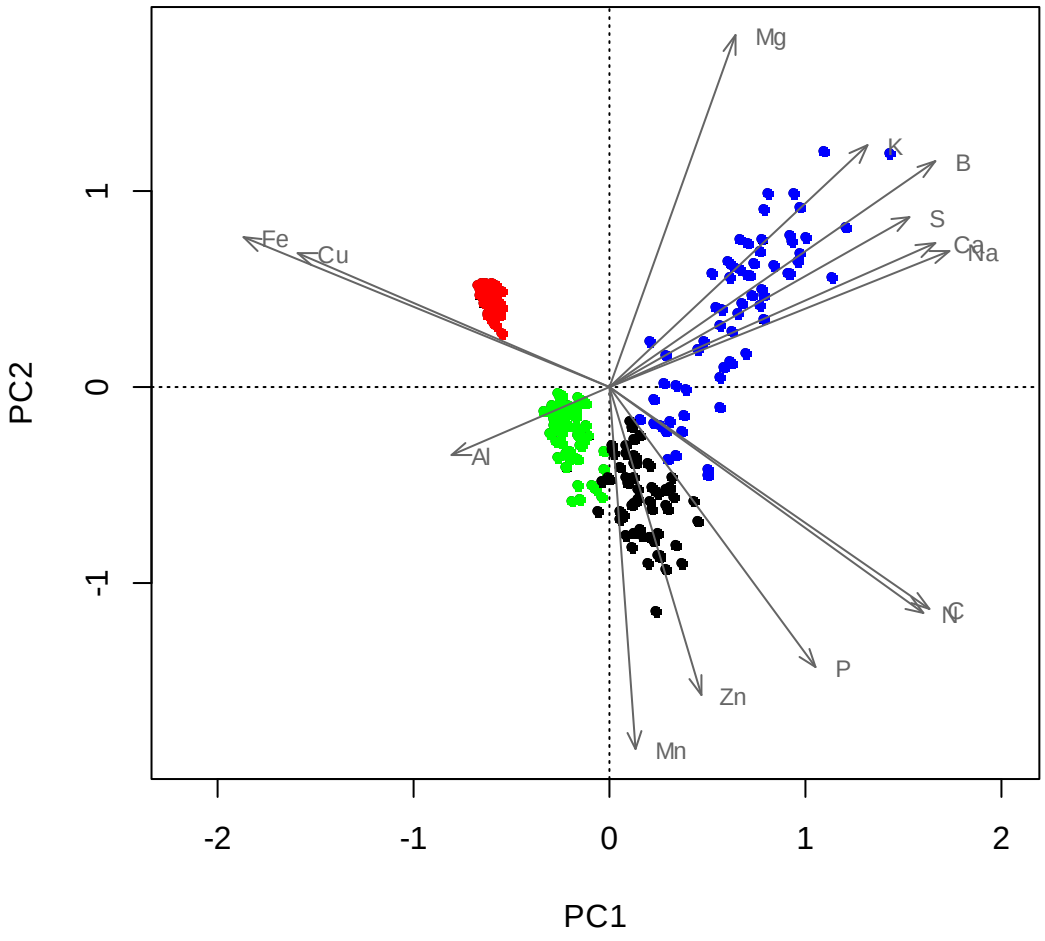

Figure 2.8. Correlation biplot of the first two principal component axes of the PCA on the soil nutrient data. Each grid is indicated by points of a certain colour. The L4 (red points) and L5 (green points) grids were lower biomass grids while the P1 (blue points) and P2 (black points) grids were higher biomass grids.

Regressions with species richness, total biomass, live biomass or litter as the response variables were done with PC1, PC2, or PC3 as the explanatory variables. Variation in litter was 82% explained by the first principal component of the soil nutrient PCA with a concave down relationship, and live biomass variation was 67% explained by PC1 with a positive linear relationship. The first principal component was able to explain 32% of the variation in species richness, also in a concave down relationship. The variation in species richness was 35% explained in a regression with PC2 in a negative linear relationship (Figure 2.9). Variation in species richness, total biomass, live biomass and litter were all less than 10% explained in regressions with PC3 (Table 2.5).

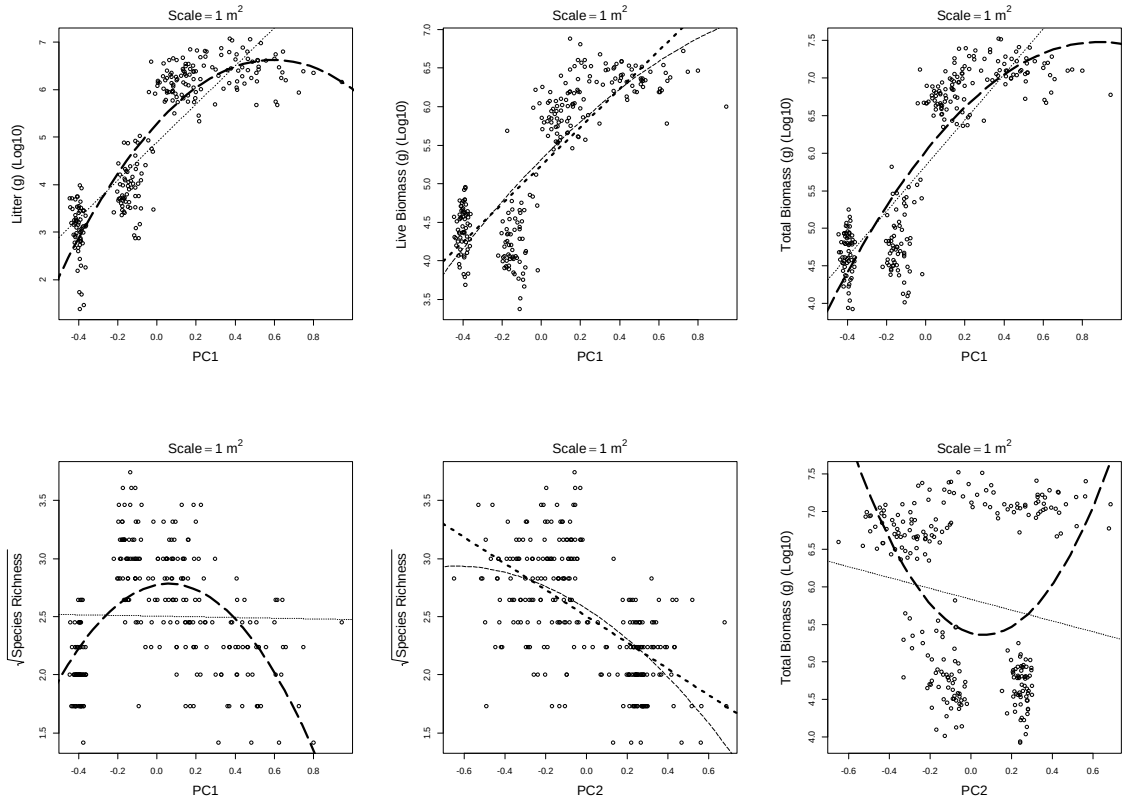

Figure 2.9. Log transformed litter, log transformed live biomass, and log transformed total biomass with fitted curves from linear regression models at 1 m^2 having PC1 as the explanatory variable (top panels); square root transformed species richness with fitted curves from linear regression models having PC1 (bottom left panel) and PC2 (bottom center panel) as the explanatory variables; and log transformed total biomass with fitted curves from linear regression models having PC2 as the explanatory variable (bottom right panel). The dotted line is the fitted linear model and the dashed line is the fitted quadratic model. The significant model in each plot is shown in bold.

Table 2.5. Bivariate regressions for PC1, PC2 and PC3 (from the soil nutrient PCA) as explanatory variables and species richness, total biomass, live biomass and litter as the response variables at the 1 m^2 scale. Form codes are as follows: CD = concave down quadratic model, CU = concave up quadratic model, POS = positive linear model, and NEG = negative linear model. For quadratic models degrees of freedom are 2 on 253 and for linear models are 1 on 254. Non-significant results are left blank.

Explanatory Variable	**Response Variable**	**Form**	**Term 1**		**Term 2**		**Model**		
			t Statistic	*p* Value	*t* Statistic	*p* Value	*F* Statistic	*p* Value	Multiple R^2
PC1	√Species Richness	CD	3.55	4.61E-04	-10.82	1.10E-22	58.63	1.20E-21	0.32
	Total Biomass (g) (log10)	CD	27.99	1.93E-79	-5.96	8.65E-09	401.19	3.42E-79	0.76
	Live Biomass (g) (log10)	POS	22.80	2.19E-63			519.84	2.19E-63	0.67
	Litter (g) (log10)	CD	33.74	1.26E-95	-10.64	4.32E-22	570.26	1.84E-94	0.82
PC2	√Species Richness	NEG	-11.81	5.89E-26			139.55	5.89E-26	0.35
	Total Biomass (g) (log10)	CU	-3.32	1.04E-03	7.11	1.21E-11	29.99	2.05E-12	0.19
	Live Biomass (g) (log10)	CU	-1.60	1.11E-01	6.99	2.41E-11	25.37	9.09E-11	0.17
	Litter (g) (log10)	CU	-5.16	4.90E-07	6.62	2.15E-10	34.12	7.60E-14	0.21
PC3	√Species Richness	NEG	-4.14	4.76E-05			17.13	4.76E-05	0.06
	Total Biomass (g) (log10)	POS	3.44	6.80E-04			11.83	6.80E-04	0.04
	Live Biomass (g) (log10)	POS	4.28	2.63E-05			18.33	2.63E-05	0.07
	Litter (g) (log10)								

Soil nutrient regressions

Carbon

At 1 m^2, soil carbon explained the greatest amount of variation in litter, 80%, in a concave down relationship (Figure 2.10). Soil carbon explained 72% and 61% of the variation in total biomass and live biomass respectively in positive linear relationships. With species richness, a concave down curve with soil carbon explained 15% of the variation. The forms of these relationships were consistent with increasing scale up to 16 m^2 for total biomass and live biomass and up to 4 m^2 for species richness. For litter the relationship switched from concave down to positive linear between 2 m^2 and 4 m^2 (Table 2.6).

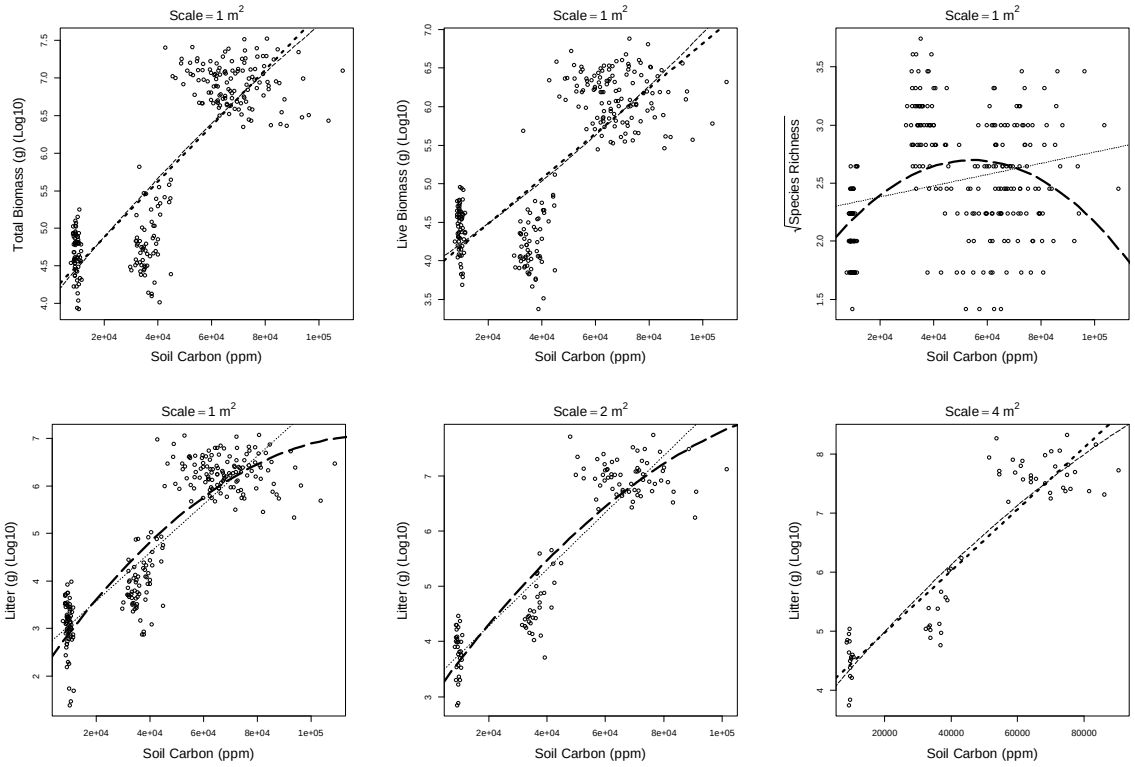

Figure 2.10. Fitted curves from linear regressions with soil carbon as the explanatory variable and log transformed total biomass (top left panel), log transformed live biomass (top center panel) and square root transformed species richness (top right panel) as response variables at the 1 m^2 scale. Fitted curves from linear regression models having soil carbon as the explanatory variable and log transformed litter as response variables at 1 m^2 (bottom left panel), 2 m^2 (bottom center panel), and 4 m^2 (bottom right panel). The dotted line is the fitted linear model and the dashed line is the fitted quadratic model. The significant model in each plot is shown in bold.

Table 2.6. Bivariate regressions of soil carbon with species richness, total biomass, live biomass and litter as the response variables. Form codes are as follows: CD = concave down quadratic model, CU = concave up quadratic model, POS = positive linear model, and NEG = negative linear model. For quadratic models degrees of freedom are 2 on: 253 at 1 m^2, 125 at 2 m^2, 61 at 4 m^2, 13 at 16 m^2, 1 at 64 m^2; and for linear models are 1 on: 254 at 1 m^2, 126 at 2 m^2, 62 at 4 m^2, 14 at 16 m^2, and 2 at 64 m^2. Grey highlights show regressions at the 1 m^2 scale. Non-significant results are left blank.

Response Variable	**Scale (m^2)**	**Form**	**Term 1**		**Term 2**		**Model**		
			t Statistic	*p* Value	*t* Statistic	*p* Value	*F* Statistic	*p* Value	Multiple R^2
√Species Richness	1	CD	6.21	2.14E-09	-5.31	2.38E-07	22.80	7.88E-10	0.15
	2	CD	5.37	3.70E-07	-4.68	7.49E-06	16.68	3.78E-07	0.21
	4	CD	4.20	8.69E-05	-3.67	5.19E-04	10.49	1.22E-04	0.26
	16								
	64								
Total Biomass (g) (log10)	1	POS	25.37	1.43E-71			643.39	1.43E-71	0.72
	2	POS	19.23	2.72E-39			369.76	2.72E-39	0.75
	4	POS	14.23	3.40E-21			202.45	3.40E-21	0.77
	16	POS	7.79	1.87E-06			60.67	1.87E-06	0.81
	64								
Live Biomass (g) (log10)	1	POS	20.06	2.78E-54			402.33	2.78E-54	0.61
	2	POS	15.04	6.72E-30			226.12	6.72E-30	0.64
	4	POS	10.99	3.44E-16			120.77	3.44E-16	0.66
	16	POS	5.72	5.29E-05			32.72	5.29E-05	0.70
	64								
Litter (g) (log10)	1	CD	12.79	3.12E-29	-4.81	2.56E-06	503.86	5.84E-89	0.80
	2	CD	8.65	2.08E-14	-2.62	9.89E-03	308.11	4.85E-49	0.83
	4	POS	18.53	5.77E-27			343.33	5.77E-27	0.85
	16	POS	11.50	1.61E-08			132.24	1.61E-08	0.90
	64								

Nitrogen

At the 1 m^2 scale soil nitrogen best explained the variation in litter accounting for 81% with a concave down relationship. Positive linear relationships explained 73% and 63% of the variation in total biomass and live biomass respectively. Soil nitrogen explained 14% of the variation in species richness in a concave down curve. The forms of relationships were consistent with increasing scale up to 16 m^2 for total biomass and live biomass and up to 4 m^2 for species richness; for litter the form of relationship switched from concave down to positive linear between 2 m^2 and 4 m^2 (Figure 2.11). The results for soil nitrogen were very similar to those of soil carbon at all scales (Table 2.7).

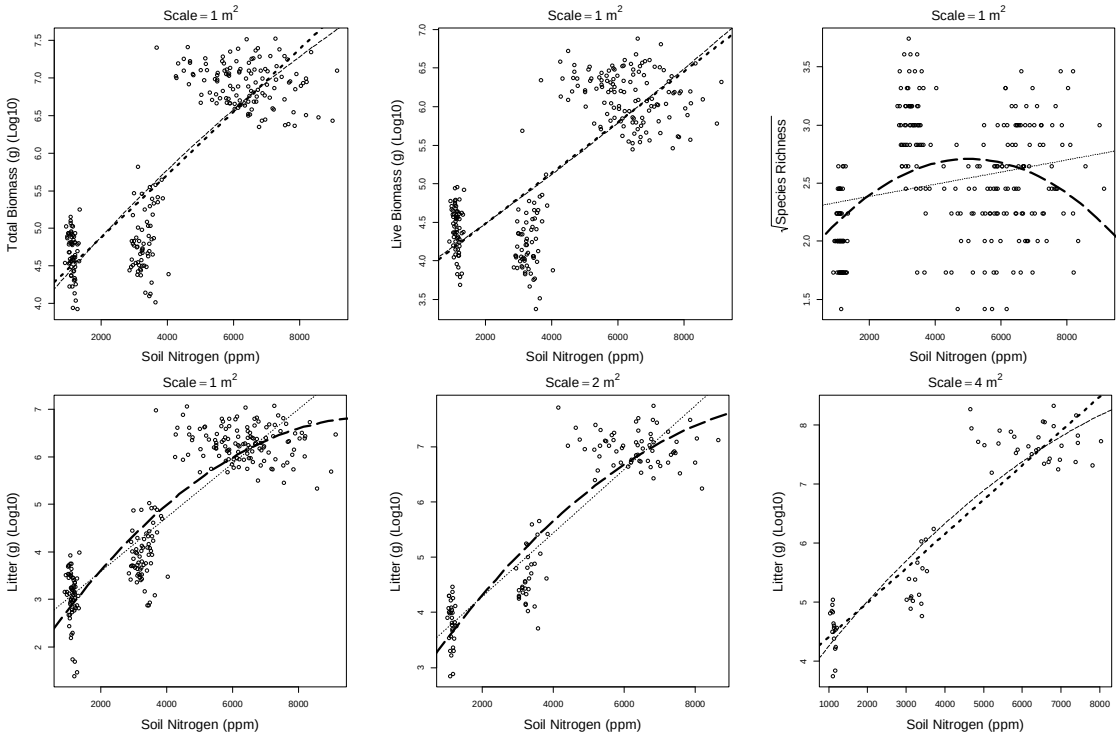

Figure 2.11. Fitted curves from linear regressions with soil nitrogen as the explanatory variable and log transformed total biomass (top left panel), log transformed live biomass (top center panel) and square root transformed species richness (top right panel) as response variables at the 1 m^2 scale. Fitted curves from linear regression models having soil nitrogen as the explanatory variable and log transformed litter as response variables at 1 m^2 (bottom left panel), 2 m^2 (bottom center panel), and 4 m^2 (bottom right panel). The dotted line is the fitted linear model and the dashed line is the fitted quadratic model. The significant model in each plot is shown in bold.

Table 2.7. Bivariate regressions of soil nitrogen with species richness, total biomass, live biomass and litter as the response variables. Form codes are as follows: CD = concave down quadratic model, CU = concave up quadratic model, POS = positive linear model, and NEG = negative linear model. For quadratic models degrees of freedom are 2 on: 253 at 1 m^2, 125 at 2 m^2, 61 at 4 m^2, 13 at 16 m^2, 1 at 64 m^2; and for linear models are 1 on: 254 at 1 m^2, 126 at 2 m^2, 62 at 4 m^2, 14 at 16 m^2, and 2 at 64 m^2. Grey highlights show regressions at the 1 m^2 scale. Non-significant results are left blank.

Response Variable	**Scale (m^2)**	**Form**	**Term 1**		**Term 2**		**Model**		
			t Statistic	*p* Value	*t* Statistic	*p* Value	*F* Statistic	*p* Value	Multiple R^2
√Species Richness	1	CD	5.87	1.37E-08	-5.09	6.91E-07	21.07	3.42E-09	0.14
	2	CD	5.06	1.46E-06	-4.47	1.71E-05	15.15	1.28E-06	0.20
	4	CD	3.90	2.40E-04	-3.45	1.01E-03	9.18	3.28E-04	0.23
	16								
	64								
Total Biomass (g) (log10)	1	POS	26.14	5.78E-74			683.14	5.78E-74	0.73
	2	POS	19.73	2.43E-40			389.09	2.43E-40	0.76
	4	POS	14.57	1.09E-21			212.27	1.09E-21	0.77
	16	POS	7.92	1.53E-06			62.79	1.53E-06	0.82
	64								
Live Biomass (g) (log10)	1	POS	20.58	4.99E-56			423.38	4.99E-56	0.63
	2	POS	15.39	9.93E-31			236.92	9.93E-31	0.65
	4	POS	11.28	1.18E-16			127.14	1.18E-16	0.67
	16	POS	5.86	4.12E-05			34.37	4.12E-05	0.71
	64								
Litter (g) (log10)	1	CD	12.48	3.54E-28	-5.36	1.87E-07	532.35	2.18E-91	0.81
	2	CD	8.61	2.61E-14	-3.25	1.50E-03	324.19	3.41E-50	0.84
	4	POS	18.53	5.69E-27			343.51	5.69E-27	0.85
	16	POS	11.22	2.21E-08			125.82	2.21E-08	0.90
	64								

Soil carbon to nitrogen ratio

At the 1 m^2 scale soil carbon to nitrogen ratio was a concave down relationship with litter, total biomass, species richness and live biomass as response variables and explained 42%, 29%, 24%, and 20% of the variation at this scale, respectively. With increases in scale the form of the significant relationship switched from concave down to a positive linear relationship. For all response variables this change occurred between 2 m^2 and 4 m^2 (Figure 2.12), except for live biomass for which it occurred between 1 m^2 and 2 m^2 (Table 2.8).

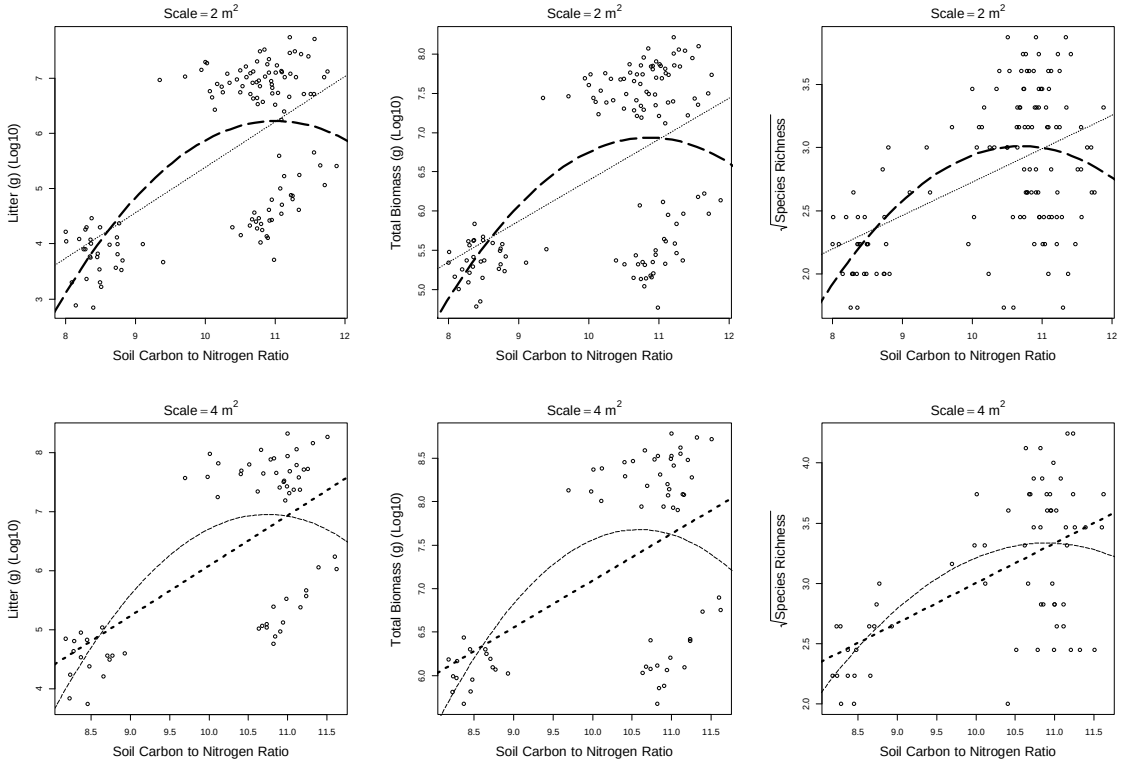

Figure 2.12. Fitted curves from linear regressions at the 2 m^2 scale (top panels) and 4 m^2 scale (bottom row) with soil carbon to nitrogen ratio as the explanatory variable, and log transformed litter (left panels), log transformed total biomass (center panels) and square root transformed species richness (right panels) as response variables. The dotted line is the fitted linear model and the dashed line is the fitted quadratic model. The significant model in each plot is shown in bold.

Table 2.8. Bivariate regressions of soil carbon to nitrogen ratio with species richness, total biomass, live biomass and litter as the response variables. Form codes are as follows: CD = concave down quadratic model, CU = concave up quadratic model, POS = positive linear model, and NEG = negative linear model. For quadratic models degrees of freedom are 2 on: 253 at 1 m^2, 125 at 2 m^2, 61 at 4 m^2, 13 at 16 m^2, 1 at 64 m^2; and for linear models are 1 on: 254 at 1 m^2, 126 at 2 m^2, 62 at 4 m^2, 14 at 16 m^2, and 2 at 64 m^2. Grey highlights show regressions at the 1 m^2 scale. Non-significant results are left blank.

Response Variable	**Scale (m^2)**	**Form**	**Term 1**		**Term 2**		**Model**		
			t Statistic	*p* Value	*t* Statistic	*p* Value	*F* Statistic	*p* Value	Multiple R^2
√Species Richness	1	CD	4.68	4.72E-06	-4.33	2.18E-05	39.69	1.02E-15	0.24
	2	CD	3.42	8.57E-04	-3.14	2.14E-03	28.16	8.00E-11	0.31
	4	POS	5.64	4.52E-07			31.78	4.52E-07	0.34
	16	POS	3.03	8.95E-03			9.20	8.95E-03	0.40
	64								
Total Biomass (g) (log10)	1	CD	4.08	5.96E-05	-3.65	3.19E-04	52.54	8.26E-20	0.29
	2	CD	3.03	2.99E-03	-2.74	7.06E-03	28.24	7.60E-11	0.31
	4	POS	4.92	6.65E-06			24.23	6.65E-06	0.28
	16								
	64								
Live Biomass (g) (log10)	1	CD	3.46	6.36E-04	-3.12	2.00E-03	32.38	3.02E-13	0.20
	2	POS	5.33	4.40E-07			28.40	4.40E-07	0.18
	4	POS	3.82	3.12E-04			14.58	3.12E-04	0.19
	16								
	64								
Litter (g) (log10)	1	CD	4.75	3.35E-06	-4.18	4.09E-05	89.91	3.17E-30	0.42
	2	CD	3.61	4.43E-04	-3.22	1.63E-03	49.68	1.32E-16	0.44
	4	POS	6.65	8.60E-09			44.24	8.60E-09	0.42
	16	POS	3.46	3.79E-03			12.00	3.79E-03	0.46
	64								

Phosphorus

At the 1 m^2 scale, linear regressions with litter and total biomass as response variables and soil phosphorus as the explanatory variable resulted in concave down curves explaining 39% and 25% of their variation respectively. These changed to positive linear relationships with increasing scale; for total biomass this occurred between the 1 m^2 and 2 m^2 scales and for litter between the 2 m^2 and 4 m^2 scales (Figure 2.13). The relationships for both species richness and live biomass with soil phosphorus as the explanatory variable were consistently positive linear and the amount of variation explained was 27% and 14% at the 1 m^2 scale respectively (Table 2.9).

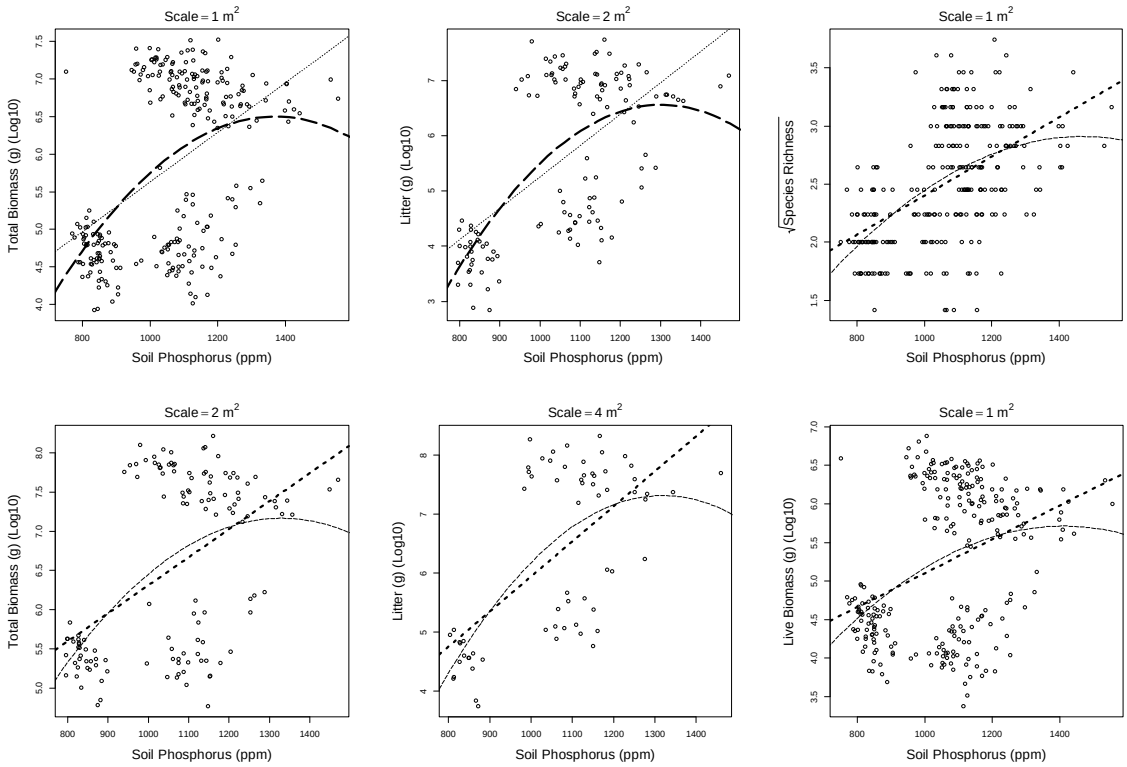

Figure 2.13. Fitted curves from linear regressions with soil phosphorus as the explanatory variable at 1 m^2 and 2 m^2 with log transformed total biomass (left panels), at 2 m^2 and 4 m^2 with log transformed litter (center panels) and with square root transformed species richness and log transformed live biomass at 1 m^2 (right panels). The dotted line is the fitted linear model and the dashed line is the fitted quadratic model. The significant model in each plot is shown in bold.

Table 2.9. Bivariate regressions of soil phosphorus with species richness, total biomass, live biomass and litter as the response variables. Form codes are as follows: CD = concave down quadratic model, CU = concave up quadratic model, POS = positive linear model, and NEG = negative linear model. For quadratic models degrees of freedom are 2 on: 253 at 1 m^2, 125 at 2 m^2, 61 at 4 m^2, 13 at 16 m^2, 1 at 64 m^2; and for linear models are 1 on: 254 at 1 m^2, 126 at 2 m^2, 62 at 4 m^2, 14 at 16 m^2, and 2 at 64 m^2. Grey highlights show regressions at the 1 m^2 scale. Non-significant results are left blank.

Response Variable	**Scale (m^2)**	**Form**	**Term 1**		**Term 2**		**Model**		
			t Statistic	*p* Value	*t* Statistic	*p* Value	*F* Statistic	*p* Value	Multiple R^2
√Species Richness	1	POS	9.81	1.83E-19			96.19	1.83E-19	0.27
	2	POS	8.32	1.24E-13			69.19	1.24E-13	0.35
	4	POS	6.76	5.63E-09			45.67	5.63E-09	0.42
	16	POS	4.43	5.71E-04			19.62	5.71E-04	0.58
	64								
Total Biomass (g) (log10)	1	CD	3.86	1.46E-04	-3.03	2.71E-03	42.33	1.39E-16	0.25
	2	POS	6.42	2.56E-09			41.18	2.56E-09	0.25
	4	POS	4.70	1.48E-05			22.11	1.48E-05	0.26
	16								
	64								
Live Biomass (g) (log10)	1	POS	6.36	9.20E-10			40.48	9.20E-10	0.14
	2	POS	4.72	6.16E-06			22.28	6.16E-06	0.15
	4	POS	3.47	9.51E-04			12.05	9.51E-04	0.16
	16								
	64								
Litter (g) (log10)	1	CD	5.85	1.52E-08	-4.73	3.66E-06	80.02	1.18E-27	0.39
	2	CD	4.16	5.92E-05	-3.39	9.34E-04	46.33	8.83E-16	0.43
	4	POS	6.37	2.59E-08			40.61	2.59E-08	0.40
	16	POS	3.50	3.56E-03			12.22	3.56E-03	0.47
	64								

Potassium

In regressions with species richness as the response variable and soil potassium as the explanatory variable 14% of the variation was explained; the form of the significant relationship was always negative linear and this held up to the 4 m^2 scale. In regressions with soil potassium as the explanatory variable and total biomass, live biomass and litter as response variables the relationship was concave up and explained 22%, 25% and 18% of the variation respectively at the 1 m^2 scale. This relationship switched to a positive linear form between 2 m^2 and 4 m^2 for total biomass and litter and between 1 m^2 and 2 m^2 for live biomass. In the case of litter, which had no significant relationship at 16 m^2, the form of the relationship switched back to concave up and was significant, at 64 m^2 (Figure 2.14, Table 2.10).

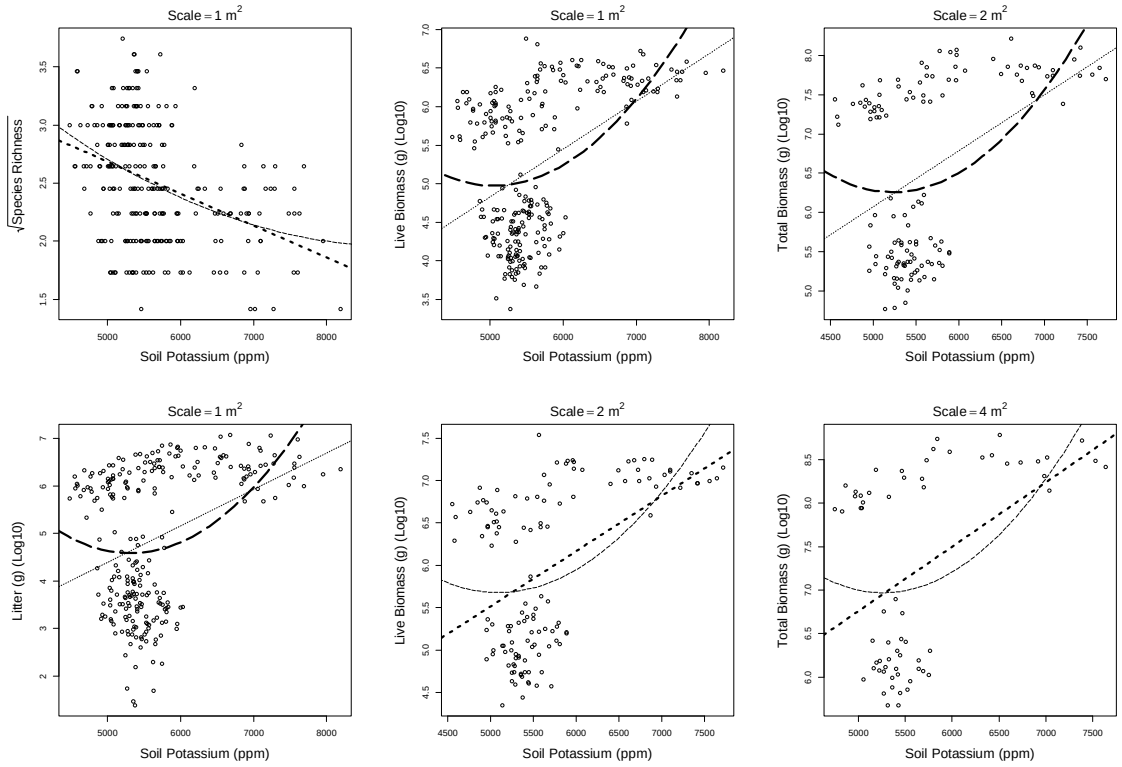

Figure 2.14. Fitted curves from linear regressions with soil potassium as the explanatory variable at 1 m^2 with square root transformed species richness and log transformed litter (left panels), at 1 m^2 and 2 m^2 with log transformed live biomass (center panels) and with log transformed total biomass at 2 m^2 and 4 m^2 (right panels). The dotted line is the fitted linear model and the dashed line is the fitted quadratic model. The significant model in each plot is shown in bold.

Table 2.10. Bivariate regressions of soil potassium with species richness, total biomass, live biomass and litter as the response variables. Form codes are as follows: CD = concave down quadratic model, CU = concave up quadratic model, POS = positive linear model, and NEG = negative linear model. For quadratic models degrees of freedom are 2 on: 253 at 1 m^2, 125 at 2 m^2, 61 at 4 m^2, 13 at 16 m^2, 1 at 64 m^2; and for linear models are 1 on: 254 at 1 m^2, 126 at 2 m^2, 62 at 4 m^2, 14 at 16 m^2, and 2 at 64 m^2. Grey highlights show regressions at the 1 m^2 scale. Non-significant results are left blank.

Response Variable	**Scale (m^2)**	**Form**	**Term 1**		**Term 2**		**Model**		
			t Statistic	*p* Value	*t* Statistic	*p* Value	*F* Statistic	*p* Value	Multiple R^2
√Species Richness	1	NEG	-6.47	5.15E-10			41.80	5.15E-10	0.14
	2	NEG	-4.91	2.75E-06			24.12	2.75E-06	0.16
	4	NEG	-3.61	6.11E-04			13.04	6.11E-04	0.17
	16								
	64								
Total Biomass (g) (log10)	1	CU	-3.02	2.76E-03	3.60	3.90E-04	35.95	1.81E-14	0.22
	2	CU	-2.29	2.36E-02	2.67	8.53E-03	19.75	3.52E-08	0.24
	4	POS	4.01	1.64E-04			16.11	1.64E-04	0.21
	16								
	64								
Live Biomass (g) (log10)	1	CU	-2.99	3.10E-03	3.61	3.64E-04	42.20	1.53E-16	0.25
	2	POS	6.12	1.11E-08			37.42	1.11E-08	0.23
	4	POS	4.50	3.06E-05			20.24	3.06E-05	0.25
	16								
	64								
Litter (g) (log10)	1	CU	-3.22	1.46E-03	3.70	2.61E-04	28.03	1.01E-11	0.18
	2	CU	-2.53	1.28E-02	2.86	5.01E-03	16.14	5.83E-07	0.21
	4	POS	3.43	1.07E-03			11.78	1.07E-03	0.16
	16								
	64	CU	-431.58	1.48E-03	436.49	1.46E-03	123076.48	2.02E-03	1.00

Boron

Soil boron explained the most variation in live biomass accounting for 54% at 1 m^2. The form of the relationship with total biomass, live biomass, and litter was concave down at 1 m^2, 2 m^2, and 4 m^2 and for total biomass and live biomass switched to positive linear at 16 m^2. For litter at 16 m^2 no form was significant. Soil boron explained 17% of the variation in species richness at 1 m^2 in a concave up relationship. This form of relationship also held at 2 m^2 but changed to negative linear at 4 m^2 (Figure 2.15, Table 2.11)

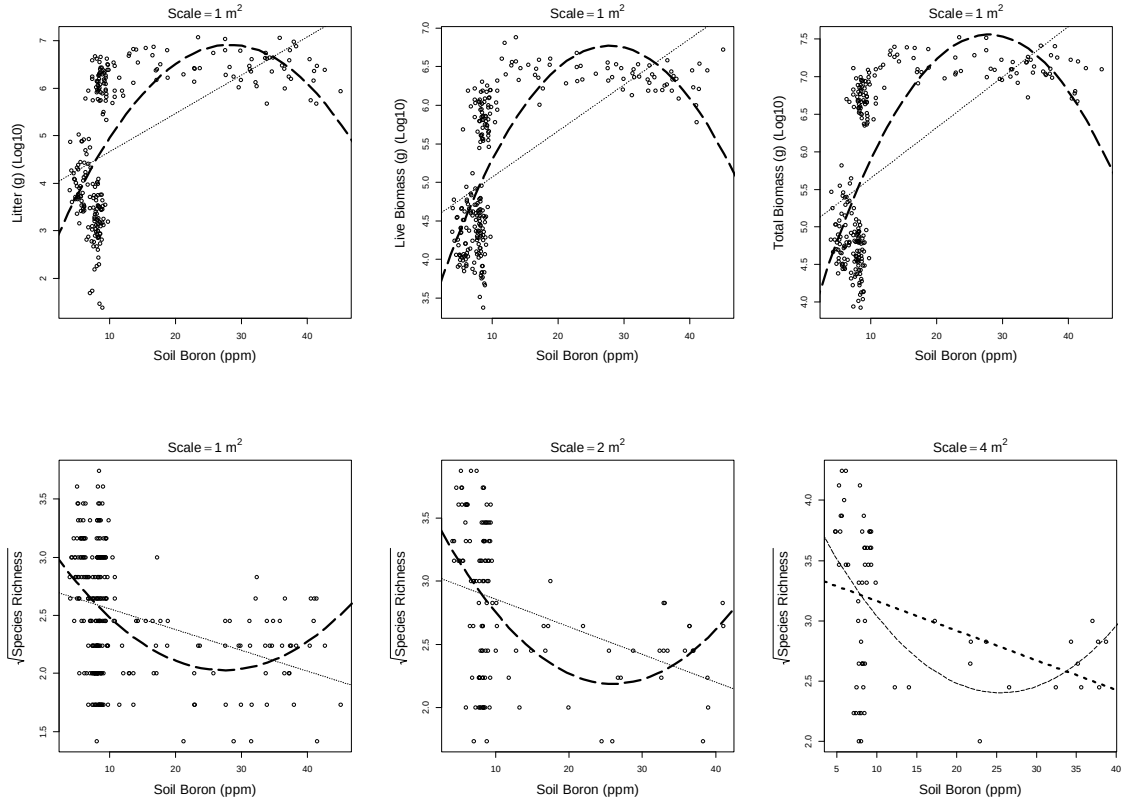

Figure 2.15. Fitted curves from linear regressions with soil boron as the explanatory variable at 1 m^2 with log transformed litter, log transformed live biomass, and log transformed total biomass as response variables (top panels), and with square root transformed species richness at 1 m^2, 2 m^2 and 4 m^2 (bottom panels). The dotted line is the fitted linear model and the dashed line is the fitted quadratic model. The significant model in each plot is shown in bold.

Table 2.11. Bivariate regressions of soil boron with species richness, total biomass, live biomass and litter as the response variables. Form codes are as follows: CD = concave down quadratic model, CU = concave up quadratic model, POS = positive linear model, and NEG = negative linear model. For quadratic models degrees of freedom are 2 on: 253 at 1 m^2, 125 at 2 m^2, 61 at 4 m^2, 13 at 16 m^2, 1 at 64 m^2; and for linear models are 1 on: 254 at 1 m^2, 126 at 2 m^2, 62 at 4 m^2, 14 at 16 m^2, and 2 at 64 m^2. Grey highlights show regressions at the 1 m^2 scale. Non-significant results are left blank.

Response Variable	**Scale (m^2)**	**Form**	**Term 1**		**Term 2**		**Model**		
			t Statistic	*p* Value	*t* Statistic	*p* Value	*F* Statistic	*p* Value	Multiple R^2
√Species Richness	1	CU	-5.02	9.78E-07	4.00	8.29E-05	26.26	4.33E-11	0.17
	2	CU	-4.20	4.97E-05	3.45	7.63E-04	17.15	2.61E-07	0.22
	4	NEG	-3.32	1.50E-03			11.04	1.50E-03	0.15
	16								
	64								
Total Biomass (g) (log10)	1	CD	10.25	7.89E-21	-7.98	4.94E-14	120.72	1.54E-37	0.49
	2	CD	7.56	7.42E-12	-5.99	2.06E-08	65.78	3.04E-20	0.51
	4	CD	5.47	8.76E-07	-4.38	4.82E-05	34.42	9.83E-11	0.53
	16	POS	3.43	4.06E-03			11.77	4.06E-03	0.46
	64								
Live Biomass (g) (log10)	1	CD	11.34	2.30E-24	-8.86	1.41E-16	145.94	7.13E-43	0.54
	2	CD	8.63	2.38E-14	-6.88	2.59E-10	83.28	1.03E-23	0.57
	4	CD	6.28	3.97E-08	-5.03	4.54E-06	44.57	1.17E-12	0.59
	16	POS	3.91	1.58E-03			15.26	1.58E-03	0.52
	64								
Litter (g) (log10)	1	CD	8.25	8.50E-15	-6.36	9.40E-10	82.33	2.88E-28	0.39
	2	CD	6.04	1.65E-08	-4.71	6.41E-06	44.95	1.96E-15	0.42
	4	CD	4.38	4.73E-05	-3.46	9.98E-04	23.39	2.88E-08	0.43
	16								
	64								

Iron

Soil iron explained the most variation in litter and accounted for 87% in a concave up relationship at 1 m^2. This relationship held at smaller scales but switched to negative linear at 16 m^2 (Figure 2.16). At 1 m^2 soil iron accounted for 85% and 79% of total biomass and live biomass respectively and for these response variables the relationship was consistently concave up at scales up to 16 m^2. A concave down curve was found at scales up to 16 m^2 for regressions with species richness as the response variable and soil iron as the explanatory variable; at 1 m^2 this accounted for 29% of the variation (Table 2.12).

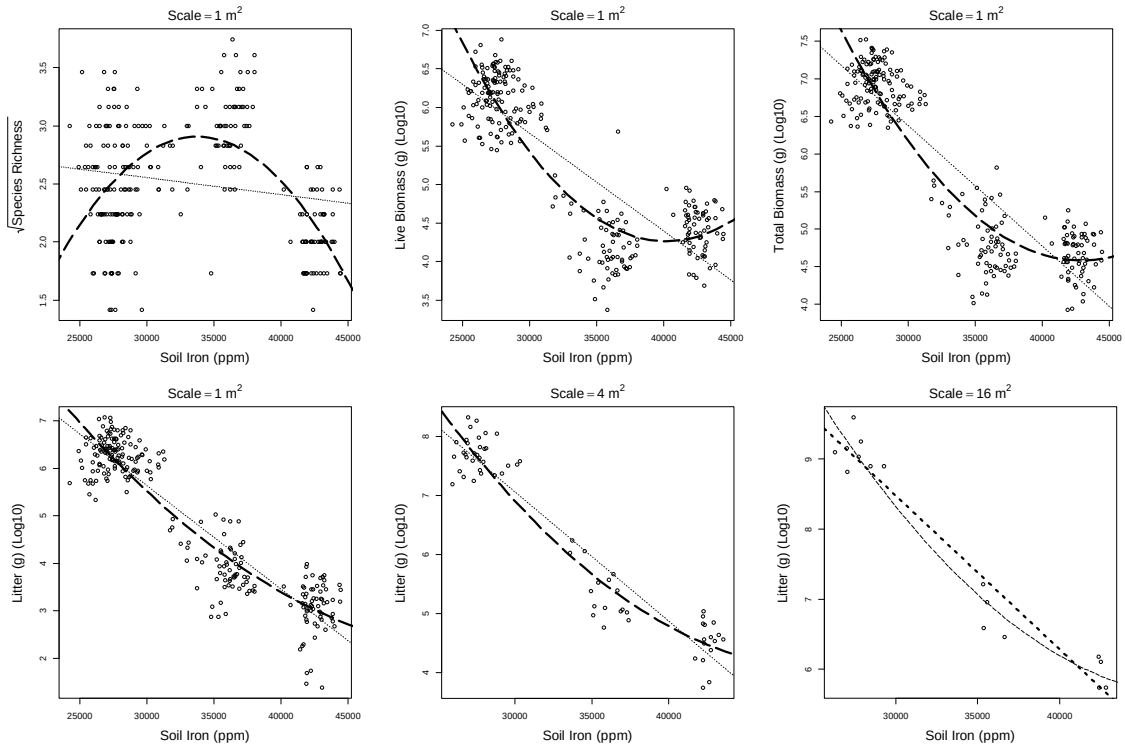

Figure 2.16. Fitted curves from linear regressions with soil iron as the explanatory variable at 1 m^2 with square root transformed species richness, log transformed live biomass, and log transformed total biomass as response variables (top panels), and at 1 m^2, 4 m^2 and 16 m^2 with log transformed litter (bottom panels). The dotted line is the fitted linear model and the dashed line is the fitted quadratic model. The significant model in each plot is shown in bold.

Table 2.12. Bivariate regressions of soil iron with species richness, total biomass, live biomass and litter as the response variables. Form codes are as follows: CD = concave down quadratic model, CU = concave up quadratic model, POS = positive linear model, and NEG = negative linear model. For quadratic models degrees of freedom are 2 on: 253 at 1 m^2, 125 at 2 m^2, 61 at 4 m^2, 13 at 16 m^2, 1 at 64 m^2; and for linear models are 1 on: 254 at 1 m^2, 126 at 2 m^2, 62 at 4 m^2, 14 at 16 m^2, and 2 at 64 m^2. Grey highlights show regressions at the 1 m^2 scale. Non-significant results are left blank.

Response Variable	**Scale (m^2)**	**Form**	**Term 1**		**Term 2**		**Model**		
			t Statistic	*p* Value	*t* Statistic	*p* Value	*F* Statistic	*p* Value	Multiple R^2
√Species Richness	1	CD	9.45	2.31E-18	-9.68	4.56E-19	52.67	7.54E-20	0.29
	2	CD	8.78	1.03E-14	-8.97	3.60E-15	44.57	2.44E-15	0.42
	4	CD	7.44	4.08E-10	-7.60	2.18E-10	31.96	3.20E-10	0.51
	16	CD	4.46	6.38E-04	-4.57	5.21E-04	12.12	1.07E-03	0.65
	64								
Total Biomass (g) (log10)	1	CU	-11.76	9.18E-26	9.49	1.84E-18	732.47	5.84E-106	0.85
	2	CU	-9.76	4.61E-17	8.03	6.18E-13	459.73	2.38E-58	0.88
	4	CU	-8.19	2.10E-11	6.83	4.52E-09	301.01	2.49E-32	0.91
	16	CU	-5.14	1.90E-04	4.34	7.98E-04	108.40	7.79E-09	0.94
	64								
Live Biomass (g) (log10)	1	CU	-12.73	5.02E-29	10.95	4.12E-23	483.19	3.96E-87	0.79
	2	CU	-10.54	5.70E-19	9.19	1.10E-15	306.15	6.75E-49	0.83
	4	CU	-8.74	2.41E-12	7.68	1.58E-10	199.86	1.65E-27	0.87
	16	CU	-5.30	1.43E-04	4.70	4.14E-04	67.89	1.32E-07	0.91
	64								
Litter (g) (log10)	1	CU	-6.55	3.23E-10	4.07	6.34E-05	818.49	3.33E-111	0.87
	2	CU	-5.89	3.39E-08	3.90	1.59E-04	570.89	1.37E-63	0.90
	4	CU	-5.15	2.96E-06	3.57	6.99E-04	378.42	4.13E-35	0.93
	16	NEG	-15.16	4.43E-10			229.76	4.43E-10	0.94
	64								

Magnesium

At the 1 m^2 scale linear regressions with soil magnesium as the explanatory variable explained the most variation in species richness, accounting for 49%. Soil magnesium explained 9%, 11%, and 10% of the variation in total biomass, live biomass and litter at the same scale. The form of the curve was concave up for every regression that was significant except in the case of live biomass where it switched to positive linear between the 1 m^2 and 2 m^2 scale and was not significant at larger scales (Figure 2.17, Table 2.13). The observation with over 20,000 ppm soil magnesium was identified by Cook's distance as an influential point; however, removing it did not change the forms of relationships that were significant.

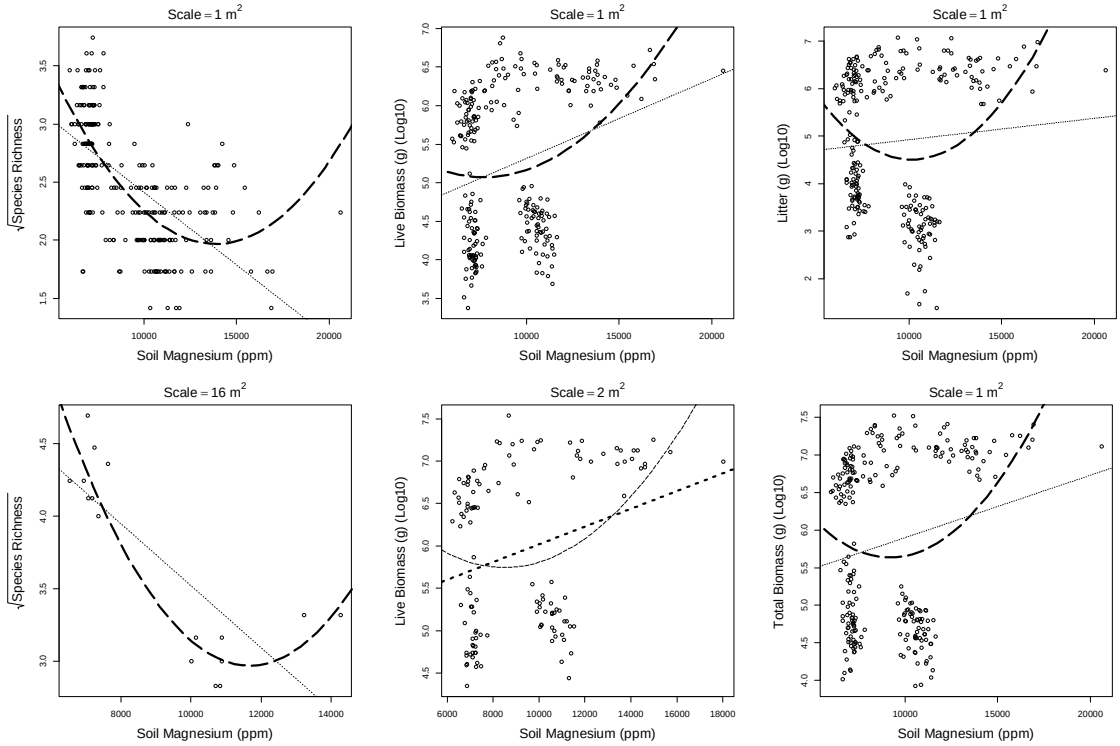

Figure 2.17. Fitted curves from linear regressions with soil magnesium as the explanatory variable at 1 m^2 and 16 m^2 with square root transformed species richness (left panels), at 1m^2 and 2 m^2 with log transformed live biomass (center panels), and log transformed litter and log transformed total biomass (right panels). The dotted line is the fitted linear model and the dashed line is the fitted quadratic model. The significant model in each plot is shown in bold.

Table 2.13. Bivariate regressions of soil magnesium with species richness, total biomass, live biomass and litter as the response variables. Form codes are as follows: CD = concave down quadratic model, CU = concave up quadratic model, POS = positive linear model, and NEG = negative linear model. For quadratic models degrees of freedom are 2 on: 253 at 1 m^2, 125 at 2 m^2, 61 at 4 m^2, 13 at 16 m^2, 1 at 64 m^2; and for linear models are 1 on: 254 at 1 m^2, 126 at 2 m^2, 62 at 4 m^2, 14 at 16 m^2, and 2 at 64 m^2. Grey highlights show regressions at the 1 m^2 scale. Non-significant results are left blank.

Response Variable	**Scale (m^2)**	**Form**	**Term 1**		**Term 2**		**Model**		
			t Statistic	*p* Value	*t* Statistic	*p* Value	*F* Statistic	*p* Value	Multiple R^2
√Species Richness	1	CU	-9.62	7.34E-19	7.45	1.52E-12	122.96	4.94E-38	0.49
	2	CU	-8.72	1.44E-14	7.14	6.73E-11	95.83	5.89E-26	0.61
	4	CU	-7.94	5.48E-11	6.73	6.71E-09	79.57	1.00E-17	0.72
	16	CU	-6.21	3.16E-05	5.33	1.37E-04	49.83	8.02E-07	0.88
	64								
Total Biomass (g) (log10)	1	CU	-3.41	7.66E-04	3.98	8.89E-05	12.97	4.33E-06	0.09
	2	CU	-3.10	2.42E-03	3.45	7.67E-04	8.57	3.24E-04	0.12
	4	CU	-2.70	8.92E-03	2.92	4.95E-03	5.60	5.83E-03	0.16
	16								
	64								
Live Biomass (g) (log10)	1	CU	-2.08	3.87E-02	2.89	4.23E-03	15.09	6.46E-07	0.11
	2	POS	3.29	1.28E-03			10.85	1.28E-03	0.08
	4								
	16								
	64								
Litter (g) (log10)	1	CU	-4.99	1.13E-06	5.28	2.84E-07	14.77	8.55E-07	0.10
	2	CU	-4.35	2.84E-05	4.53	1.37E-05	10.73	4.99E-05	0.15
	4	CU	-3.66	5.31E-04	3.77	3.75E-04	7.33	1.40E-03	0.19
	16								
	64								

Manganese

Of the response variables, soil manganese was able to explain the greatest amount of variation in species richness; at the 1 m^2 scale it accounted for 25% and had a positive linear relationship. Soil manganese explained 8%, 6%, and 12% of total biomass, live biomass and litter respectively (Figure 2.18). The relationship remained positive linear between soil manganese and species richness from 1 m^2 up to 16 m^2 after which it became insignificant. For total biomass and live biomass the relationship was concave up at 1 m^2 and 2 m^2 and insignificant at larger scales. For litter, the relationship was concave up at 1 m^2, positive linear at 2 m^2 and was not significant at larger scales (Table 2.14).

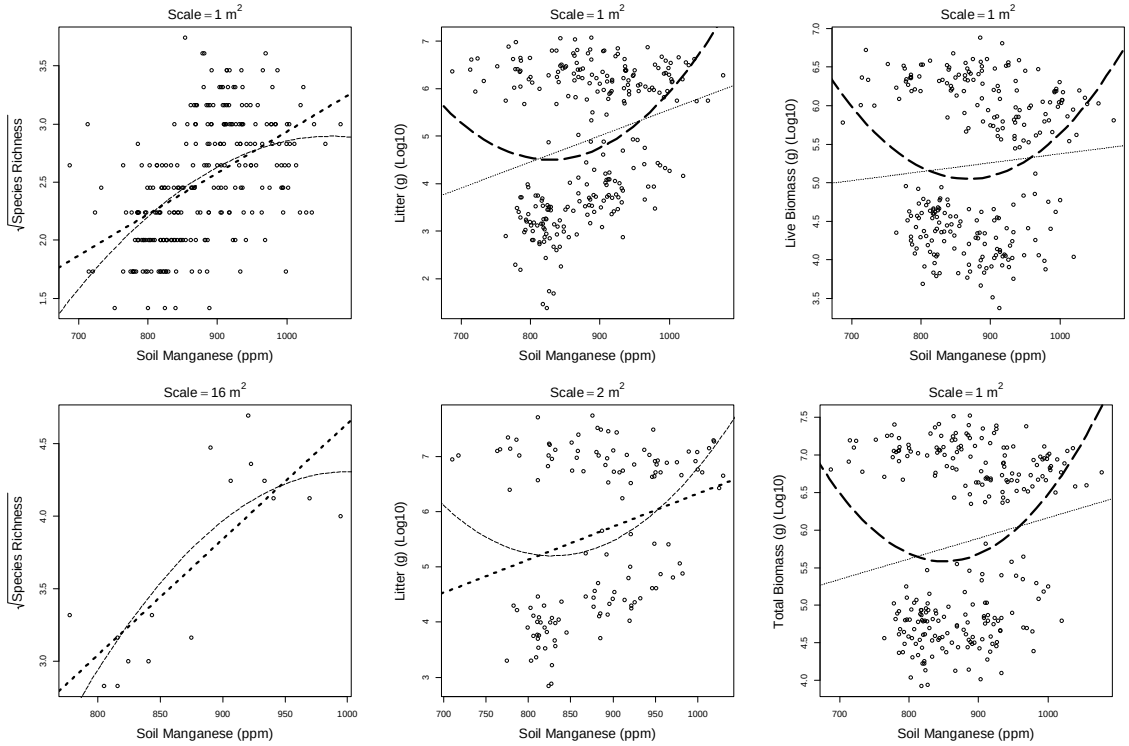

Figure 2.18. Fitted curves from linear regressions with soil manganese as the explanatory variable at 1 m^2 and 16 m^2 with square root transformed species richness (left panels), at 1m^2 and 2 m^2 with log transformed litter (center panels), and log transformed live biomass and log transformed total biomass (right panels). The dotted line is the fitted linear model and the dashed line is the fitted quadratic model. The significant model in each plot is shown in bold.

Table 2.14. Bivariate regressions of soil manganese with species richness, total biomass, live biomass and litter as the response variables. Form codes are as follows: CD = concave down quadratic model, CU = concave up quadratic model, POS = positive linear model, and NEG = negative linear model. For quadratic models degrees of freedom are 2 on: 253 at 1 m^2, 125 at 2 m^2, 61 at 4 m^2, 13 at 16 m^2, 1 at 64 m^2; and for linear models are 1 on: 254 at 1 m^2, 126 at 2 m^2, 62 at 4 m^2, 14 at 16 m^2, and 2 at 64 m^2. Grey highlights show regressions at the 1 m^2 scale. Non-significant results are left blank.

Response Variable	**Scale (m^2)**	**Form**	**Term 1**		**Term 2**		**Model**		
			t Statistic	*p* Value	*t* Statistic	*p* Value	*F* Statistic	*p* Value	Multiple R^2
√Species Richness	1	POS	9.20	1.36E-17			84.63	1.36E-17	0.25
	2	POS	8.43	6.68E-14			71.10	6.68E-14	0.36
	4	POS	7.61	1.86E-10			57.96	1.86E-10	0.48
	16	POS	4.72	3.27E-04			22.30	3.27E-04	0.61
	64								
Total Biomass (g) (log10)	1	CU	-3.70	2.67E-04	3.85	1.49E-04	11.74	1.33E-05	0.08
	2	CU	-2.64	9.34E-03	2.74	6.97E-03	6.22	2.66E-03	0.09
	4								
	16								
	64								
Live Biomass (g) (log10)	1	CU	-3.66	3.05E-04	3.74	2.28E-04	8.03	4.14E-04	0.06
	2	CU	-2.70	7.82E-03	2.76	6.71E-03	4.43	1.38E-02	0.07
	4								
	16								
	64								
Litter (g) (log10)	1	CU	-3.36	9.15E-04	3.59	3.94E-04	17.04	1.14E-07	0.12
	2	POS	3.36	1.02E-03			11.31	1.02E-03	0.08
	4								
	16								
	64								

Soil and leaf nutrient PCA and PCA regressions

The percentage of variation in the soil and leaf nutrient data accounted for by the first two PCA axes is 70.0% and rises to 79.5% if PC3 is included. Alone, PC1 explains 42.9% of the variation in the soil and leaf nutrient data while PC2 alone explains 27.1%. The percentage of variation in the data explained by PC3 alone is 9.5% (Table 2.15).

Table 2.15. Results for the first four axes from a PCA of the soil and leaf nutrient data collected from four 3 m × 3 m subsamples within the four 8 m × 8 m grids (L4, L5, P1 and P2).

	PC1	**PC2**	**PC3**	**PC4**
Eigenvalues	7.7210	4.8719	1.7125	1.0511
Proportion Explained	0.4289	0.2707	0.0951	0.0584
Cumulative Proportion	0.4289	0.6996	0.7948	0.8531

The Kaiser-Guttman criterion for the PCA of the soil and leaf nutrient data shows the first four axes were greater than the average eigenvalue but in the broken stick model only the first two axes were greater than the corresponding pieces of broken stick (APPENDIX E).

The distance biplot of the first two axes of the PCA on the soil and leaf nutrient data indicates that soil sodium, calcium, potassium, boron, magnesium and iron are nutrients that have contributed more than average to the ordination space (Figure 2.19). Soil carbon and nitrogen point the opposite direction of iron and these are well aligned with PC1. None of the leaf nutrients contribute more than average to the PCA. Soil magnesium again lines up with PC2.

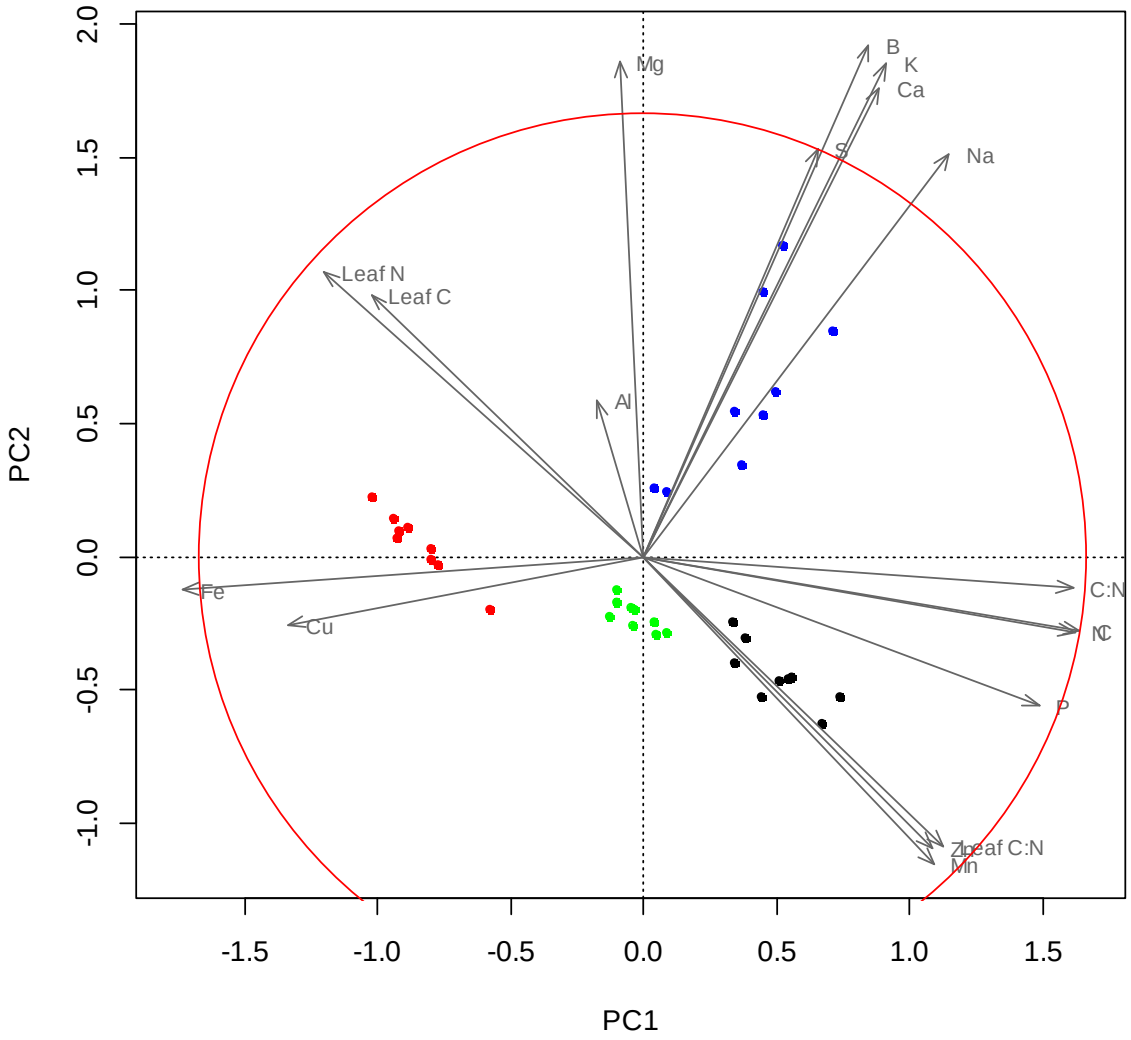

Figure 2.19. Distance biplot of the first two principal component axes from the PCA on the soil and leaf nutrient data. The red circle is the circle of equilibrium contribution. Each grid is indicated by points of a certain colour. The L4 (red points) and L5 (green points) grids were lower biomass grids while the P1 (blue points) and P2 (black points) grids were higher biomass grids.

The correlation biplot shows soil sodium, calcium, potassium, boron and magnesium (at a slightly larger angle) grouped together in a similar direction indicating positive correlation (Figure 2.20). Again, these nutrients are associated with the P2 grid. The L4 grid is again tightly associated with soil iron which is not tightly correlated with any other nutrients but is

slightly positively associated with leaf carbon and nitrogen content, however these variables contributed less than average to the PCA ordination space. Soil aluminum aligns strongly with PC3; variation in this element dominates this axis (APPENDIX E).

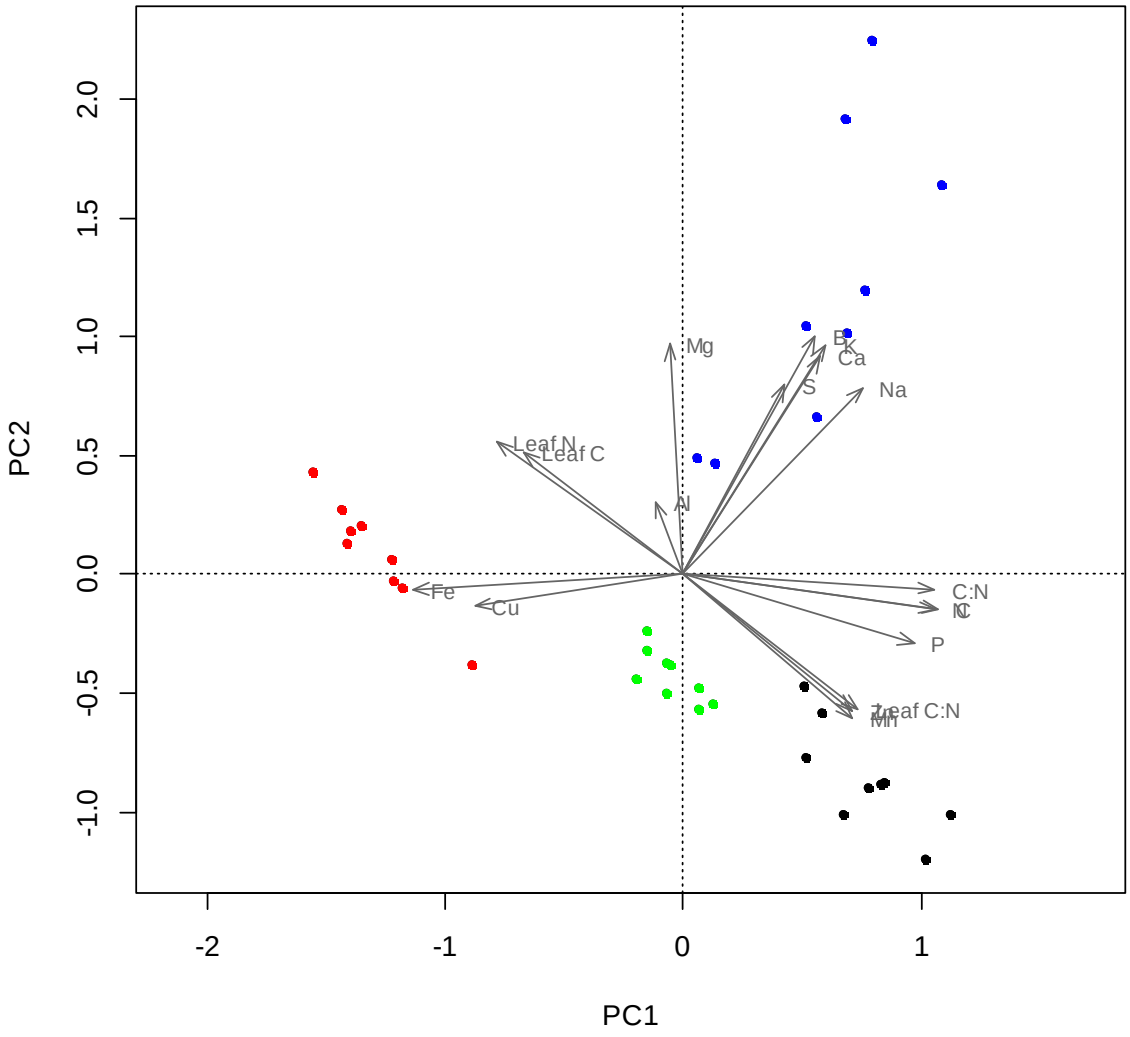

Figure 2.20. Correlation biplot of the first two principal component axes of the soil and leaf nutrient data. Each grid is indicated by points of a certain colour. The L4 (red points) and L5 (green) grids were lower biomass grids while the P1 (blue points) and P2 (black points) grids were higher biomass grids.

At the 1 m^2 scale the first principal component explained the most variation in litter with a positive linear relationship accounting for 76% of the variation in the data. Total biomass and live biomass gave high R^2 values with PC1 which accounted for 75% and 71% of the variation respectively with concave up relationships. The second principal component explained 37%, 35%, and 33% of the variation in live biomass, total biomass and litter respectively with concave up relationships. Variation in species richness was 34% explained by a negative linear relationship with PC2 as the explanatory variable (Figure 2.21, Table 2.16).

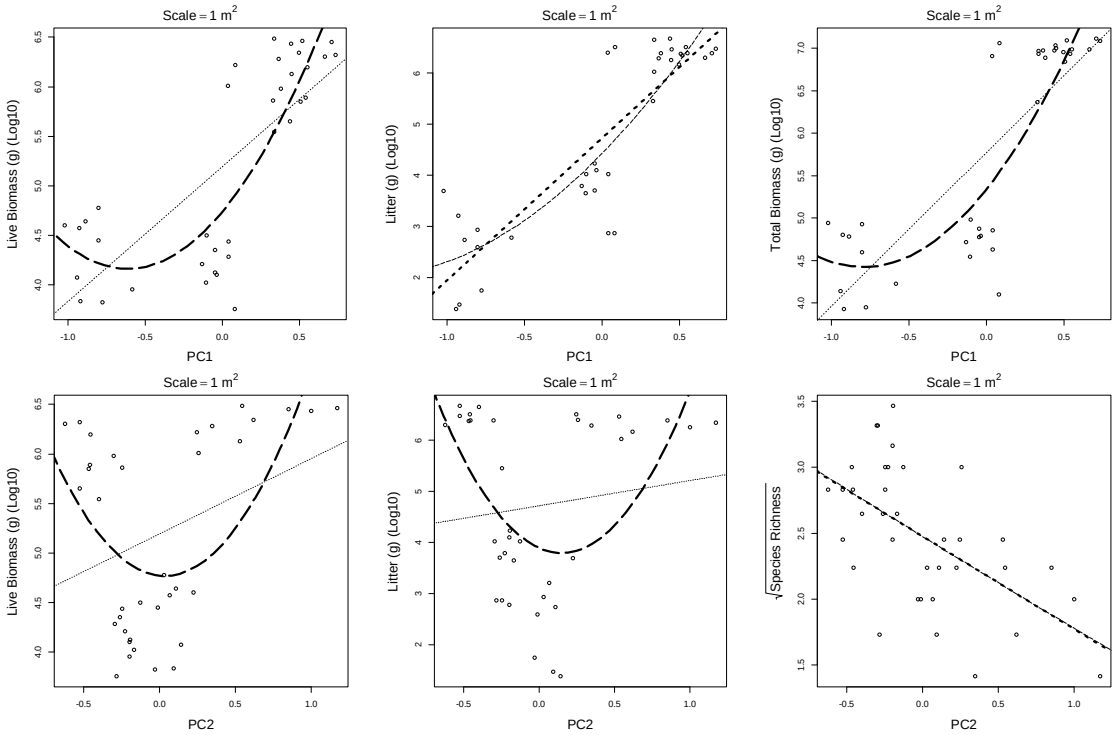

Figure 2.21. Log transformed live biomass, log transformed litter and log transformed total biomass with fitted curves from linear regression models at 1 m^2 having PC1 as the explanatory variable (top panels); and, log transformed live biomass, log transformed litter and square root transformed species richness with fitted curves from linear regression models having PC2 as the explanatory variable (bottom panels). The principal components are from the PCA on the soil and leaf nutrient data. The dotted line is the fitted linear model and the dashed line is the fitted quadratic model. The significant model in each plot is shown in bold.

Table 2.16. Bivariate regressions with PC1, PC2 and PC3 (from the soil and leaf nutrient PCA) as explanatory variables and species richness, total biomass, live biomass and litter as the response variables at the 1 m^2 scale. Form codes are as follows: CD = concave down quadratic model, CU = concave up quadratic model, POS = positive linear model, and NEG = negative linear model. For quadratic models degrees of freedom are 2 on 33 and for linear models are 1 on 34. Non-significant results are left blank.

Explanatory Variable	**Response Variable**	**Form**	**Term 1**		**Term 2**		**Model**		
			t Statistic	*p* Value	*t* Statistic	*p* Value	*F* Statistic	*p* Value	Multiple R^2
PC1	√Species Richness								
	Total Biomass (g) (log10)	CU	9.60	4.43E-11	3.37	1.95E-03	50.65	8.75E-11	0.75
	Live Biomass (g) (log10)	CU	8.93	2.56E-10	4.05	2.91E-04	41.20	1.07E-09	0.71
	Litter (g) (log10)	POS	10.48	3.49E-12			109.78	3.49E-12	0.76
PC2	√Species Richness	NEG	-4.16	2.05E-04			17.29	2.05E-04	0.34
	Total Biomass (g) (log10)	CU	-1.20	2.39E-01	3.87	4.87E-04	8.71	9.18E-04	0.35
	Live Biomass (g) (log10)	CU	-0.41	6.87E-01	3.68	8.20E-04	9.74	4.74E-04	0.37
	Litter (g) (log10)	CU	-1.80	8.06E-02	3.95	3.82E-04	8.19	1.29E-03	0.33
PC3	√Species Richness								
	Total Biomass (g) (log10)								
	Live Biomass (g) (log10)								
	Litter (g) (log10)								

Soil and leaf carbon, nitrogen and carbon to nitrogen ratios PCA and regressions

The percentage of variation in the soil and leaf carbon, nitrogen and carbon to nitrogen ratio nutrient data accounted for by the first two PCA axes is 87.3% and rises to 94.4% if PC3 is included. The first axis alone explains 70.2% of the variation while the second alone explains 17.1%. The percentage of variation in the data explained by the third axis alone is 7.1% (Table 2.17).

Table 2.17. Results for the first four axes from a PCA on soil and leaf carbon, nitrogen, and carbon to nitrogen ratio data collected from four 3 m × 3 m subsamples within the four 8 m × 8 m soil grids (L4, L5, P1 and P2).

	PC1	**PC2**	**PC3**	**PC4**
Eigenvalues	4.2127	1.0234	0.4253	0.2940
Proportion Explained	0.7021	0.1706	0.0709	0.0490
Cumulative Proportion	0.7021	0.8727	0.9436	0.9926

The Kaiser-Guttman criterion of the PCA of the soil and leaf carbon, nitrogen and carbon to nitrogen ratio nutrient data suggests that the first two axes are relevant while the broken stick model indicates only the first axis contains important information (APPENDIX E).

The distance biplot of the first two axes of the PCA of the soil and leaf carbon, nitrogen and carbon to nitrogen ratio nutrient data indicates that soil carbon and nitrogen, as well as leaf nitrogen, are nutrients that have contributed more than average to the ordination space (Figure 2.22). Leaf carbon, soil carbon to nitrogen ratio and leaf carbon to nitrogen ratio contribute less than average to the PCA ordination space.

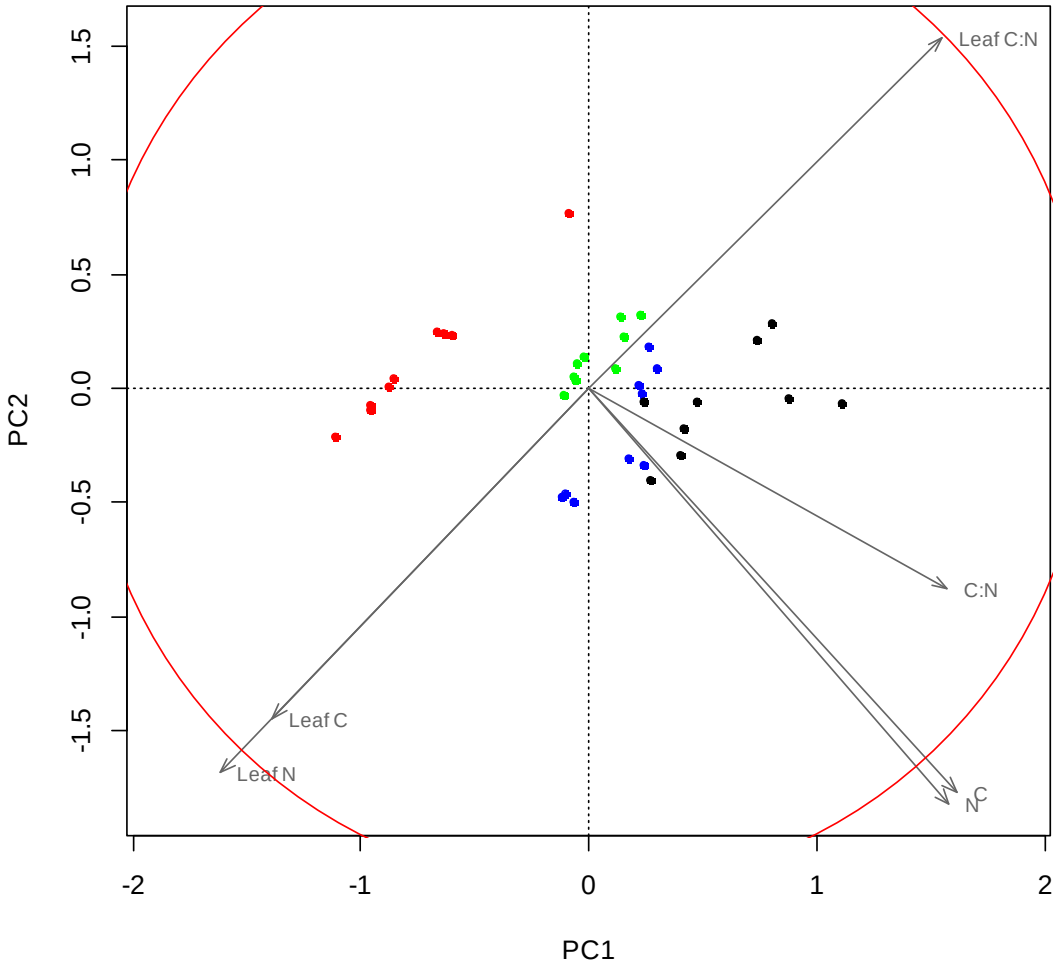

Figure 2.22. Distance biplot of the first two principal component axes from the PCA of the soil and leaf carbon, nitrogen and carbon to nitrogen ratio nutrient data. The red circle is the circle of equilibrium contribution. Each grid is indicated by points of a certain colour. The L4 (red points) and L5 (green points) grids were lower biomass grids while the P1 (blue points) and P2 (black points) grids were higher biomass grids.

The correlation biplot (Figure 2.23) shows that soil carbon and nitrogen are slightly negatively correlated with leaf carbon and nitrogen. High leaf carbon and nitrogen is

associated with the lower biomass L4 grid while high soil carbon and nitrogen are correlated with the higher biomass P1 and P2 grids.

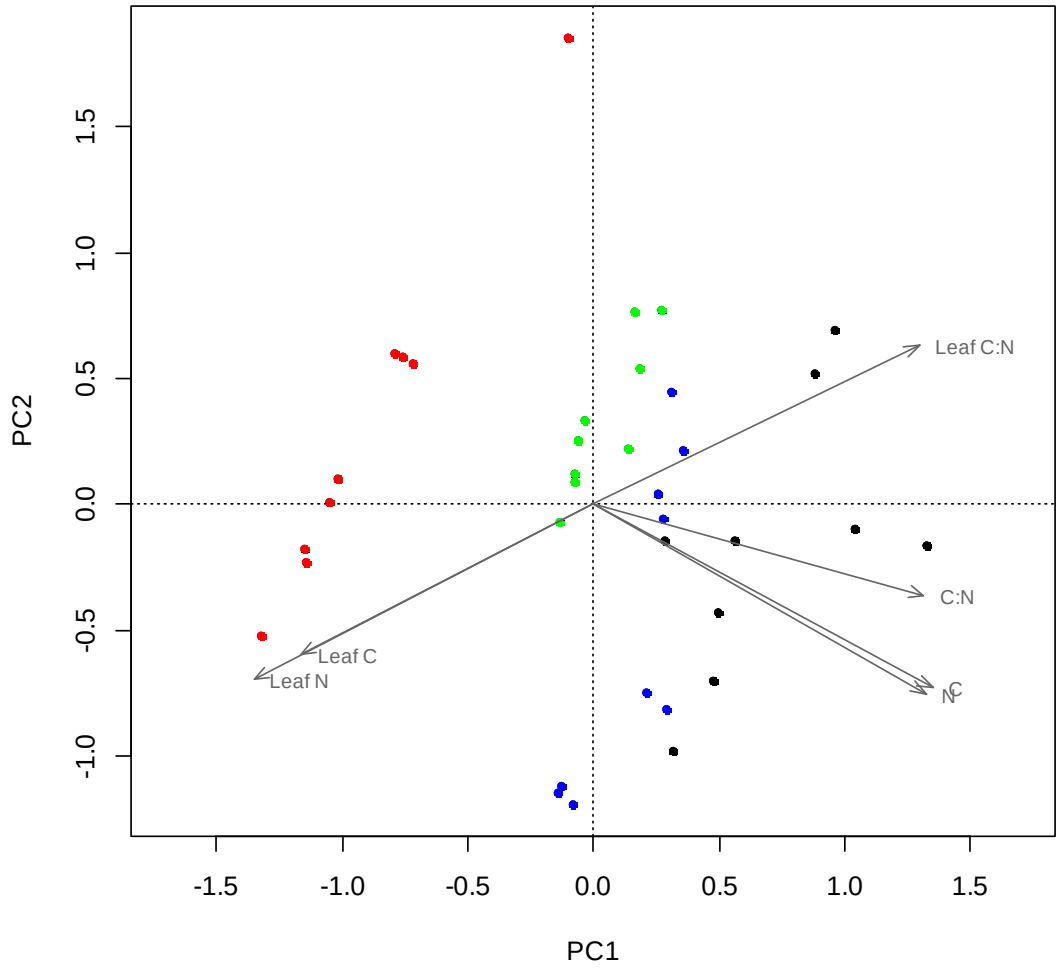

Figure 2.23. Correlation biplot of the first two principal component axes from the PCA of the soil and leaf carbon, nitrogen and carbon to nitrogen ratio nutrient data. Each grid is indicated by points of a certain colour. The L4 (red points) and L5 (green points) grids were lower biomass grids while the P1 (blue points) and P2 (black points) grids were higher biomass grids.

At the 1 m^2 scale, regressions with PC1 as the explanatory variable explained the most variation in litter accounting for 56% of the variation with a positive linear form (Figure

2.24). The relationships with total biomass and live biomass were also positive linear and accounted for 45% and 36% of the variation respectively. Relationships between the same response variables, in regressions with PC2, were all negative linear; there were no significant relationships between any of the PCA axes and species richness. The variation in total biomass and live biomass were both 27% explained by PC2; variation in litter was 23% explained by PC2 (Table 2.18).

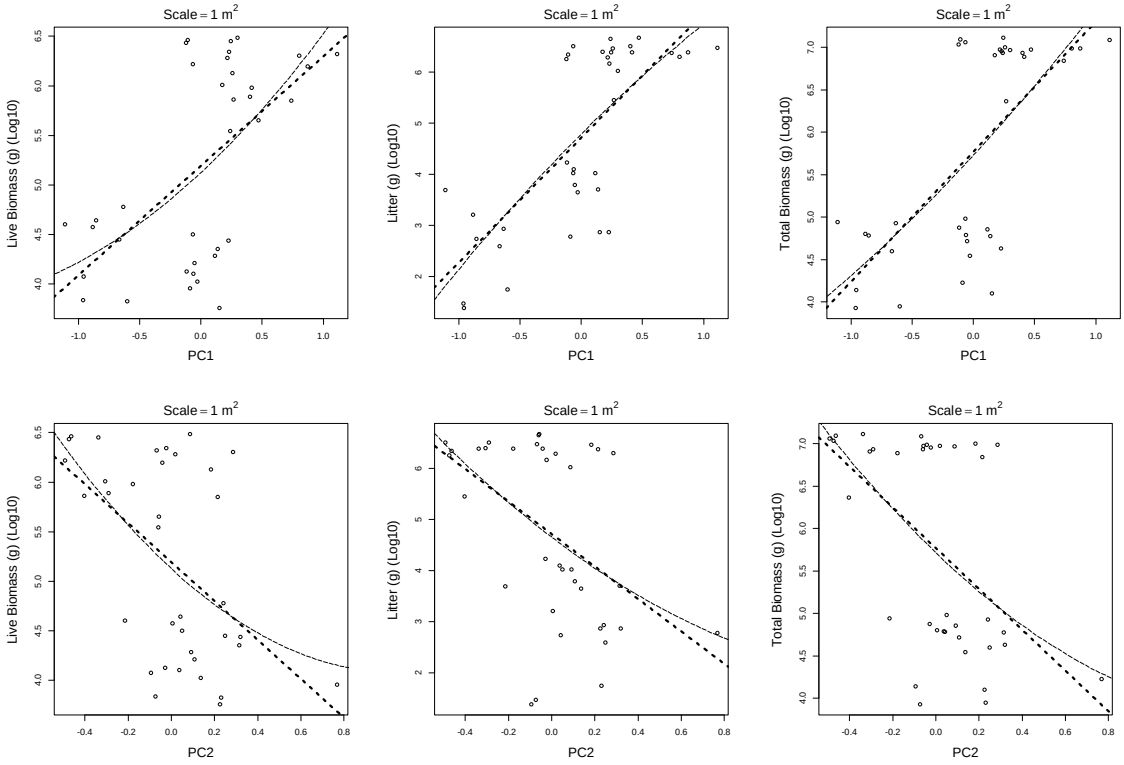

Figure 2.24. Fitted curves from linear regression models at 1 m^2 having log transformed live biomass, log transformed litter and log transformed total biomass as response variables and PC1 (top panels); and PC2 (bottom panels) as the explanatory variables. The principal components are from the PCA on only the soil and leaf carbon, nitrogen, and carbon to nitrogen ratios. The dotted line is the fitted linear model and the dashed line is the fitted quadratic model. The significant model in each plot is shown in bold.

Table 2.18. Bivariate regressions for PC1, PC2 and PC3 (from the soil and leaf carbon, nitrogen and carbon to nitrogen ratio nutrient PCA) as explanatory variables and species richness, total biomass, live biomass and litter as the response variables at the 1 m^2 scale. Form codes are as follows: CD = concave down quadratic model, CU = concave up quadratic model, POS = positive linear model, and NEG = negative linear model. For quadratic models degrees of freedom are 2 on 33 and for linear models are 1 on 34. Non-significant results are left blank.

Explanatory Variable	**Response Variable**	**Form**	**Term 1**		**Term 2**		**Model**		
			t Statistic	*p* Value	*t* Statistic	*p* Value	*F* Statistic	*p* Value	Multiple R^2
PC1	√Species Richness								
	Total Biomass (g) (log10)	POS	5.32	6.62E-06			28.29	6.62E-06	0.45
	Live Biomass (g) (log10)	POS	4.35	1.18E-04			18.90	1.18E-04	0.36
	Litter (g) (log10)	POS	6.57	1.59E-07			43.13	1.59E-07	0.56
PC2	√Species Richness								
	Total Biomass (g) (log10)	NEG	-3.55	1.15E-03			12.61	1.15E-03	0.27
	Live Biomass (g) (log10)	NEG	-3.58	1.07E-03			12.80	1.07E-03	0.27
	Litter (g) (log10)	NEG	-3.17	3.18E-03			10.08	3.18E-03	0.23
PC3	√Species Richness								
	Total Biomass (g) (log10)								
	Live Biomass (g) (log10)								
	Litter (g) (log10)								

At the 1 m^2 scale, soil carbon accounted for 23% of the variation in leaf carbon in a negative linear relationship. Soil nitrogen explained 27% of the variation in leaf nitrogen, also, in a negative linear relationship (Figure 2.25). The explanatory variable soil carbon to nitrogen ratio was able to explain 34% of the variation in leaf carbon to nitrogen ratio and this relationship was positive linear (Table 2.19).

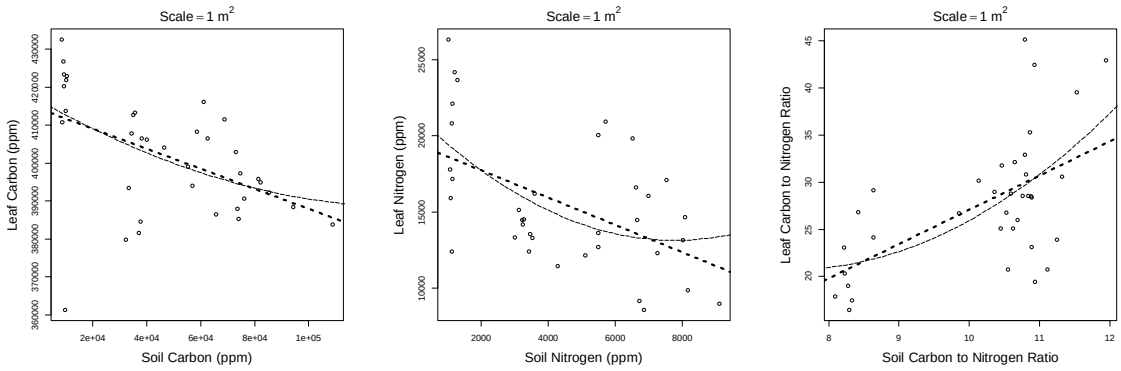

Figure 2.25. Fitted curves from linear regression models at 1 m^2 having leaf carbon as the response variable and soil carbon as the explanatory variable (left panel); leaf nitrogen as the response variable and soil nitrogen as the explanatory variable (center panel), and leaf carbon to nitrogen ratio as the response variable and soil carbon to nitrogen ratio as the explanatory variable (bottom panel). The dotted line is the fitted linear model and the dashed line is the fitted quadratic model. The significant model in each plot is shown in bold.

Table 2.19. Bivariate regressions for soil carbon, nitrogen and carbon to nitrogen ratio as explanatory variables and leaf carbon, nitrogen, and carbon to nitrogen ratio as response variables at the 1 m^2 scale. Form codes are as follows: CD = concave down quadratic model, CU = concave up quadratic model, POS = positive linear model, and NEG = negative linear model. For quadratic models degrees of freedom are 2 on 33 and for linear models are 1 on 34. Non-significant results are left blank.

Variables	**Form**	**Term 1**		**Term 2**		**Model**		
		t Statistic	*p* Value	*t* Statistic	*p* Value	*F* Statistic	*p* Value	Multiple R^2
C (ppm)	NEG	-3.22	2.82E-03			10.36	2.82E-03	0.23
N (ppm)	NEG	-3.57	1.09E-03			12.74	2.85E-11	0.27
C:N	POS	4.19	1.89E-04			17.53	6.79E-28	0.34

DISCUSSION

Study limitations

This work can provide insights into relationships between species richness, productivity, and soil nutrient resources; however, in order to provide a clear context for conclusions, acknowledgment of a few study limitations is necessary before moving on to interpretation of results. Sampling in each grid was conducted only once at, or shortly after, the height of the growing season. The transient nature of spring ephemerals and other species with low biomass, and human error, may have caused some species to be missed during counts. As such species richness has probably been slightly underestimated. Also, samples of litter and live biomass from areas with large bunchgrasses most likely underestimated total biomass, live biomass and litter, because the bases of the large bunchgrasses were not collected (Figure 2.5).

While measurements of total nutrients can reveal broad patterns, it is important to recognize that much of the nutrients in the soil may be present in insoluble forms which are unavailable for plant absorption. Leaves were measured for carbon and nitrogen content; however, roots are known to be a major repository (~90%) of vegetative carbon and nitrogen in grasses (Schuman et al. 1999). Additionally, biomass samples were oven dried at 80 C° for 48 hours before elemental analysis of total carbon and nitrogen which may have caused some of the nitrogen to volatilize in the form of ammonia. Nitrogen volatilization from cut grass can occur at temperatures as low as 10 °C and occurs more rapidly at higher temperatures (Whitehead et al. 1988). Bias may have been introduced into the leaf carbon and nitrogen results because rates of volatilization may depend, in part, on initial concentrations, and potentially on specific characteristics of the vegetation itself.

Plots from the same grid cannot be considered completely independent samples. In many of the regressions with total biomass, live biomass and litter (but not species richness) there were clear groupings of points which likely reflect this lack of independence. In regressions of these response variables with soil carbon to nitrogen ratio, phosphorus, potassium, magnesium and manganese, these groupings were largely missed by fitted curves but

sometimes still returned high R^2 values. Care was taken to assess and report whether fitted lines were actually a good fit to the data as, in these instances, regression analysis is not appropriate.

Generally, it is not considered good practice to compare R^2 values between models with different data transformations or for model selection; however, this rule is usually referred to in the context of model selection where the outcome of dropping one variable from a model is being weighed against its retention. Here, comparison is used only to convey an impression of model fit and not to build complex models. The limitations that accompany aggregation of plots to investigate scale are examined in more detail in the 'Scale' section near the end of the discussion.

Species richness and biomass relationships

The relationship between species richness and total biomass was expected to be unimodal as predicted by the HBM (Al-Mufti et al. 1977, Grime 1979). In the regressions that had total biomass and litter as explanatory variables and species richness as the response variable, the expected unimodal curve was apparent but had relatively low R^2 values both for the full 14-grid dataset and the 4-grid soil dataset. These results are not consistent with the findings of Adler et al. (2011) as they concluded that there was no clear relationship between biomass and species richness at any scale; fine scale, regional, or global. Interestingly, the relationship between live biomass and species richness was consistently negative linear and accounted for very little of the variation in species richness, only as much as 4% at the 1 m^2 scale. This draws attention to the potential difference and importance of the choice to include, or exclude, litter when collecting samples to test the HBM. In this study at the 1 m^2 scale, the form of the significant relationship was different between litter and live biomass in regressions with species richness, the first principal component from the soil nutrient PCA, soil carbon, soil nitrogen, soil phosphorus, and the first principal component from the PCA of all soil nutrients with leaf carbon, leaf nitrogen and leaf carbon to nitrogen ratio. In five out of six of these cases live biomass had significant linear relationships while litter gave significant concave down relationships. Four of the five linear cases for live biomass were positive linear relationships. The case where live biomass produced a negative linear

relationship occurred in regressions with species richness. Total biomass did not consistently take the same form as either live biomass or litter. Thus, litter could be an important component of the productivity proxy in resolving the unimodal curve predicted by the HBM, as pointed out by Fridley et al. (2012), and may explain some of the inconsistencies in the results of different studies, such as those of Adler et al. (2011) and others (e.g. Moore and Keddy 1989, Gough et al. 1994; for meta-analyses see: Mittelbach et al. 2001; Gillman and Wright 2006; Pärtel, Laanisto, and Zobel 2007). Certainly, there is potential for the significant form to differ between including and excluding litter. The results from regressions of total biomass with species richness from this study correspond with others that find support for the HBM (e.g. Al-Mufti et al. 1977, Wheeler and Giller 1982, Walker and Peet 1983, Tilman 1986, Austin 1987, Day et al. 1988, Wilson and Shay 1990, Shipley et al. 1991, Wheeler and Shaw 1991). Where relationships were significant, forms were consistent across increasing scales for both the 14-grid and 4-grid datasets.

Patterns in the PCA of the soil nutrient data were consistent with those that would be expected to coincide with the HBM. The first principal component appeared to represent productivity; regressions with PC1 as the explanatory variable and litter, live biomass and total biomass as the response variables support this observation with strong R^2 values (0.82, 0.67, and 0.76, respectively). Although there is evidence of curvature in the litter and total biomass relationships with PC1, the majority of the fitted curve is fairly straight and the maximum occurs at high values of the PC1 axis (Figure 2.9). It may be that there is proportionally less litter towards the high biomass end of the PC1 axis because of higher decomposition rates and grazing in high productivity sites; this may reduce the build-up of the litter layer in spite of the high level of productivity. In low productivity sites breakdown of litter could be slower because of the drier nature of these sites. In regressions with PC1 as the explanatory variable, the form of the relationship with species richness resulted in a classic humped-shape curve which explained 32% of the variation in the data. Regressions of species richness, total biomass, live biomass and litter with the second principal component indicated that PC2 may represent species richness. Of the response variables, this axis was able to explain a considerable amount, 35%, of variation in species richness with a negative linear relationship (Figure 2.9). This indicates that species richness decreases from

the bottom of the PCA biplot to the top (Figure 2.7). The relationships of the biomass variables with PC2 were all concave up and explained ~20% of the variation in these variables, the lowest R^2 values overall for regressions with both PC1 and PC2. Given that the principal component analysis was based entirely on the nutrient data, the apparent representation of biomass and species richness by PC1 and PC2 emphasizes the innate structuring of herbaceous communities on soil nutrients. Soil resources have impacts on patterns of vegetation and likewise the vegetation that grows feeds back to influence future soil nutrient profiles.

Soil nutrients

Carbon

As predicted, soil carbon explained a high proportion of the variation in both total biomass (72% at 1 m^2) and live biomass (61% at 1 m^2) in positive linear relationships. These findings are in accordance with texts and literature and are intuitive given that greater production results in higher levels of litter being laid down and eventually incorporated into the soil. This leads to greater soil organic carbon (and nitrogen) which in turn has many benefits for plant growth including soil moisture retention, ion exchange capacity, and slow release of nutrients (Batjes 1996, Brady and Weil 1996, Wolkovich et al. 2010). Soil carbon was strongly related to litter (80% at 1 m^2) in a concave down curve; however, the maximum of this curve did not occur inside the range of the data and the fitted curve is more or less linear for the majority of its range (Figure 2.10). Still, it appears that the increasing curvature at high litter levels with increasing soil carbon is a reflection of greater heterogeneity in soil carbon at high productivity levels which results in elongation of the cloud points of litter values along the soil carbon axis.

Soil nutrients are not homogenously distributed through space. Different species have different nutrient requirements so soil nutrient heterogeneity is important to species richness (Willems et al. 1993, Janssens et al. 1998, Aarssen 2001). Increased heterogeneity of environmental conditions is also thought to contribute to increased productivity (Šímová et al. 2013). Heterogeneity has been suggested to play a role in the scale dependence of the species richness productivity relationship because the degree of environmental heterogeneity

often varies with scale (Chesson 1998, Chase and Leibold 2002, Chalcraft et al. 2004). In small plots the distribution of soil nutrients is likely to be relatively homogenous, however, large plots are more likely to capture spatial heterogeneity by including patches with various nutrient quantities. At large scales species turnover and richness increase because of the aggregation of different patches of resources. So far, studies evaluating the effect of heterogeneity on species richness and productivity have produced mixed results (Šímová et al. 2013). Newman (1973) and Tilman (1988) state that heterogeneity varies in a humped-shape pattern across habitats of increasing fertility. Perhaps, the curve detected at the extent of the biomass range in this study (~1850 g/m^2) is indicative of a humped-shape relationship in soil heterogeneity with increasing soil nutrients.

In the distance biplot of PC1 and PC2 from the soil nutrients PCA, soil carbon was indicated to be an important variable as it contributed more than average to the ordination space. As predicted, soil carbon was tightly grouped with soil nitrogen indicating a positive correlation between these two soil nutrients; soil phosphorus was also in close proximity. This is logical because soil nitrogen and soil phosphorus are both commonly limiting nutrients and they, like carbon, are tightly linked to biomass production. Plant available nitrogen and the composition of soil organic matter are key factors in nutrient cycling rates and primary productivity (Brady and Weil 1996). The patterns shown for soil carbon, soil nitrogen, soil phosphorus and soil potassium in the soil nutrient PCA are consistent with those expected to coincide with the HBM as PC1 seems to represent productivity, PC2 seems to represent inverted species richness, and soil carbon, soil nitrogen, soil phosphorus, and soil potassium are oriented towards the high productivity end of PC1.

Soil carbon produced a concave down relationship in the regression with species richness as the response variable at the 1 m^2 scale, as predicted. Although this relationship was (perhaps) somewhat weaker than expected, explaining only 15% of the variation in species richness, this concave down relationship had a clear maximum in the midrange of soil carbon values and was quite curved, producing a unimodal curve as expected to coincide with the HBM.

In regressions at the 1 m^2 scale, carbon always explained over 60% of the variation in total biomass, live biomass and litter. With increasing scale these relationships were consistently positive linear for total biomass and live biomass up to 16 m^2 and went from being concave down to positive linear for litter between 2 m^2 and 4 m^2. The minimum amount of variation in species richness that was explained by soil carbon was 15%; these relationships were consistently concave down at scales increasing up to 4 m^2 and were insignificant at greater scales. No significant relationships were found at the 64 m^2 scale for regressions with any of the nutrients with only one exception (potassium) which will be discussed in due course. These results correspond well with the observation by Waide et al. (1999) that unimodal relationships commonly occur across community boundaries or when plots are from multiple community types.

Nitrogen

The prediction that soil nitrogen would positively relate to total biomass and live biomass was supported as was the expectation that species richness would be related to soil nitrogen by a unimodal curve. At all scales, patterns that emerged for soil nitrogen were identical to those of soil carbon; the values of individual results were also extremely similar. This supports the prediction that soil carbon and nitrogen would be highly positively correlated and could be expected because of the role of soil nitrogen in plant growth that causes it to be tightly associated with biomass production and, therefore, also highly correlated to soil carbon in natural systems. The strong positive correlation between soil nitrogen and biomass variables suggests that nitrogen probably is limiting in these study sites. Litter produced a curved relationship with soil nitrogen (as it did with carbon) where a positive linear one was expected. The explanation for this follows the same logic as for the curved relationship between litter and soil carbon. Soil nitrogen patterns were consistent with those expected to coincide with the HBM, results from the Rothemsted Park Grass experiment (Crawley et al. 2005) and other literature (Kirchner 1977, Goldberg and Miller 1990, Bobbink 1991, Wilson and Tilman 1993, Chapin et al. 1995, Wedin and Tilman 1996, Gough et al. 2000, Baer et al. 2003, Cornwell and Grubb 2003).

Soil carbon to nitrogen ratio

At the 1 m^2 scale, soil carbon to nitrogen ratio was not related to total biomass, live biomass and litter by a positive linear relationship as was expected to coincide with the HBM; instead, a significant concave down curve resulted explaining 29%, 20% and 42% of the variation respectively. As predicted, and in accordance with the HBM, soil carbon to nitrogen ratio was related to species richness by a concave down curve and explained a similar amount of the variation in the data (24% at 1 m^2) to regressions between soil carbon to nitrogen ratio and productivity variables; however, this fitted line appears to be a more true fit of the data than the fitted lines from regressions with biomass variables (Figure 2.12). Although results for soil carbon, nitrogen and carbon to nitrogen ratio were not completely predicted, they do not contradict information presented by Brady and Weil (1996) or Chapin et al. (1993). With increasing scale the concave down forms became positive linear for all variables (species richness, total biomass, live biomass and litter). In the PCA of all soil nutrients and leaf nutrients, soil carbon to nitrogen ratio aligned well with PC1 which seemed to represent productivity and was perpendicular to PC2 which seems to represent inverted species richness.

Given the similarity of the soil carbon and nitrogen regression results and the closeness of these nutrients in the PCA biplots, it was interesting that the form of relationships between soil carbon and nitrogen in regressions with the productivity variables varied from those of soil carbon to nitrogen ratio in regressions with the productivity variables. With total and live biomass, soil carbon and nitrogen gave positive linear forms as opposed to concave down forms produced in regressions with soil carbon to nitrogen ratio. At the 1 m^2 scale, soil carbon and nitrogen explained more of the variation in the productivity variables, between 61% - 81% compared to between 20% - 42%, explained by soil carbon to nitrogen ratio.

Phosphorus

Soil phosphorus was predicted to have a positive linear relationship with productivity variables because it is the second most commonly limiting nutrient in natural systems and is often tightly linked to biomass production. This hypothesis was supported for live biomass

at the 1 m^2, 2 m^2 and 4 m^2 scales; however, this hypothesis was not supported at the 1 m^2 scale for total biomass or at the 1 m^2 and 2 m^2 scales for litter where concave down forms were significant. Maxima for these curves were also at the end of the range of measured values and increasing productivity was associated with an increase in the variation of soil phosphorus. Again, an expected humped-shape relationship in soil heterogeneity as predicted by the environmental heterogeneity hypothesis (Newman 1973, Tilman 1988) may help to explain this observation, as in the cases of soil carbon and nitrogen. For total biomass and litter at the 2 m^2 and 4 m^2 and at the 4 m^2 and 16 m^2 scales, respectively, the relationship became positive linear, corresponding with predictions, and was not significant at larger scales.

Although the concave down curve between litter and soil phosphorus gave relatively strong R^2 values, it was a poor fit to the data; the fitted line for soil phosphorus and species richness also gave similar R^2 values and appears to be a more true fit of the data (Figure 2.13). The prediction that soil phosphorus would show a concave down relationship with species richness, as predicted by the HBM and as found by Janssens et al. (1998), was not supported; nor was the somewhat commonly reported negative linear relationship found (Janssens et al. 1998, Venterink et al. 2001, Lambers et al. 2010). In regressions between soil phosphorus and species richness a positive linear form was evident from 1 m^2 - 16 m^2. Although our results do not support previous studies, it is quite difficult to draw conclusions based on total phosphorus measurements or to compare them with studies based on extractable phosphorus given that only ~0.01% of the total phosphorus present in soils is actually available for use by plants.

Measuring plant available phosphorus in the soil would likely have been more telling in terms of the questions raised in this study. It could be that other nutrients, such as nitrogen, are more limiting and phosphorus therefore exerts little control over vegetation dynamics such as productivity and species richness in this system. Or maybe phosphorus is relatively limiting and sampling a greater range of biomass would reveal that the pattern observed here is only the increasing phase of a humped-shape relationship between phosphorus and species richness. Because insoluble precipitates form when iron and phosphate interact (Dalton et al. 1983) the orientation of phosphorus in the opposite direction of iron in the soil nutrient PCA

may be an indication that phosphorus is not readily available, especially at lower productivity levels, and provide some support for the latter suggestion. As it is, results do not fully correspond with those expected to coincide with the HBM.

Potassium

It was predicted that soil potassium may show a positive linear relationship with biomass variables because it is the third most commonly limiting nutrient in natural systems and, like soil phosphorus and nitrogen, is often tightly correlated with biomass production. This hypothesis was not supported at the 1 m^2 scale for live biomass or at the 1 m^2 or 2 m^2 scales for total biomass and litter where the form of relationship was concave up. The relationship became positive linear, as predicted by the HBM, only at intermediate scales (2 m^2 - 4 m^2).

The regressions between potassium and litter were not significant at 16 m^2 but showed a significant concave up curve at the 64 m^2 scale and returned a perfect R^2 value of 1.00 (Table 2.10). This is very likely a spurious result of fitting regression lines to only four data points. The figures of fitted regression lines for soil potassium and litter across scales support this conclusion (Figure G.5).

Potassium was predicted to potentially show a humped-shape curve with species richness in accordance with the HBM because of its potential positive linear relationship with productivity variables. This hypothesis was not supported as regressions between soil potassium and species richness were consistently negative linear in form at the 1 m^2, 2 m^2 and 4 m^2 scales.

Although regressions of soil potassium with productivity variables gave stronger R^2 values than regressions with species richness, the fitted lines were a poor fit for two groups of points, one at low and one at high productivity, that were scattered over the lower half of the range of soil potassium values. The fitted lines from regressions of soil potassium and species richness were a more convincing fit to the data points (Figure 2.14).

Given that soil potassium normally has less influence over community diversity than soil phosphorus (because it is usually less limiting) and that in this system either phosphorus is

limiting over a wider range of biomass than was sampled or is not as limiting as nitrogen and therefore is not limiting enough to exert control over diversity, it is unlikely that potassium exerts strong control over vegetation dynamics such as productivity and species richness in the study area. Like phosphorus, in the soil nutrient PCA potassium was aligned slightly better with PC2 than with PC1 and was oriented towards the high biomass end of PC1 but towards the low species richness end of PC2. This may provide some support that the regressions between species richness and soil potassium are a more true fit to the data than those with total biomass, live biomass and litter.

Boron

Soil boron explained high levels of variation in live biomass, a minimum of 52%, in a concave down curve at 1 m^2, 2 m^2, and 4 m^2 scales and in a positive linear relationship at 16 m^2; and explained moderate levels of the variation in total biomass and litter. Soils that have less than 10 ppm are considered to be low in soil boron and those with greater levels, high in soil boron (Power and Woods 1997). Powers and Woods were not clear as to whether 10 ppm referred to total or available boron but they do state that most soils are low in boron and that high soil boron tends to be the result of volcanic activity. It is interesting that all plots with soil boron levels greater than ~11 ppm had high values for productivity variables, though, conclusions are difficult to draw because they are also all from the same grid. A minimum of 15% of the variation in species richness was explained by soil boron and the form of the relationship switched from being concave up at 1 m^2 and 2 m^2 to negative linear at the 4 m^2 scale. In the PCA of the soil nutrients soil boron was about equally aligned with PC1 and PC2 and oriented towards the high productivity end of PC1 and the low species richness end of PC2.

Iron

Relationships between soil iron and total biomass, live biomass and litter were very strong, accounting for at least 79% of variation at the 1 m^2 scale with concave up relationships. This form was apparent across scales up to 16 m^2, with the exception of litter in which case the form of relationship switched from concave up to negative linear at the 16 m^2 scale.

Additionally, for litter, unlike for total biomass and live biomass, the minima of the concave up curves did not occur within the range of the data. Soil iron was also able to explain a considerable amount of the variation in species richness, a minimum of 29%, and concave down relationships emerged across scales up to 16 m^2; in this case there was a clear maximum nearly in the center of the range of data (Figure 2.16).

The plots that had the greatest concentrations of iron also had the lowest concentrations of soil phosphorus and the lowest levels of total biomass, live biomass, and litter. Although iron toxicity is not certain, the results of the current study do not contradict those of Ward et al. (2008) which showed that when soil phosphorus is deficient (because there was very little to begin with or due to the formation of precipitates with iron) there is greater incidence of iron toxicity. In the correlation biplot of the soil nutrient PCA, iron, carbon, and nitrogen were slightly more aligned with PC1 than PC2, and phosphorus was oriented towards the high productivity end of PC1. Iron was oriented in the opposite direction from the others, indicating negative correlation between iron and these soil nutrients. Productivity decreases and species richness is unimodal with increasing soil iron concentrations suggesting that decreasing soil iron concentrations could also potentially be substituted for increasing productivity variables in the HBM.

Magnesium

There were no initial predictions about what patterns of soil magnesium should coincide with the HBM. The relationships between soil magnesium and total biomass and litter were concave up at scales of 4 m^2 or smaller and explained 10% of the variation or less at the 1 m^2 scale. The concave up relationship with live biomass switched to positive linear at the 2 m^2 scale. Relationships between soil magnesium and species richness were also concave up and were considerably stronger, explaining 49% of the variation in the data at the 1 m^2 scale. Fitted lines for species richness were also a truer fit to the data than fitted lines for magnesium with the productivity variables. Over most of the measured range of soil magnesium, increasing magnesium was associated with decreasing species richness, but there does appear to be a slight increase in species richness at the high end of the range (Figure 2.17). The soil nutrient PCA is in agreement with the regression findings as magnesium was

fairly well aligned with PC2 and oriented in the direction that corresponds with lower species richness and very slightly oriented towards the high productivity side of PC1. Given that magnesium is commonly added as a liming agent along with calcium, and that one of the main reasons to limit soil acidity through liming is to prevent aluminum and manganese toxicity (Brady and Weil 1996), it makes sense that magnesium is oriented in the opposite direction to soil aluminum and manganese in the PCA of soil nutrients (Figure 2.8). In terms of the HBM, if one presumes causation (which may not be the case) it seems that variation in soil magnesium has the potential to influence the height of the unimodal curve such that high magnesium corresponds with lower species richness.

Manganese

There were no a priori assumptions about what patterns in soil manganese should coincide with the HBM. Soil manganese explained fairly little of the variation in the total biomass, live biomass and litter, as much as 12% at the 1 m^2 and 2 m^2 scales, after which relationships became insignificant. These relationships were all concave up except for with litter at the 2 m^2 scale which was positive linear; generally the fitted lines for these relationships went between an upper and a lower cloud of points (Figure 2.18). Fitted lines for regressions between manganese and species richness were a truer fit to the data. Relationships between soil manganese and species richness were all positive linear at scales up to 16 m^2 and gave higher R^2 values than relationships with the productivity variables explaining 25% of the variation in the data at the 1 m^2 scale. The PCA of the nutrient data also reflected this pattern as manganese was nearly parallel to PC2, oriented in the direction of higher species richness and away from soil magnesium. It appears that soil manganese may also have the potential to influence the height of the unimodal curve such that high manganese corresponds with high species richness.

Leaf nutrients

Leaf carbon and nitrogen content were predicted to increase with increasing productivity and with increasing soil nitrogen and carbon content due to increasing soil fertility and turnover of species. This prediction was not supported by the regressions of leaf carbon with soil carbon, and leaf nitrogen with soil nitrogen, as leaf carbon and nitrogen decreased with

increasing productivity (soil carbon and nitrogen were positively correlated with productivity, and leaf carbon and nitrogen decreased with increasing soil carbon and nitrogen). These results contradicted those of Wedin and Tilman (1996) and Poorter et al. (1990) as well as information reviewed by Chapin (1980). The PCA of the leaf nutrients with all soil nutrients did not support this prediction either, as leaf carbon and nitrogen were oriented away from soil carbon and nitrogen and in the direction of low productivity on the PC1 axis. Leaf nitrogen and carbon were also oriented in the direction of lower species richness on the PC2 axis. Leaf carbon to nitrogen ratio was oriented almost exactly in the opposite direction of leaf carbon and leaf nitrogen content which were tightly grouped indicating they are highly positively correlated, as predicted. The PCA of only leaf carbon, nitrogen and carbon to nitrogen ratio with soil carbon, nitrogen and carbon to nitrogen ratio also supported the prediction that leaf carbon and nitrogen content would be highly positively correlated as these variables were tightly grouped in the correlation biplot of PC1 and PC2; however, the prediction that leaf carbon to nitrogen ratio would be negatively related to soil carbon to nitrogen ratio and productivity was not supported. Instead, a positive linear relationship was found. The simplest explanation for the discrepancies between my results and predictions for leaf carbon, nitrogen and carbon to nitrogen ratio is that oven-drying the biomass prior to elemental analysis caused some of the nitrogen to volatilize from samples at varying rates based on plant characteristics and initial nitrogen concentrations.

The results of regressions with the axes of the soil nutrient PCA with leaf nitrogen, carbon and carbon to nitrogen ratio showed similar patterns to that of the PCA of only soil nutrients. Again the first principal component seemed to represent productivity as, in regressions, PC1 was able to explain over 71% of the variation in the productivity variables. A positive linear relationship explained 76% of the variation in litter. The significant concave up curves that occurred for total biomass and live biomass had minimums well within the first half of the range of PC1 so that over the majority of the plot the fitted line is increasing. Regressions with PC1 and species richness did not return significant relationships; however, with PC2, a negative linear relationship emerged accounting for 34% of the variation in the data. Unlike the soil nutrient PCA, the second principal component explained similar amounts of the variation the productivity variables to species richness with concave up curves. The

similarity between patterns found in the PCA of soil nutrients and the PCA with leaf carbon, nitrogen, carbon to nitrogen ratio and soil nutrients is not surprising since the majority of the input data is the same. Differences likely arise more because of the difference in the number of plots that were sampled and less due to contributions by leaf nutrients and leaf carbon to nitrogen ratio. Again, the apparent representation of productivity by PC1 and of species richness by PC2, in combination with the strengths and forms of relationships that occurred in the regressions, indicates that there are patterns (structure) in the soil nutrients that align with those expected to coincide with the HBM.

Scale

Assessment of the prediction that increasing scale would weaken and potentially break the unimodal relationship between species richness and productivity was inconclusive. Multiple R^2 values often increased at larger scales, suggesting better model fit. In opposition, significant relationships often went from curved forms to linear forms before becoming insignificant at the largest scales. This pattern probably does not reflect a real pattern that exists in nature; instead, it is likely attributable to decreasing sample size with increasing scale of investigation. The reduction in the number of degrees of freedom results in larger *p* values, and therefore fewer significant results, at large scales. One less parameter is estimated (allowing one more degree of freedom) in a linear model than in a quadratic model which may explain why the models selected tended to switch from quadratic to linear before becoming insignificant.

Objective three, as stated in the introduction, cannot be adequately addressed with this dataset; however, the regularity with which concave curves became linear relationships before becoming insignificant draws attention to an interesting possibility. Perhaps a cause of the positive linear forms often reported in the literature at large scales (Pianka 1966, Currie 1991, Chase and Leibold 2002) is, in part, that studies at large scales typically have fewer samples than those at small scales. This results in loss of power to distinguish relationships rather than detection of a change in the relationship itself.

Summary

Species richness was related to total biomass with a unimodal curve as predicted by the HBM. Soil nutrients relating strongly to productivity included carbon, nitrogen and iron and related to species richness as would be expected to coincide with the HBM. Soil phosphorus and potassium had less clear relationships potentially because nitrogen exerts more control over community structure as it may be more limiting in this system. Leaf nitrogen and carbon were negatively related to productivity, counter to expectations, but this was probably due to nitrogen volatilization prior to elemental analysis. Soil magnesium and manganese had opposite relationships with species richness such that high magnesium corresponded to low species richness and high manganese corresponded with high species richness. It is possible that these nutrients contribute to determination of the height of the species richness curve. Regression analyses and principal component analyses were in consistent agreement. The principal component analyses based on soil nutrients revealed biomass and species richness as the first two axes, indicating strong connections between community species richness-productivity dynamics and soil nutrient resources. Regressions between species richness, total biomass, and live biomass, and between species richness and the first two principal components, were also in broad agreement with the HBM. It appeared that relationships were breaking down with increasing scales but this was attributable in large part to a reduction in degrees of freedom with plot aggregation at larger scales. It was not possible to resolve scale relationships within the limitations of the study design; however, it became apparent that the emergence of positive linear relationships in the literature for studies at larger scales may be partially due to smaller sample sizes.

CHAPTER 3: CONCLUSION

Context and general findings

Biodiversity is crucial to ecosystem functioning because of its control of ecological processes; so much so, that the study of biodiversity in ecosystem function has become a field of research unto itself (Cardinale et al. 2011). Interest in this area of work has been driven by the massive, global, unprecedented losses of biological diversity in recent decades, and by the dependence of people on biodiversity for the ecosystem services it provides. The vegetation in plant communities acts as the base of the entire food web and feeds back to influence the environment by contributing to soil formation and nutrient levels. A systems' level of biodiversity determines how effectively nutrients and other limiting resources (e.g. light, water) are transmitted into biomass and the extent to which ecosystem services may be provided (Cardinale et al. 2011).

Species diversity has an important role in determining the functioning of ecosystems as a whole because the characteristics of individual species influence what processes occur and to what extent (Chapin et al. 2000). Higher levels of biodiversity usually result in greater ecosystem stability and can support greater diversity at higher trophic levels (Haddad et al. 2001). In the face of continuously intensifying land use, maintaining high diversity of species and representation of different functional groups is necessary to preserve ecosystem function (Loreau et al. 2001).

The patterns found in this study are in line with what was already known, that species richness, primary productivity and resource availability are closely connected in natural communities. The relationship between species richness and total biomass in these study sites is unimodal as predicted by the HBM; however, given the wealth of other research on the subject, this finding does not contribute significantly towards resolving the debate surrounding the model. Nutrients such as carbon and nitrogen were strongly positively related to productivity and also showed humped-shape relationships with species richness. These results were also expected and do not advance science notably. Magnesium, manganese, and phosphorus appeared to correlate more with the height of the species

richness curve, and these findings present interesting opportunities for future research. In spite of effort to isolate the influence of scale on the relationship between species richness and productivity, this work has not helped to clarify the forms associated with specific scales. Alternatively, it suggests that some of the confusion surrounding scale in the literature may be related to sample size. Conclusions about the HBM, the role of soil nutrient resources in structuring communities, and the scales at which these relationships apply, have important implications for ecology and management and there are several directions future research could take.

Management implications

On many landscapes, people have the power to affect disturbance, productivity, and land use, all of which are among the most influential drivers of global loss of species richness (Sala et al. 2000). As such, studies looking at nutrient resources in relation to species richness and productivity have important messages for management efforts. Knowledge of the importance of species diversity and how different levels of disturbance (such as cattle grazing) can influence species numbers, gives the ability to optimize agriculture and species richness. The same is true of fertilizer application with regards to species richness; some can be beneficial, but driving lands to be very highly productive will likely come at a cost to biodiversity. These lessons extend to conservation and reclamation as well. Preserving biodiversity to keep ecosystem services is a major goal of conservation and an understanding of what combination of conditions will promote high levels of species richness continues to be fundamental in directing efforts to conserve species and in restoration of damaged habitats.

Future directions

As with all research, the work presented here began by building on a foundation of numerous previous studies and ends by drawing attention to several areas for future work. Because up to 90% of vegetation in temperate grasslands occurs below ground in the form of roots rhizomes and shoot-bases (Pärtel et al. 2012) and because roots are the repository of the majority (~90%) of vegetative carbon and nitrogen in grasses (Schuman et al. 1999), studies investigating the below ground species richness, root-biomass and root-nutrient content will continue to provide further evaluations of the extent to which the HBM applies. Future work

of this type should also focus on the amount of plant available nutrients as well as total nutrients present in the soil. This would help to resolve the amount of nutrients actually available for plant uptake and conversion into biomass versus the amount that may be trapped in insoluble forms or released slowly over time. Collection of additional information such as soil pH would also be advisable as pH holds strong influence over availability of soil nutrients. Manipulative nutrient addition experiments investigating the influence of magnesium and manganese on species richness would be useful to determine the role these nutrients have in determining diversity. To address the problems of independence and replication with regard to the investigation of scale, work should be done in which there is high replication of independent soil nutrient, biomass and species richness sampling. In doing this, care should be taken to keep sample size equal and adequate between each scale investigated. Lastly, because sample size may be playing an important role in the form of relationships that have been found in studies conducted at different scales, a meta-analysis looking into the type of pattern resolved with respect to both scale and sample number could be a significant step in explaining discrepancies in the literature.

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APPENDIX A: MORAN'S I CORRELOGRAMS

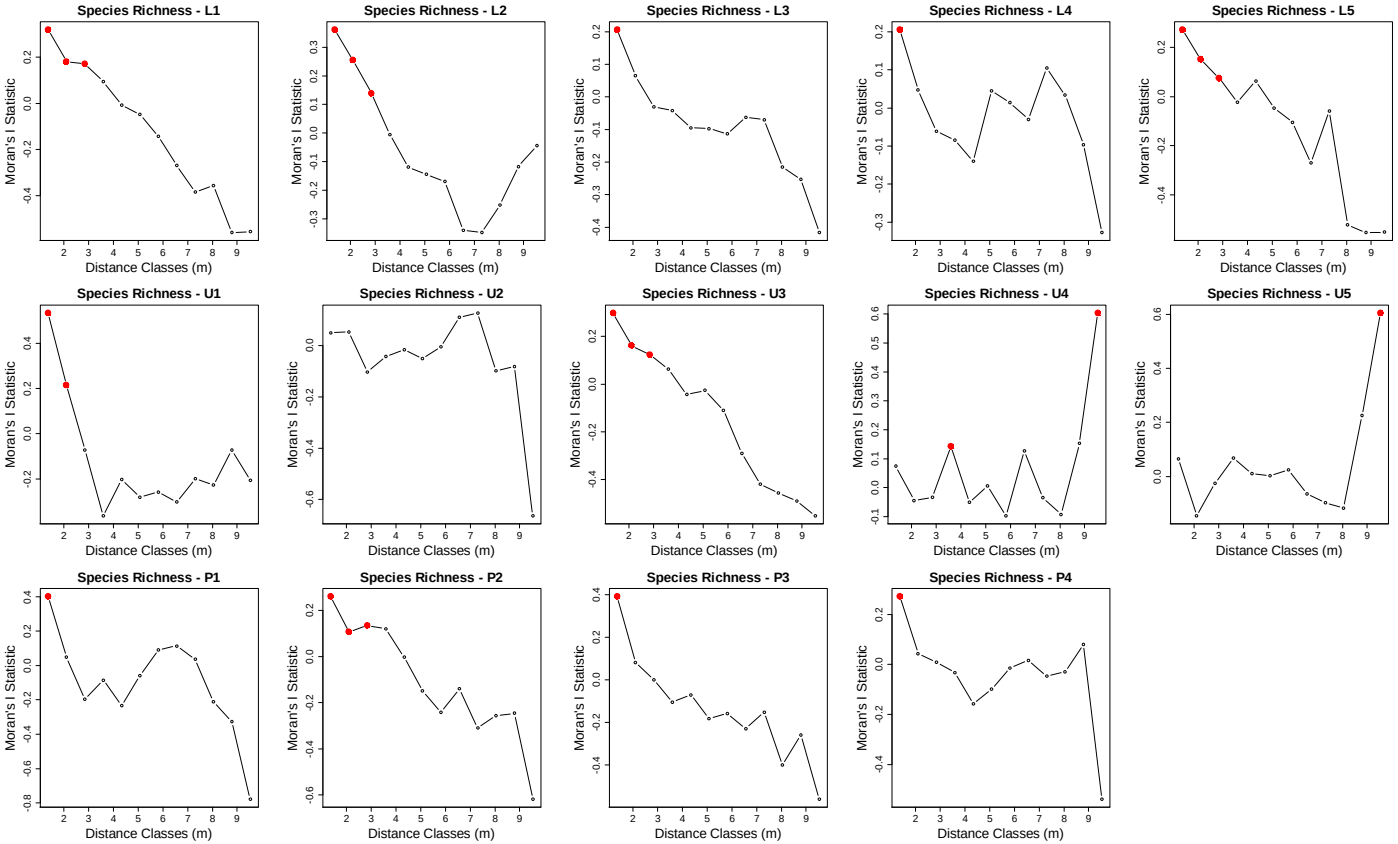


Figure A.1. Correlograms of Moran's I Statistic plotted against distance classes for species richness in each grid. Red filled points indicate significant correlation, hollow points indicate non-significant values.

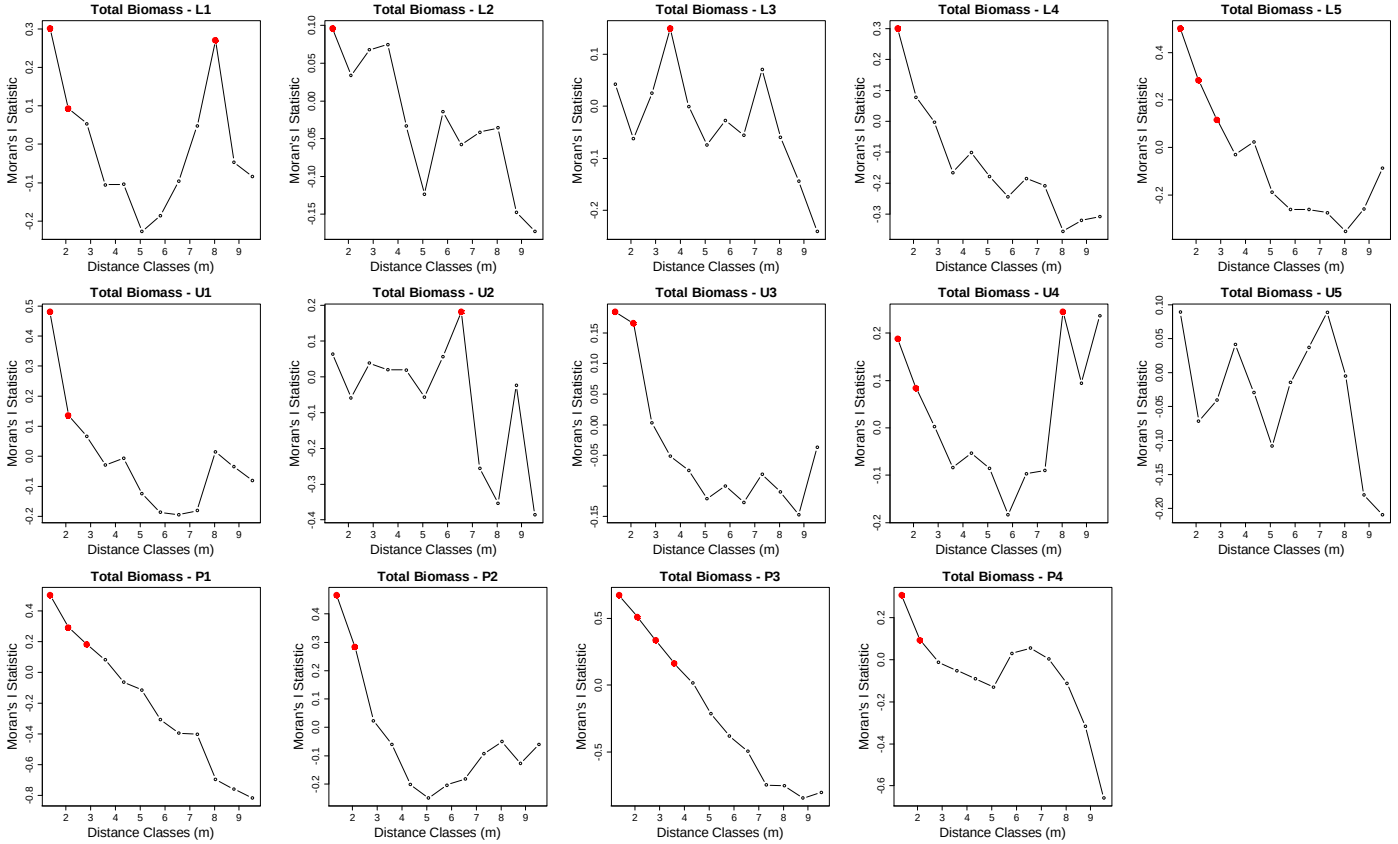


Figure A.2. Correlograms of Moran's I Statistic plotted against distance classes for total biomass in each grid. Red filled points indicate significant correlation, hollow points indicate non-significant values.

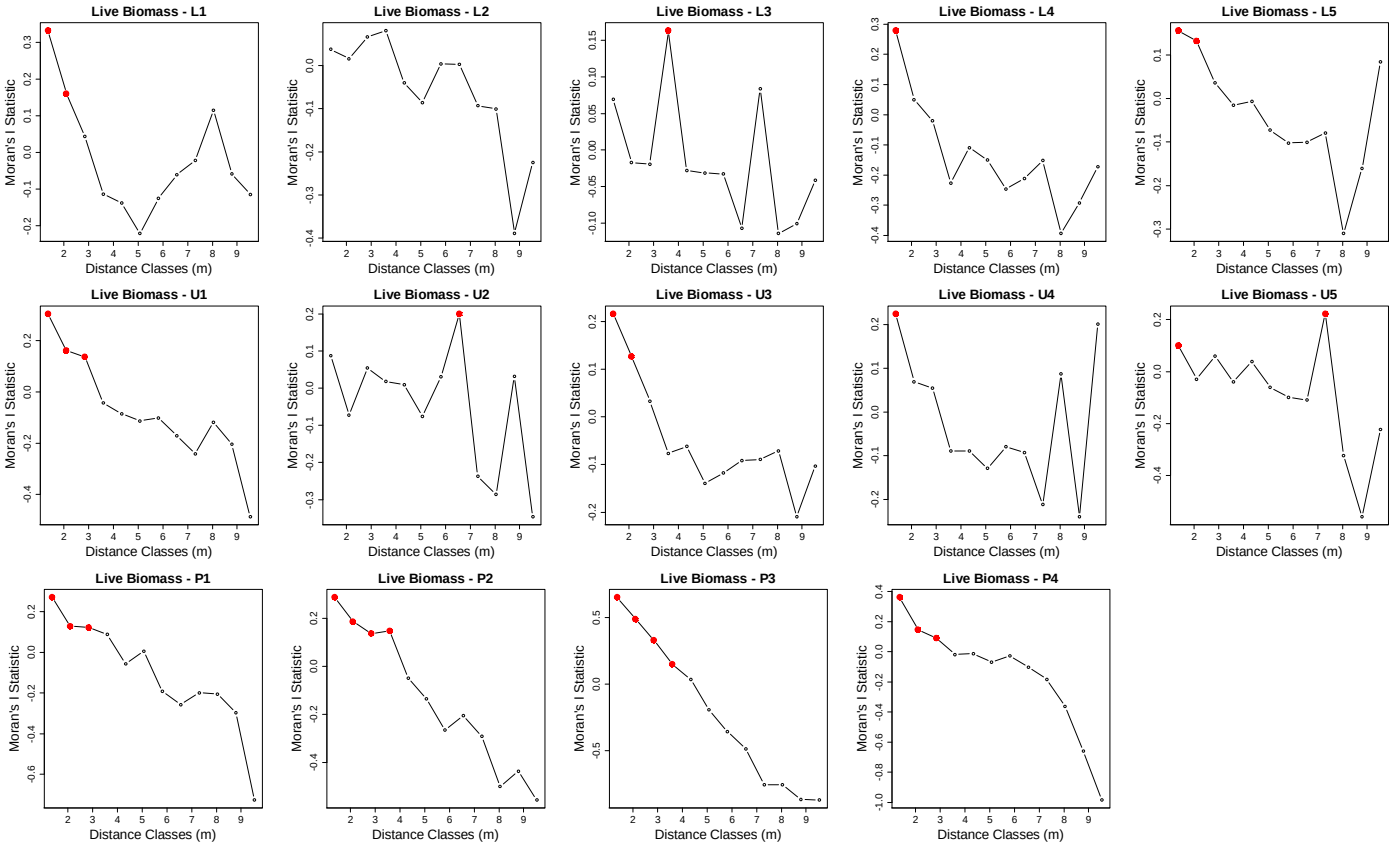


Figure A.3. Correlograms of Moran's I Statistic plotted against distance classes for live biomass in each grid. Red filled points indicate significant correlation, hollow points indicate non-significant values.

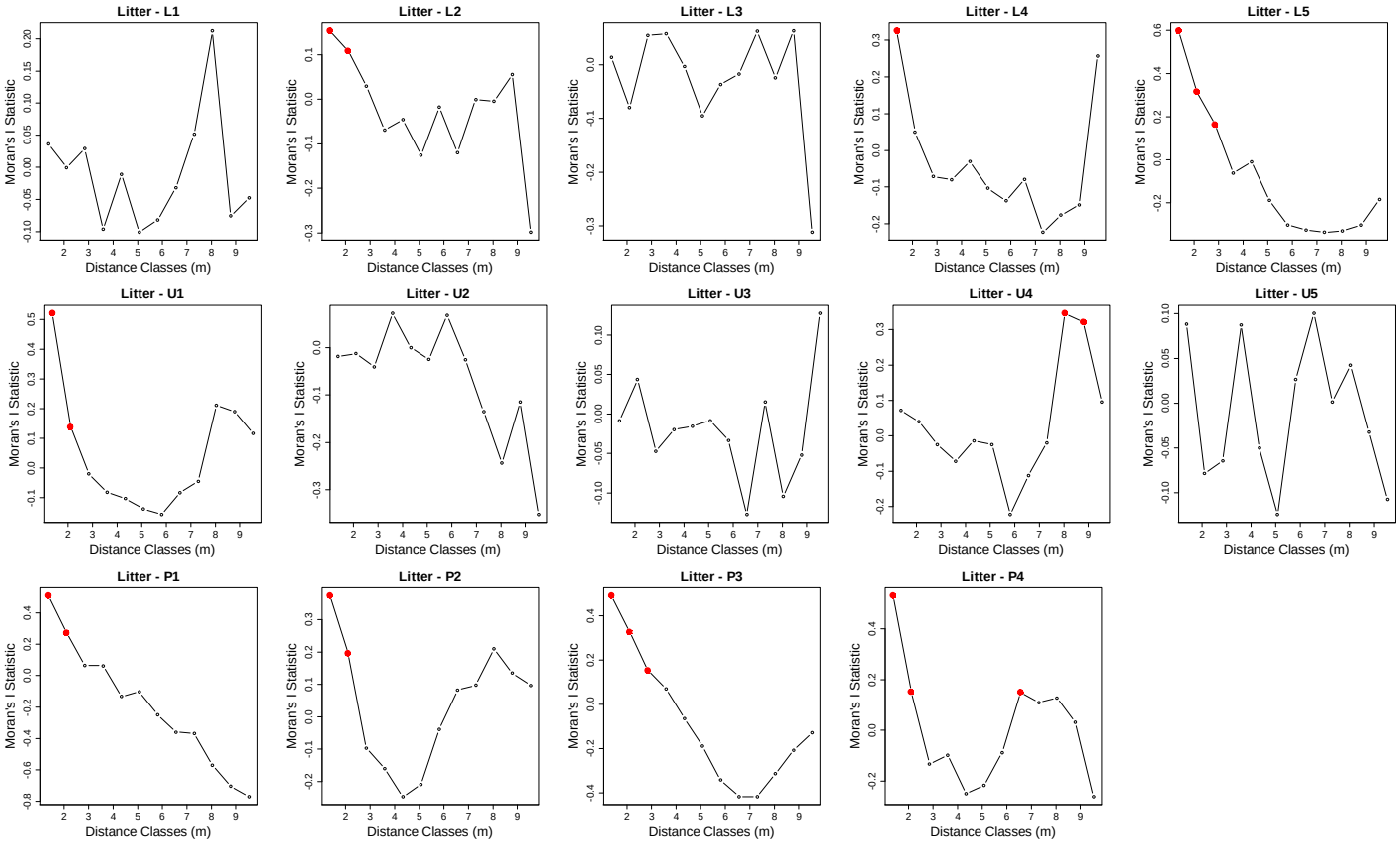
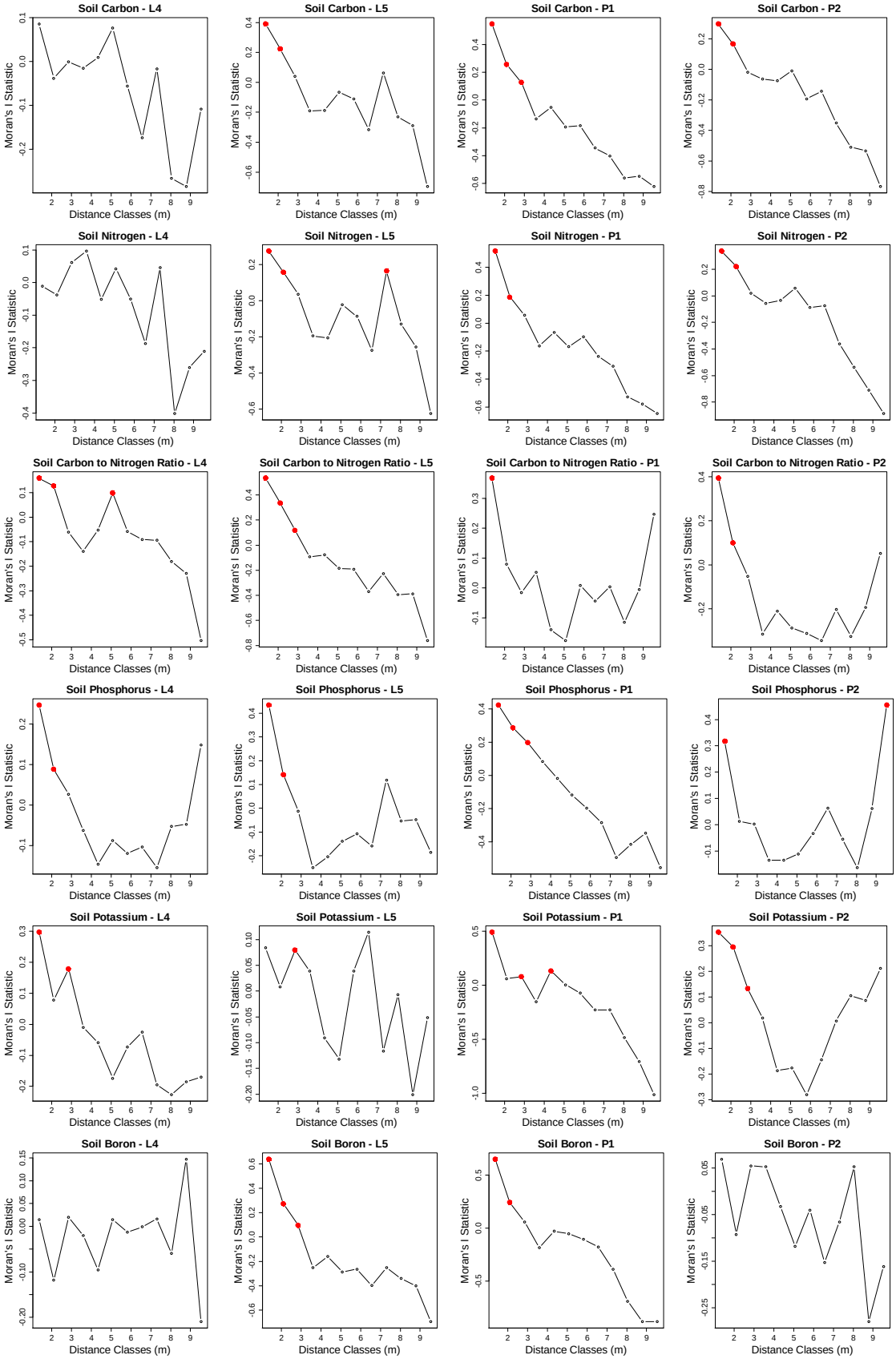


Figure A.4. Correlograms of Moran's I Statistic plotted against distance classes for litter in each grid. Red filled points indicate significant correlation, hollow points indicate non-significant values.


Soil Carbon - L4
Soil Carbon - L5
Soil Carbon - P1
Soil Carbon - P2
Soil Nitrogen - L4
Soil Nitrogen - L5
Soil Nitrogen - P1
Soil Nitrogen - P2
Soil Carbon to Nitrogen Ratio - L4
Soil Carbon to Nitrogen Ratio - L5
Soil Carbon to Nitrogen Ratio - P1
Soil Carbon to Nitrogen Ratio - P2
Soil Phosphorus - L4
Soil Phosphorus - L5
Soil Phosphorus - P1
Soil Phosphorus - P2
Soil Potassium - L4
Soil Potassium - L5
Soil Potassium - P1
Soil Potassium - P2
Soil Boron - L4
Soil Boron - L5
Soil Boron - P1
Soil Boron - P2
Moran's I Statistic
Distance Classes (m)

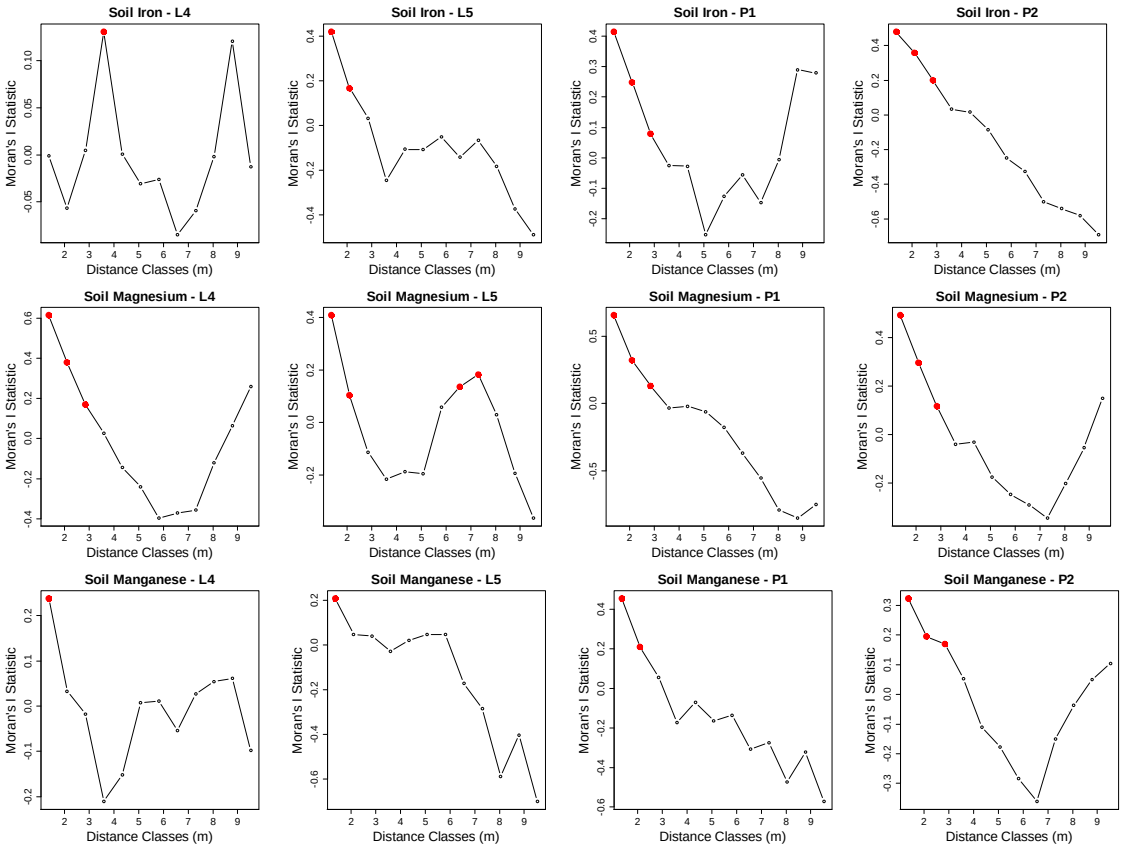
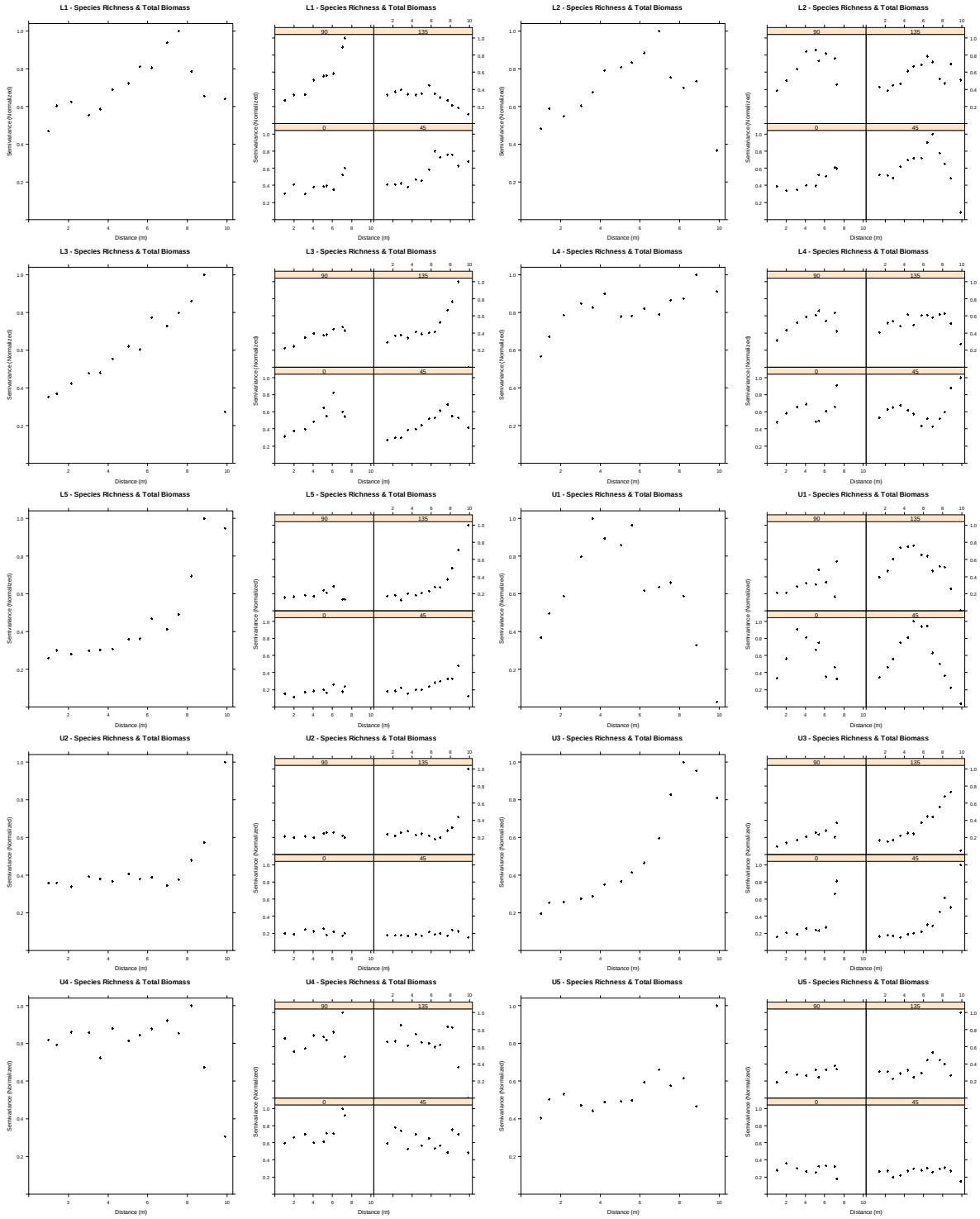


Figure A.5. Correlograms of Moran's I Statistic plotted against distance classes for soil nutrients for each grid that had soil samples taken. Carbon (row 1), nitrogen (row 2), carbon to nitrogen ratio (row 3), phosphorus (row 4), potassium (row 5), boron (row 6), iron (row 7), magnesium (row 8) and manganese (row 9). Red filled points indicate significant correlation, hollow points indicate non-significant values.

APPENDIX B: SEMI-VARIOGRAMS



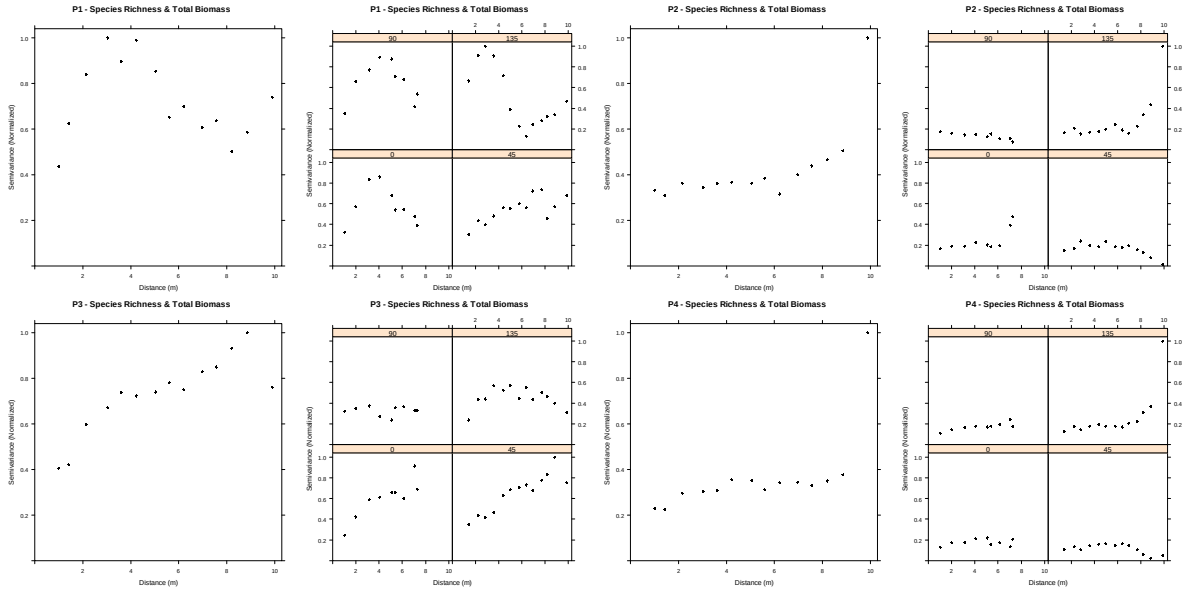
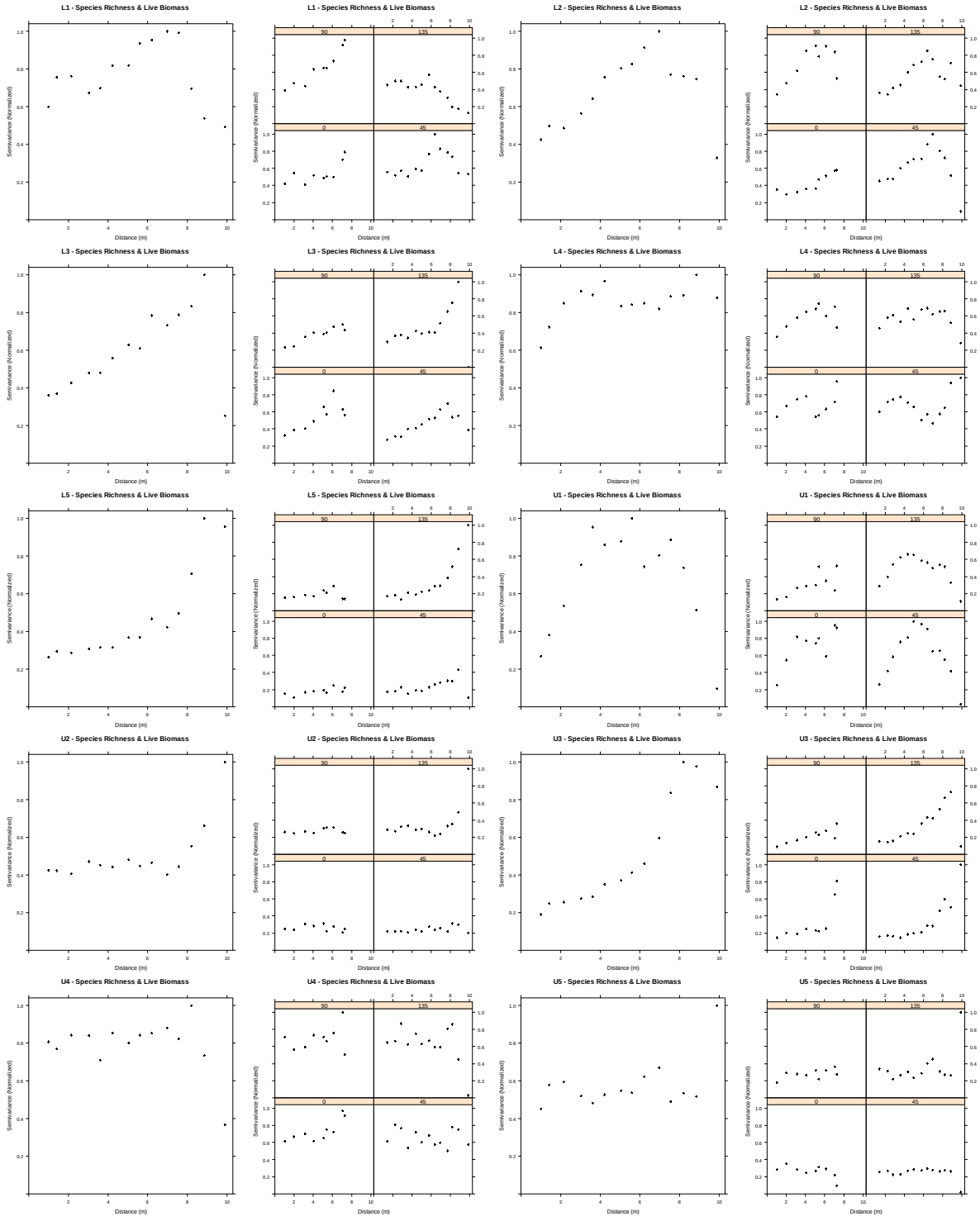


Figure B.1. Normalized semi-variograms of the standardized residuals computed for linear regressions, with square root transformed species richness as the response variable and log transformed total biomass as the explanatory variable, for each grid (L1-5, U1-5, P1-4). The second and fourth columns show directional semi-variograms at 0, 45, 90, and 135º.


L1 - Species Richness & Live Biomass
L1 - Species Richness & Live Biomass
L2 - Species Richness & Live Biomass
L2 - Species Richness & Live Biomass
L3 - Species Richness & Live Biomass
L3 - Species Richness & Live Biomass
L4 - Species Richness & Live Biomass
L4 - Species Richness & Live Biomass
L5 - Species Richness & Live Biomass
L5 - Species Richness & Live Biomass
U1 - Species Richness & Live Biomass
U1 - Species Richness & Live Biomass
U2 - Species Richness & Live Biomass
U2 - Species Richness & Live Biomass
U3 - Species Richness & Live Biomass
U3 - Species Richness & Live Biomass
U4 - Species Richness & Live Biomass
U4 - Species Richness & Live Biomass
U5 - Species Richness & Live Biomass
U5 - Species Richness & Live Biomass
Semivariance (Normalized)
Distance (m)
90
135
0
45

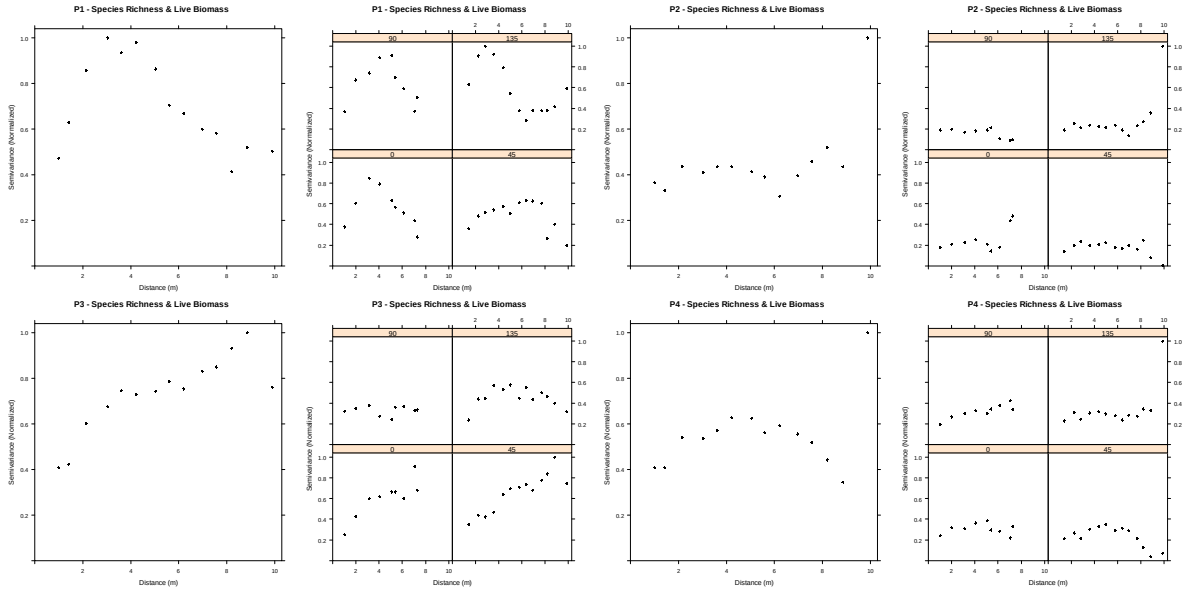
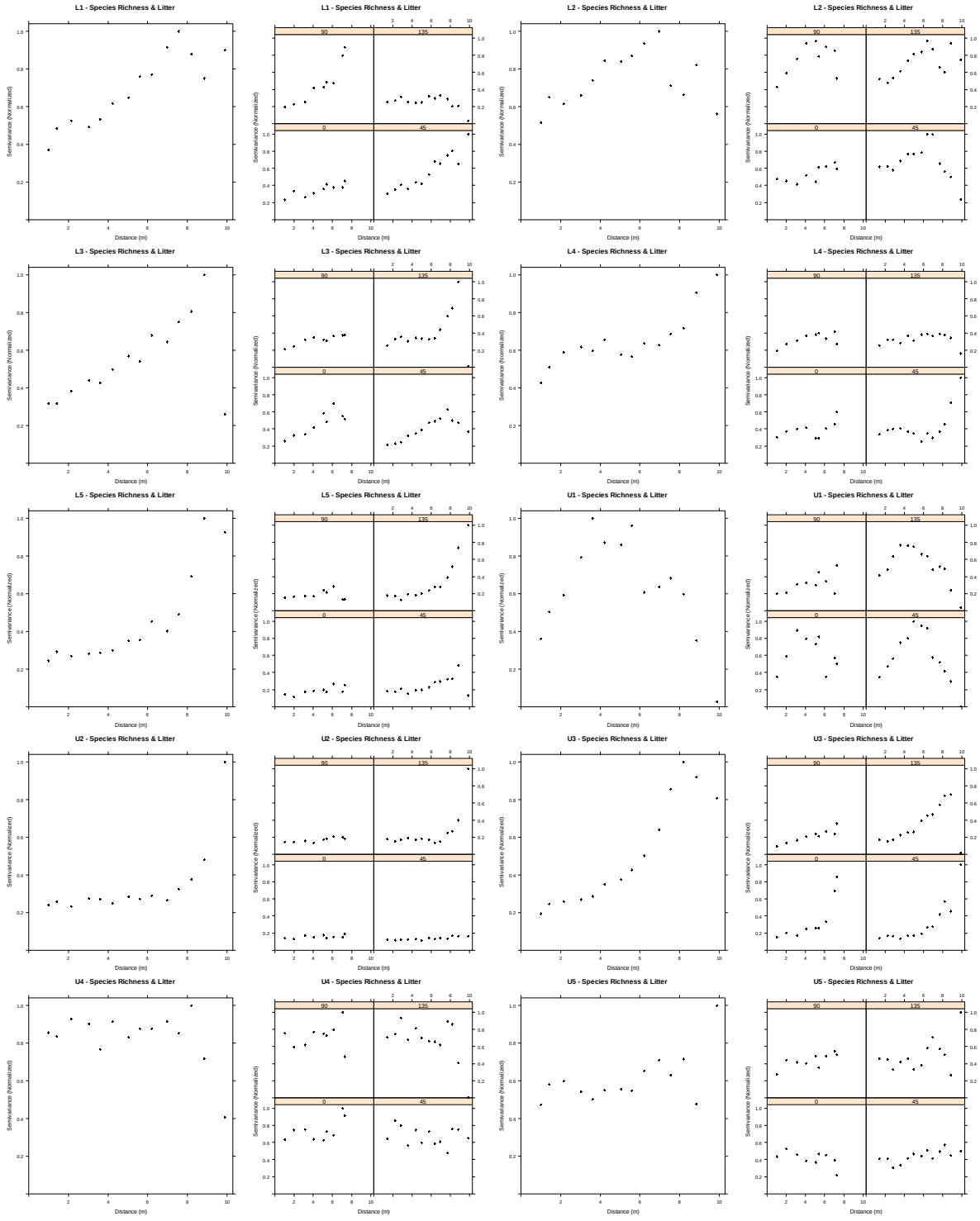


Figure B.2. Normalized semi-variograms of the standardized residuals computed for linear regressions, with square root transformed species richness as the response variable and log transformed live biomass as the explanatory variable, for each grid (L1-5, U1-5, P1-4). The second and fourth columns show directional semi-variograms at 0, 45, 90, and 135º.


L1 - Species Richness & Litter
L1 - Species Richness & Litter
L2 - Species Richness & Litter
L2 - Species Richness & Litter
L3 - Species Richness & Litter
L3 - Species Richness & Litter
L4 - Species Richness & Litter
L4 - Species Richness & Litter
L5 - Species Richness & Litter
L5 - Species Richness & Litter
U1 - Species Richness & Litter
U1 - Species Richness & Litter
U2 - Species Richness & Litter
U2 - Species Richness & Litter
U3 - Species Richness & Litter
U3 - Species Richness & Litter
U4 - Species Richness & Litter
U4 - Species Richness & Litter
U5 - Species Richness & Litter
U5 - Species Richness & Litter
Semivariance (Normalized)
Distance (m)
90
135
0
45

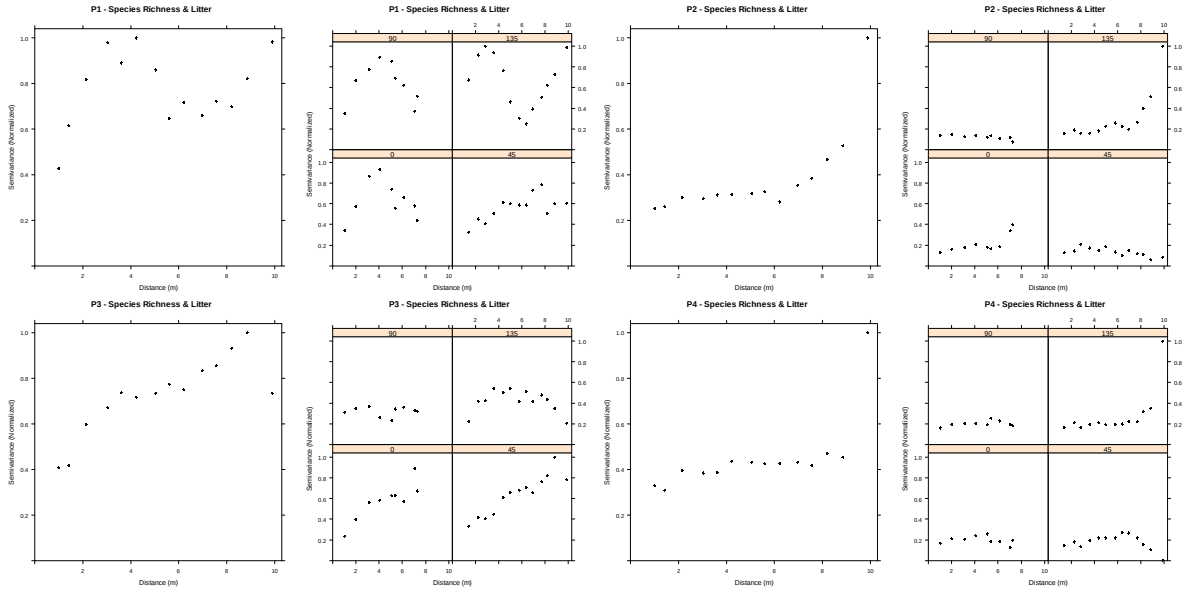


Figure B.3. Normalized semi-variograms of the standardized residuals computed for linear regressions, with square root transformed species richness as the response variable and log transformed litter as the explanatory variable, for each grid (L1-5, U1-5, P1-4). The second and fourth columns show directional semi-variograms at 0, 45, 90, and 135º.

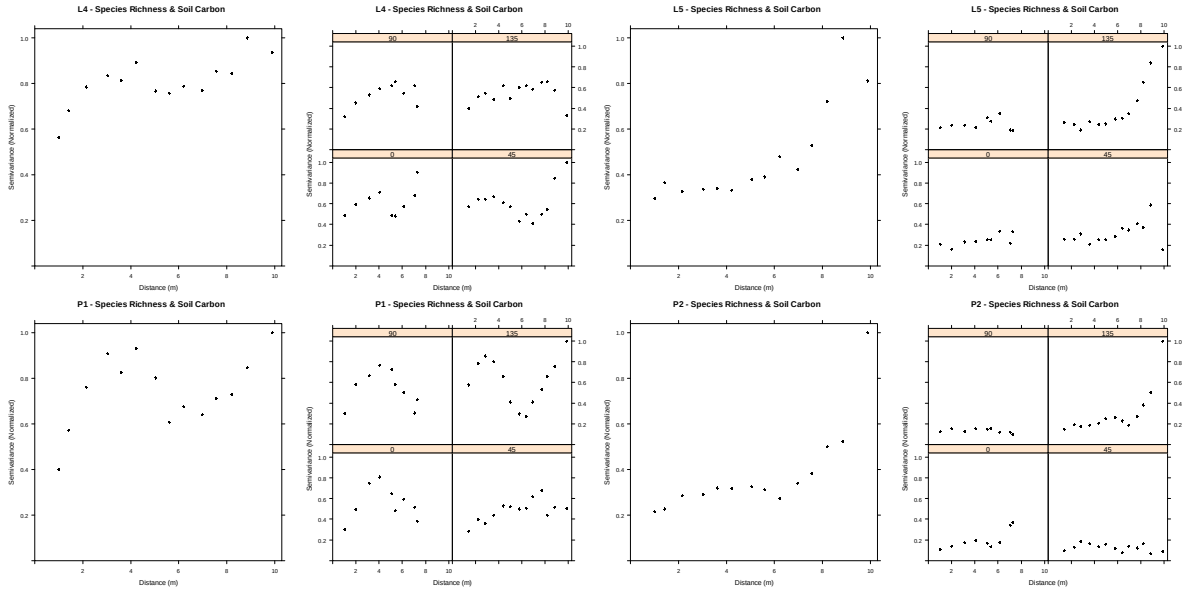


Figure B.4. Normalized semi-variograms of the standardized residuals computed for linear regressions, with square root transformed species richness as the response variable and soil carbon as the explanatory variable, for each grid that involved soil sampling (L4, L5, P1 and P2). The second and fourth columns show directional semi-variograms at 0, 45, 90, and 135º.

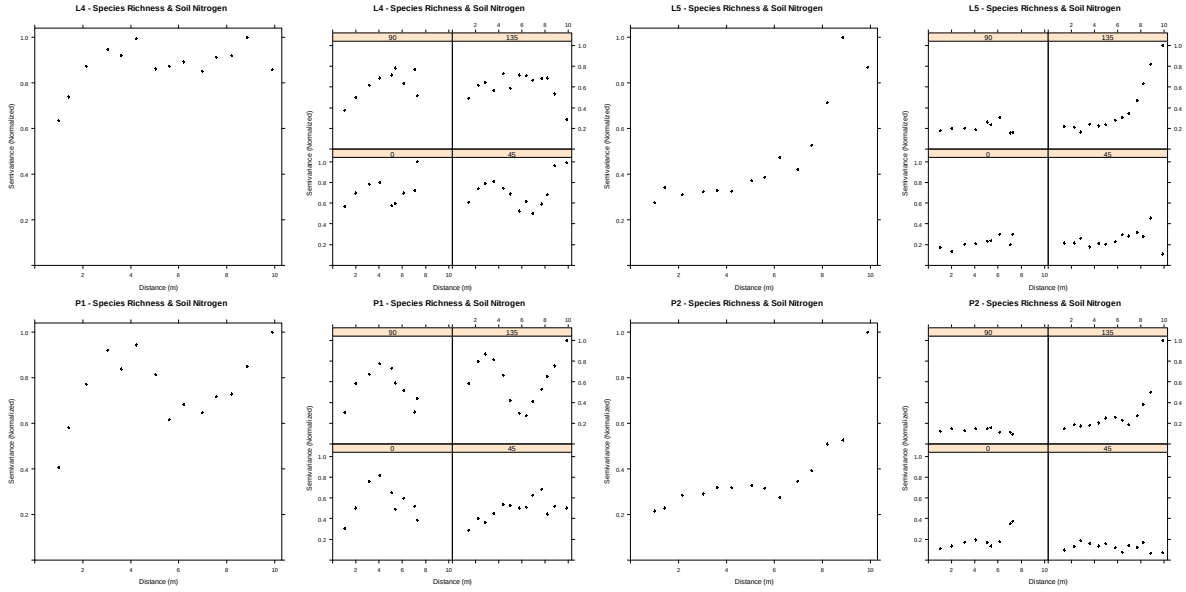


Figure B.5. Normalized semi-variograms of the standardized residuals computed for linear regressions, with square root transformed species richness as the response variable and soil nitrogen as the explanatory variable, for each grid that involved soil sampling (L4, L5, P1 and P2). The second and fourth columns show directional semi-variograms at 0, 45, 90, and 135º.

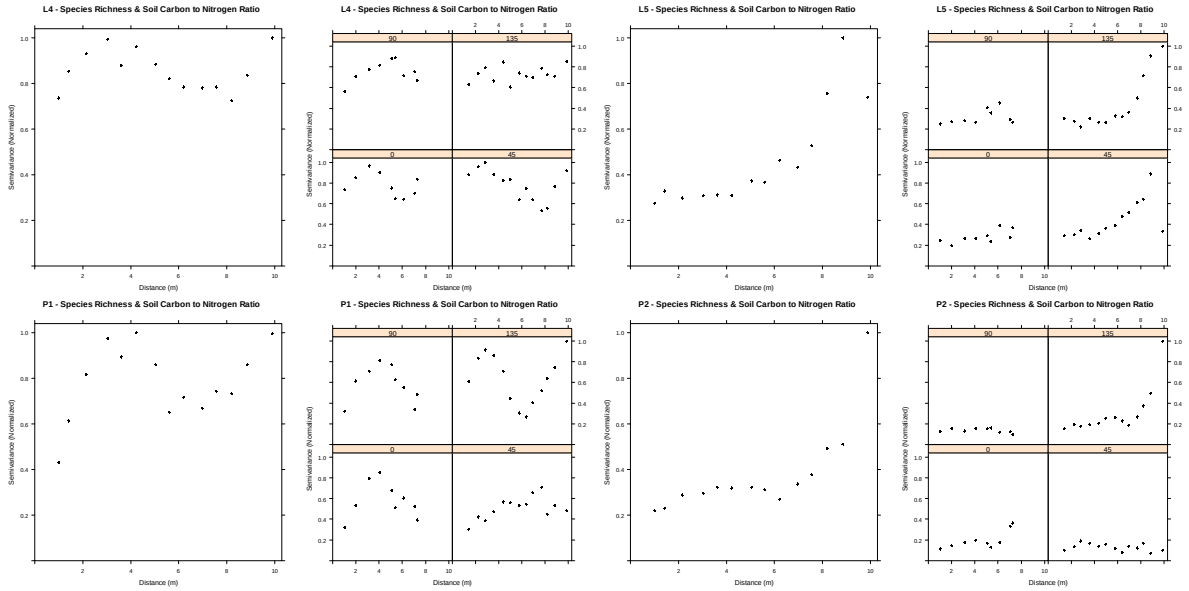


Figure B.6. Normalized semi-variograms of the standardized residuals computed for linear regressions, with square root transformed species richness as the response variable and soil carbon to nitrogen ratio as the explanatory variable, for each grid that involved soil sampling (L4, L5, P1 and P2). The second and fourth columns show directional semi-variograms at 0, 45, 90, and 135º.

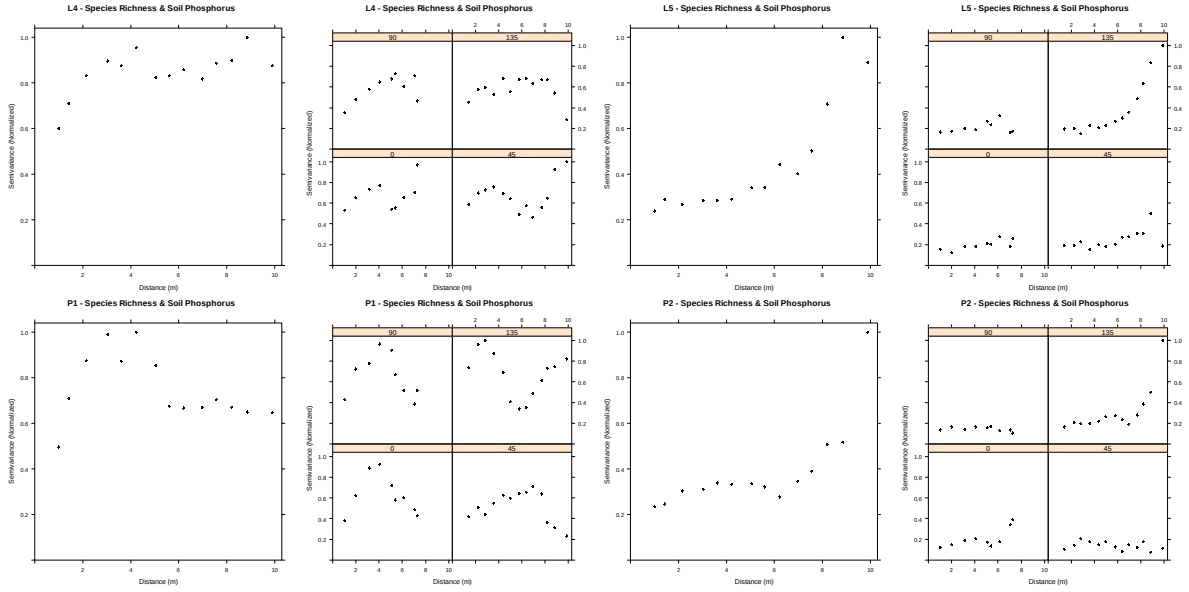


Figure B.7. Normalized semi-variograms of the standardized residuals computed for linear regressions, with square root transformed species richness as the response variable and soil phosphorus as the explanatory variable, for each grid that involved soil sampling (L4, L5, P1 and P2). The second and fourth columns show directional semi-variograms at 0, 45, 90, and 135º.

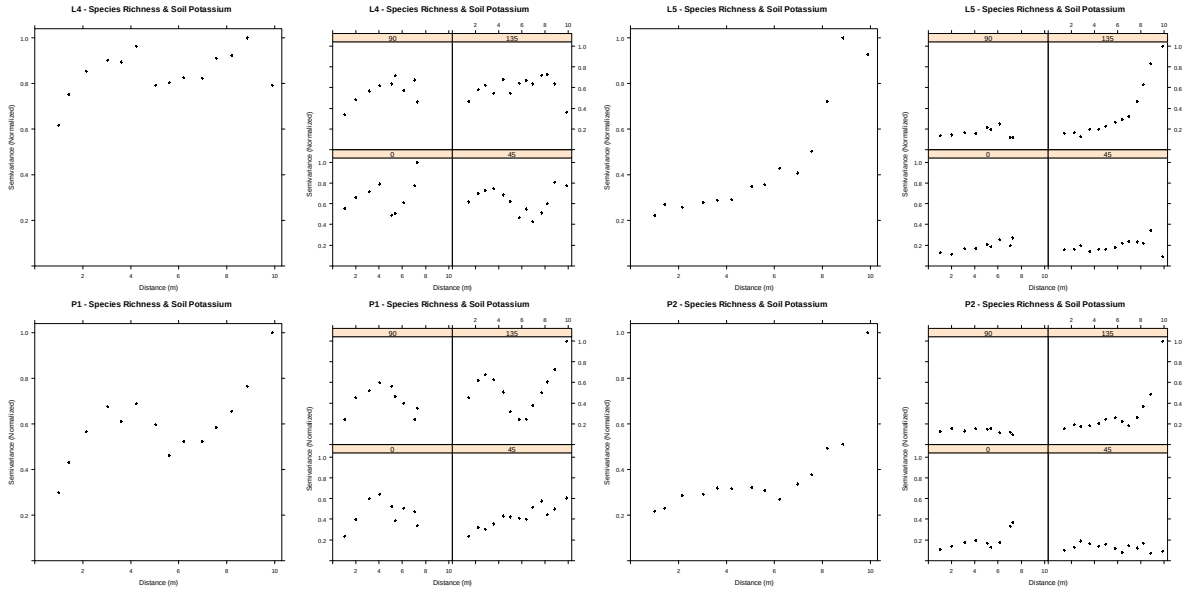


Figure B.8. Normalized semi-variograms of the standardized residuals computed for linear regressions, with square root transformed species richness as the response variable and soil potassium as the explanatory variable, for each grid that involved soil sampling (L4, L5, P1 and P2). The second and fourth columns show directional semi-variograms at 0, 45, 90, and 135º.

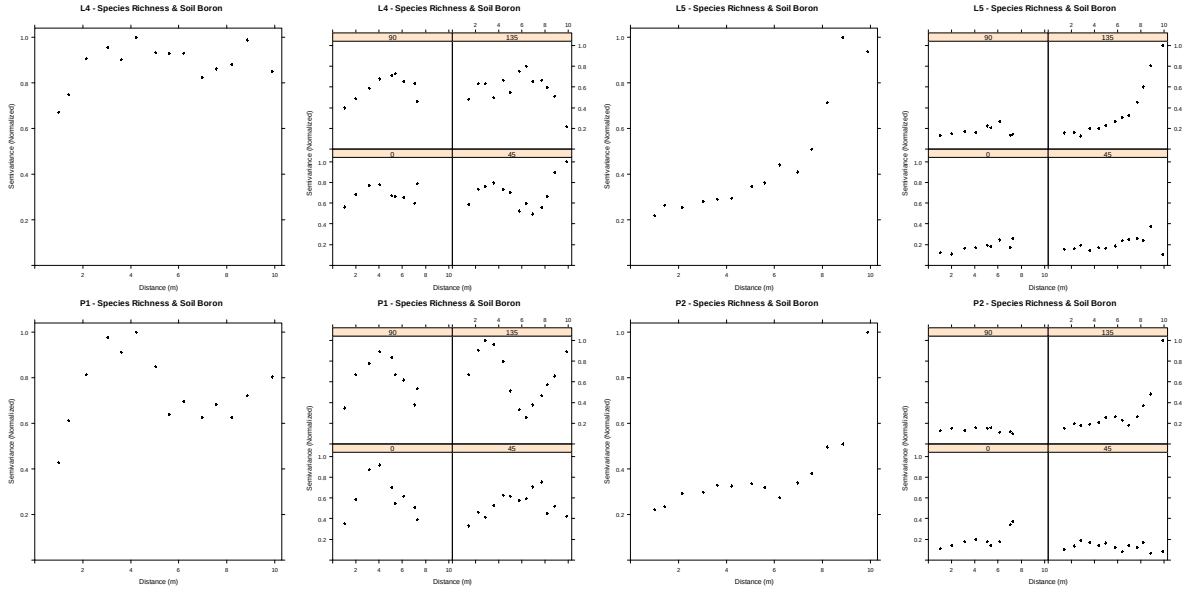


Figure B.9. Normalized semi-variograms of the standardized residuals computed for linear regressions, with square root transformed species richness as the response variable and soil boron as the explanatory variable, for each grid that involved soil sampling (L4, L5, P1 and P2). The second and fourth columns show directional semi-variograms at 0, 45, 90, and 135º.

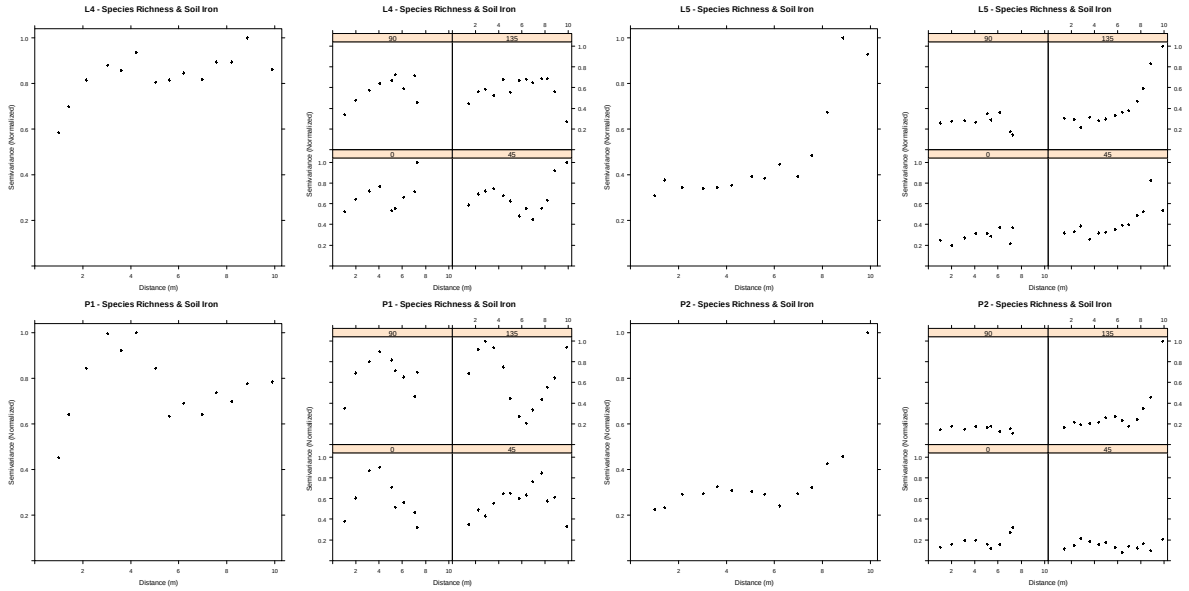


Figure B.10. Normalized semi-variograms of the standardized residuals computed for linear regressions, with square root transformed species richness as the response variable and soil iron as the explanatory variable, for each grid that involved soil sampling (L4, L5, P1 and P2). The second and fourth columns show directional semi-variograms at 0, 45, 90, and 135º.

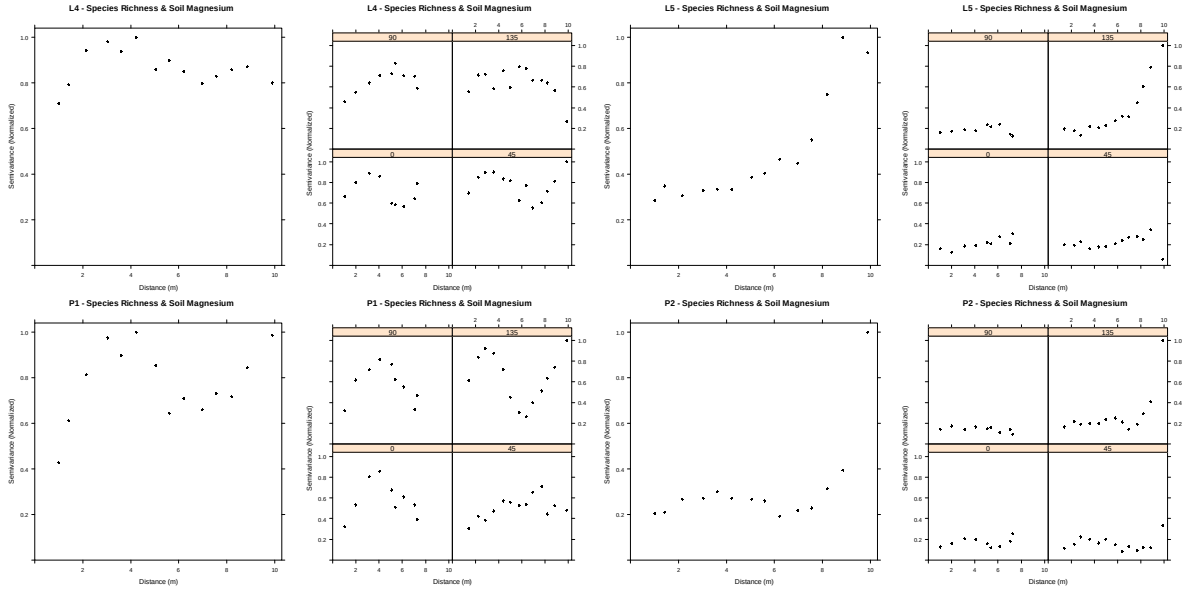


Figure B.11. Normalized semi-variograms of the standardized residuals computed for linear regressions, with square root transformed species richness as the response variable and soil magnesium as the explanatory variable, for each grid that involved soil sampling (L4, L5, P1 and P2). The second and fourth columns show directional semi-variograms at 0, 45, 90, and 135º.

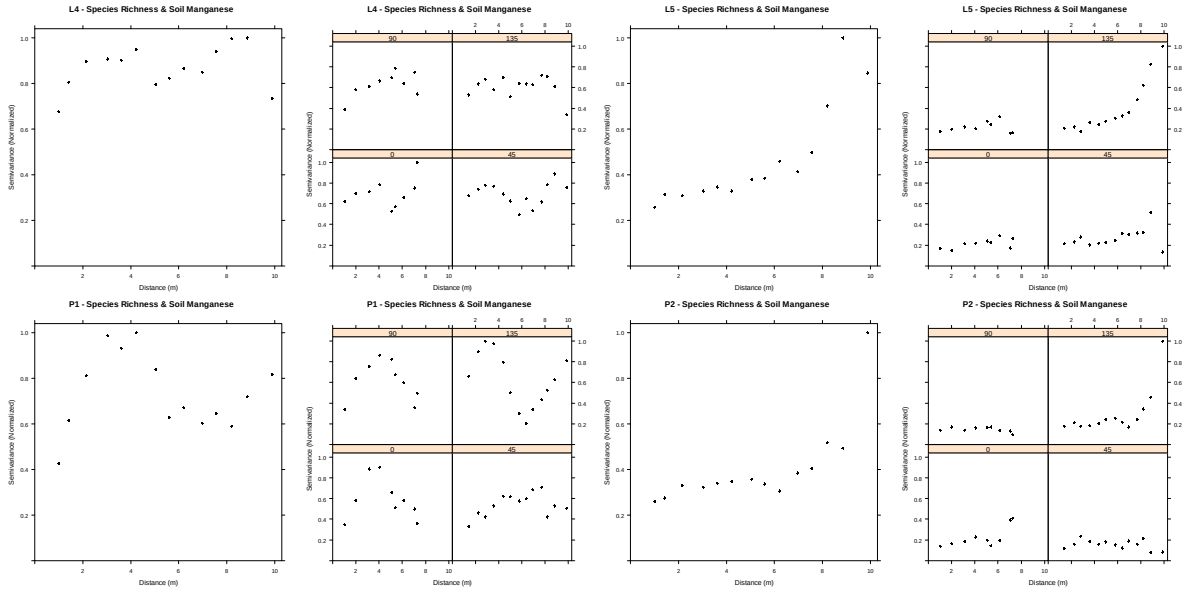


Figure B.12. Normalized semi-variograms of the standardized residuals computed for linear regressions, with square root transformed species richness as the response variable and soil manganese as the explanatory variable, for each grid that involved soil sampling (L4, L5, P1 and P2). The second and fourth columns show directional semi-variograms at 0, 45, 90, and 135º.

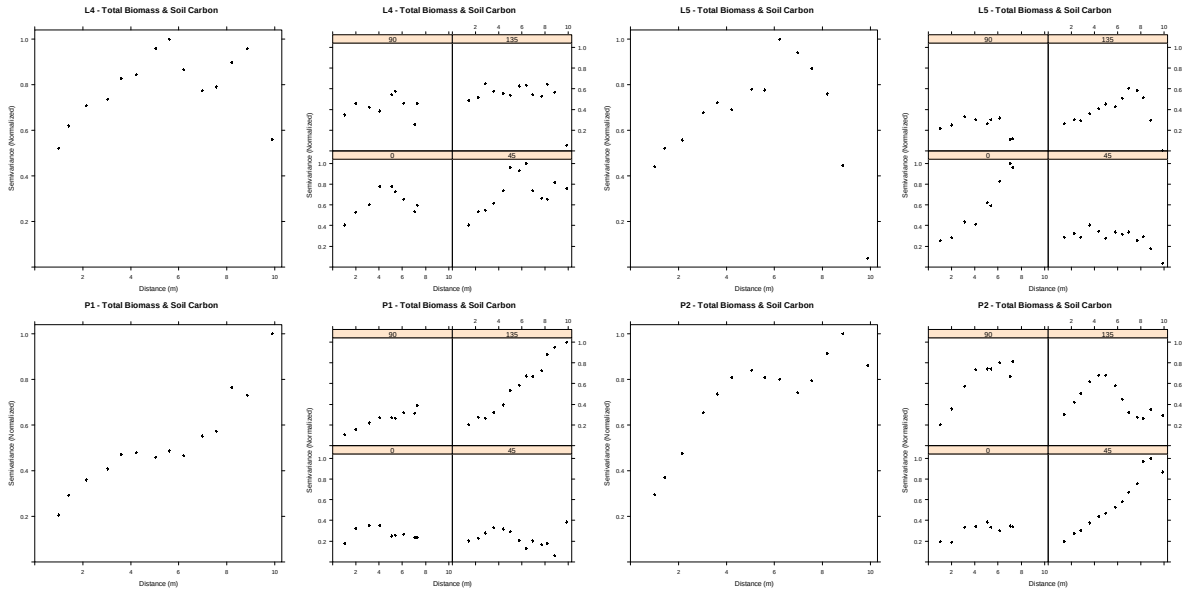


Figure B.13. Normalized semi-variograms of the standardized residuals computed for linear regressions, with log transformed total biomass as the response variable and soil carbon as the explanatory variable, for each grid that involved soil sampling (L4, L5, P1 and P2). The second and fourth columns show directional semi-variograms at 0, 45, 90, and 135º.

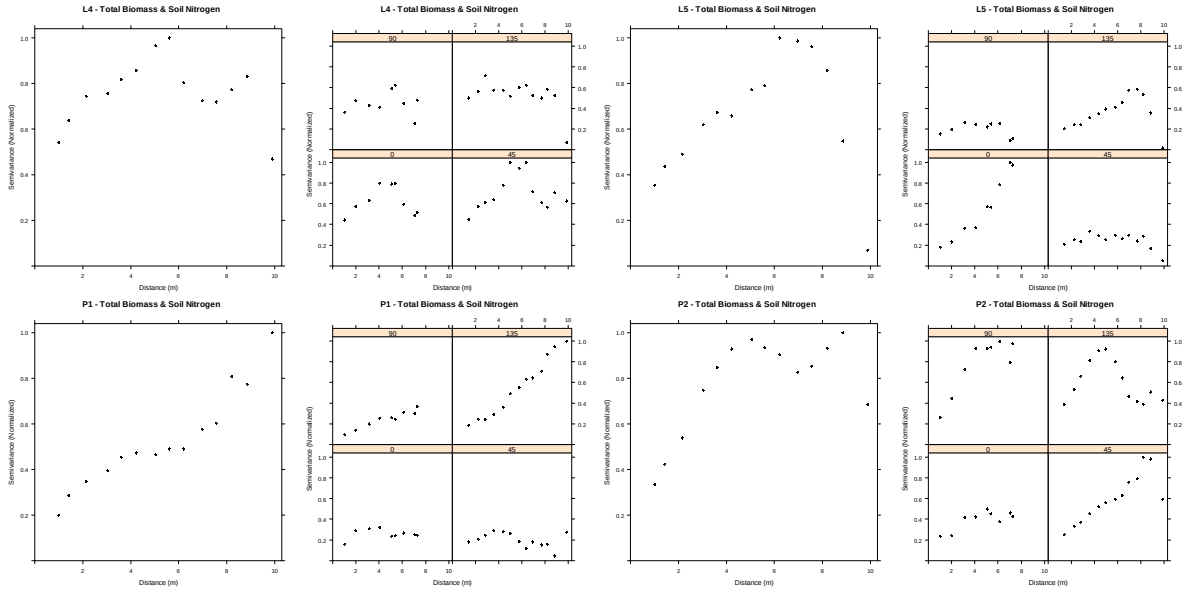


Figure B.14. Normalized semi-variograms of the standardized residuals computed for linear regressions, with log transformed total biomass as the response variable and soil nitrogen as the explanatory variable, for each grid that involved soil sampling (L4, L5, P1 and P2). The second and fourth columns show directional semi-variograms at 0, 45, 90, and 135º.

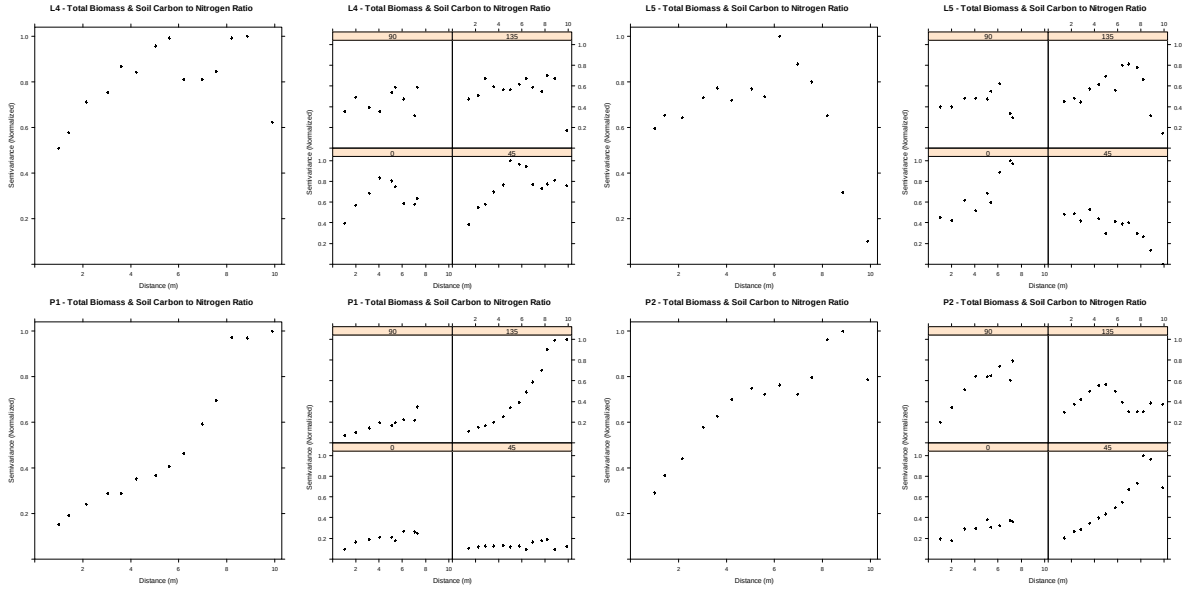


Figure B.15. Normalized semi-variograms of the standardized residuals computed for linear regressions, with log transformed total biomass as the response variable and soil carbon to nitrogen ratio as the explanatory variable, for each grid that involved soil sampling (L4, L5, P1 and P2). The second and fourth columns show directional semi-variograms at 0, 45, 90, and 135º.

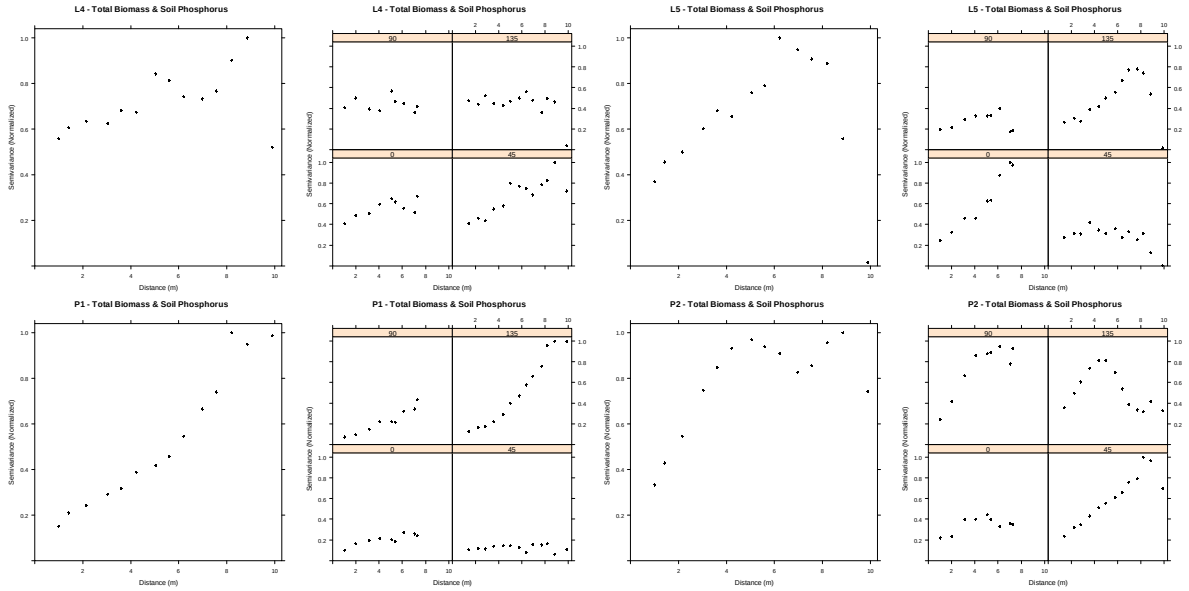


Figure B.16. Normalized semi-variograms of the standardized residuals computed for linear regressions, with log transformed total biomass as the response variable and soil phosphorus as the explanatory variable, for each grid that involved soil sampling (L4, L5, P1 and P2). The second and fourth columns show directional semi-variograms at 0, 45, 90, and 135º.

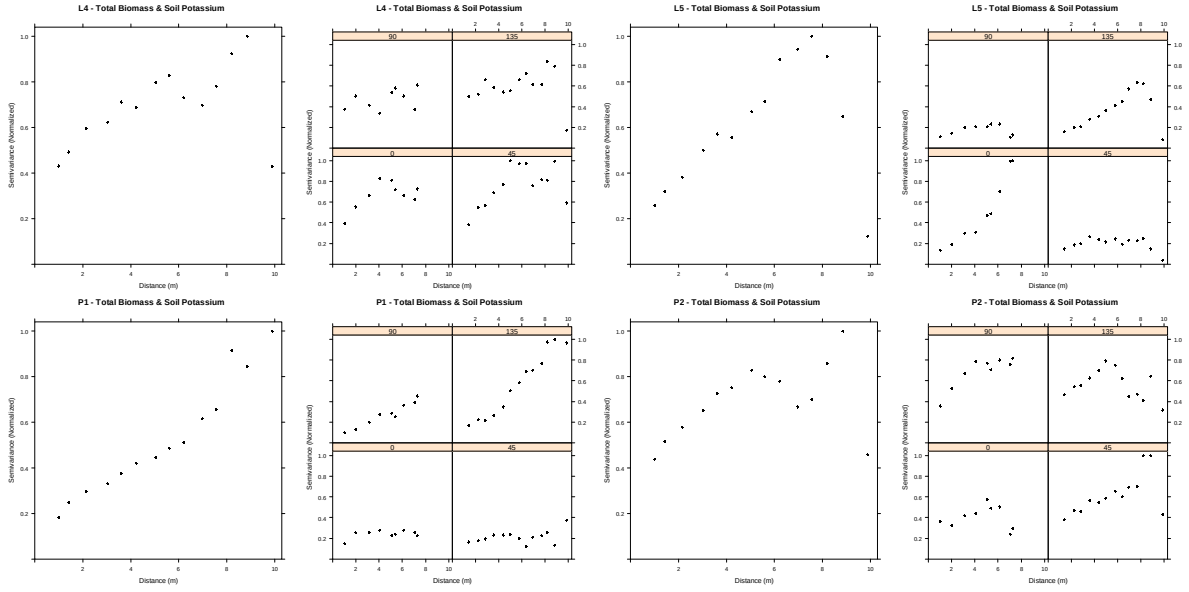


Figure B.17. Normalized semi-variograms of the standardized residuals computed for linear regressions, with log transformed total biomass as the response variable and soil potassium as the explanatory variable, for each grid that involved soil sampling (L4, L5, P1 and P2). The second and fourth columns show directional semi-variograms at 0, 45, 90, and 135º.

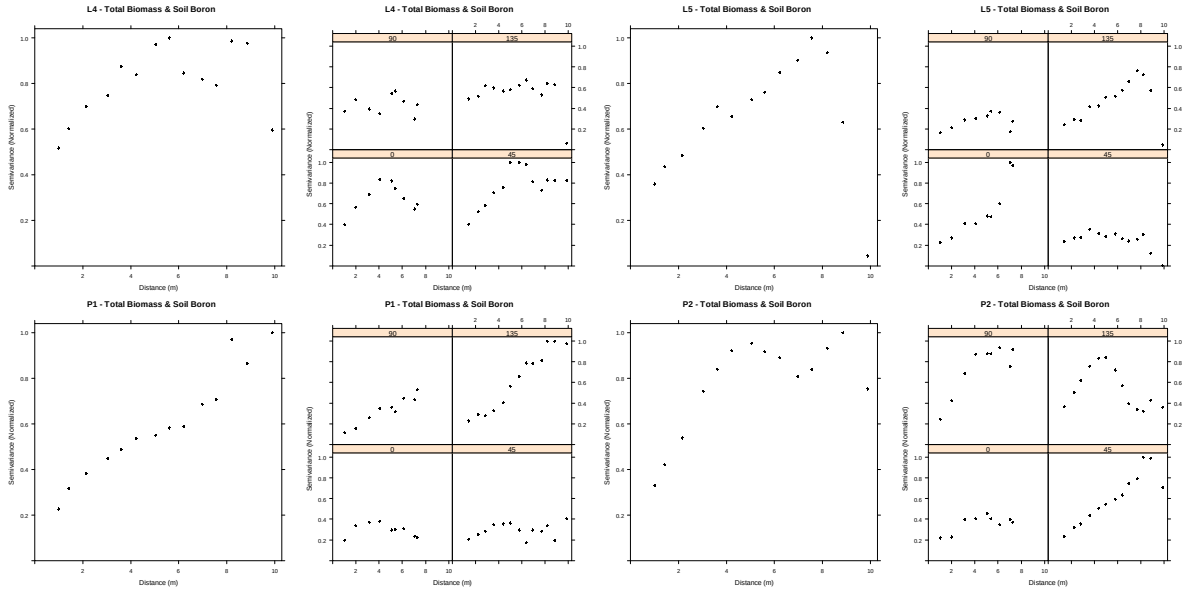


Figure B.18. Normalized semi-variograms of the standardized residuals computed for linear regressions, with log transformed total biomass as the response variable and soil boron as the explanatory variable, for each grid that involved soil sampling (L4, L5, P1 and P2). The second and fourth columns show directional semi-variograms at 0, 45, 90, and 135º.

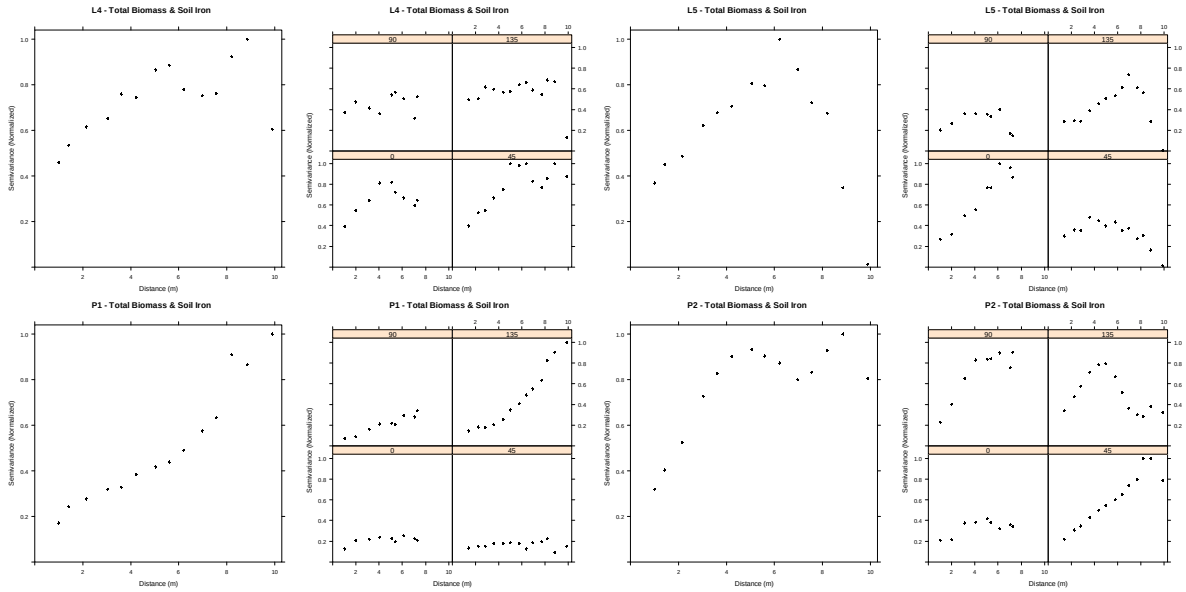


Figure B.19. Normalized semi-variograms of the standardized residuals computed for linear regressions, with log transformed total biomass as the response variable and soil iron as the explanatory variable, for each grid that involved soil sampling (L4, L5, P1 and P2). The second and fourth columns show directional semi-variograms at 0, 45, 90, and 135º.

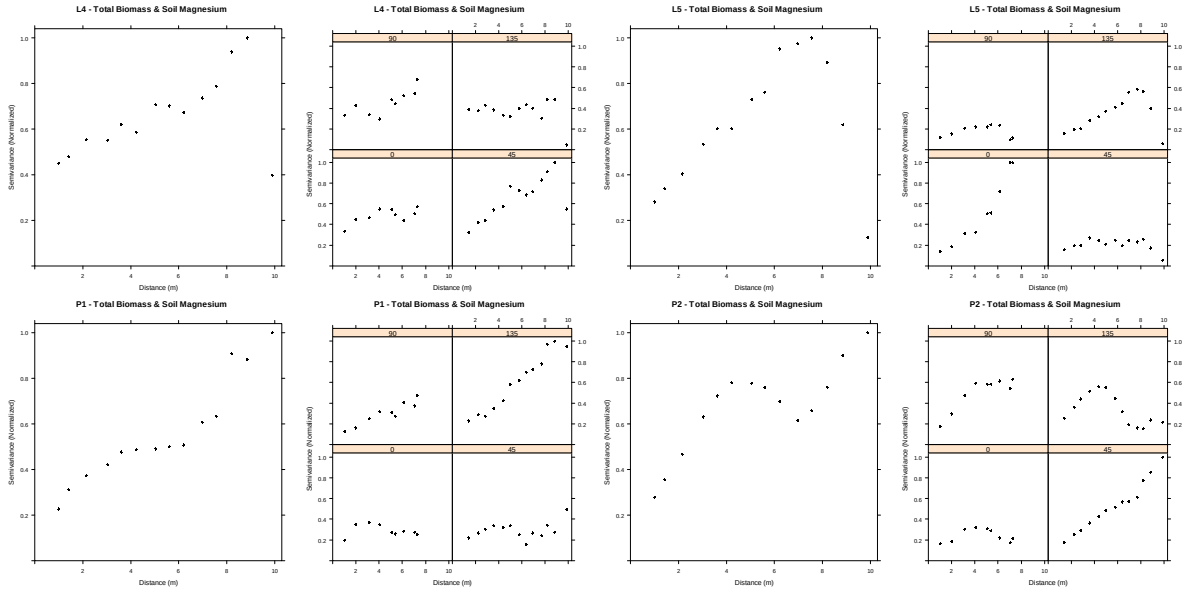


Figure B.20. Normalized semi-variograms of the standardized residuals computed for linear regressions, with log transformed total biomass as the response variable and soil magnesium as the explanatory variable, for each grid that involved soil sampling (L4, L5, P1 and P2). The second and fourth columns show directional semi-variograms at 0, 45, 90, and 135º.

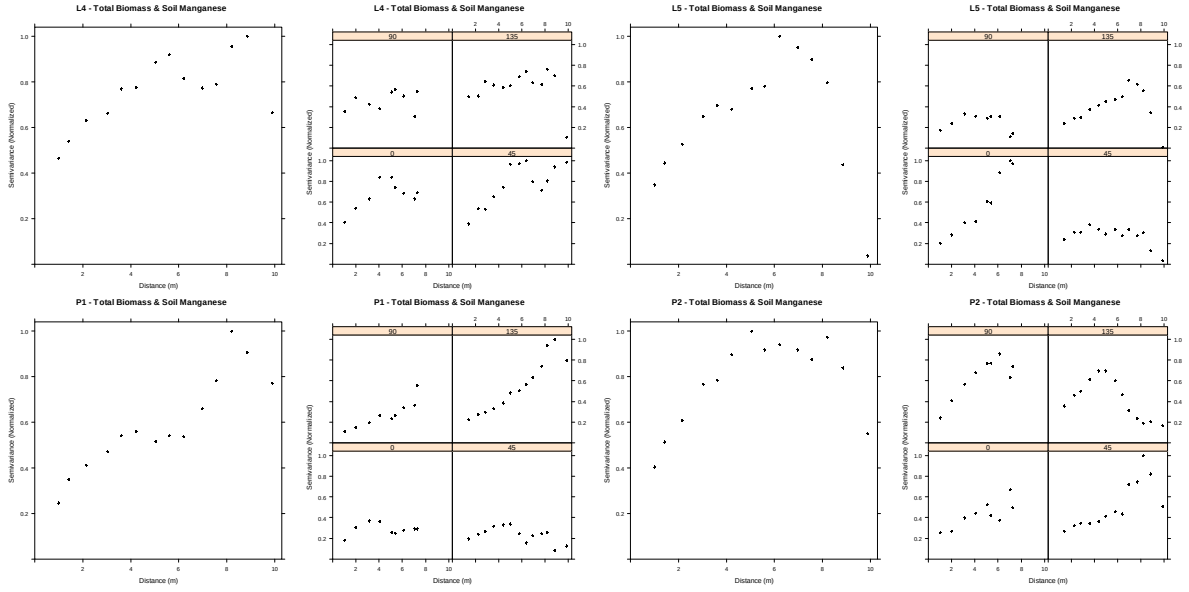


Figure B.21. Normalized semi-variograms of the standardized residuals computed for linear regressions, with log transformed total biomass as the response variable and soil manganese as the explanatory variable, for each grid that involved soil sampling (L4, L5, P1 and P2). The second and fourth columns show directional semi-variograms at 0, 45, 90, and 135º.

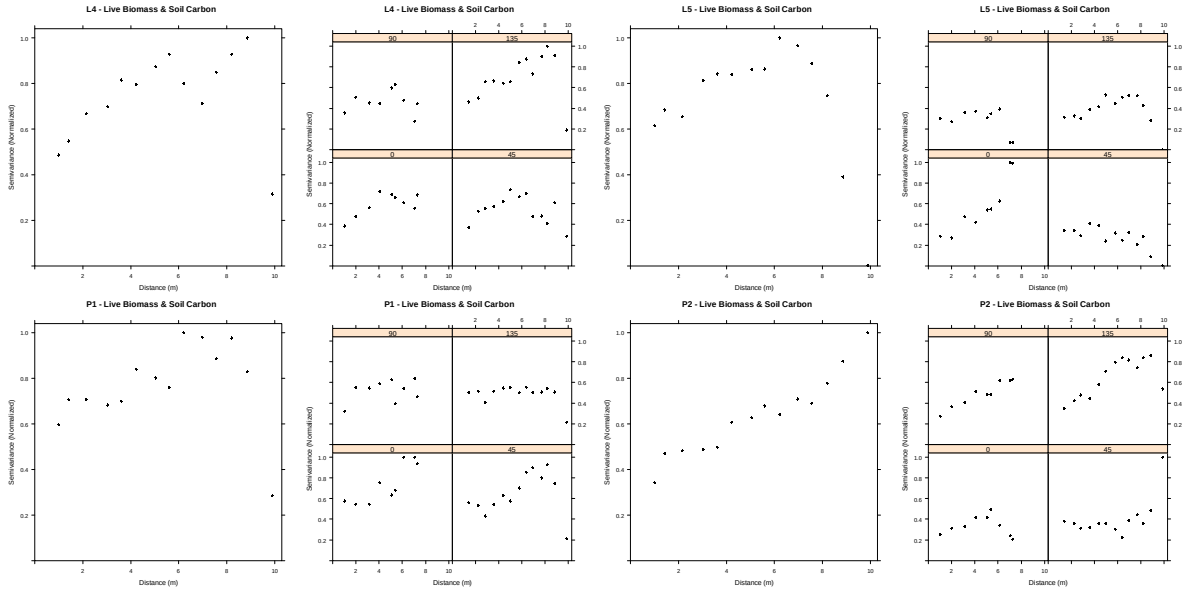


Figure B.22. Normalized semi-variograms of the standardized residuals computed for linear regressions, with log transformed live biomass as the response variable and soil carbon as the explanatory variable, for each grid that involved soil sampling (L4, L5, P1 and P2). The second and fourth columns show directional semi-variograms at 0, 45, 90, and 135º.

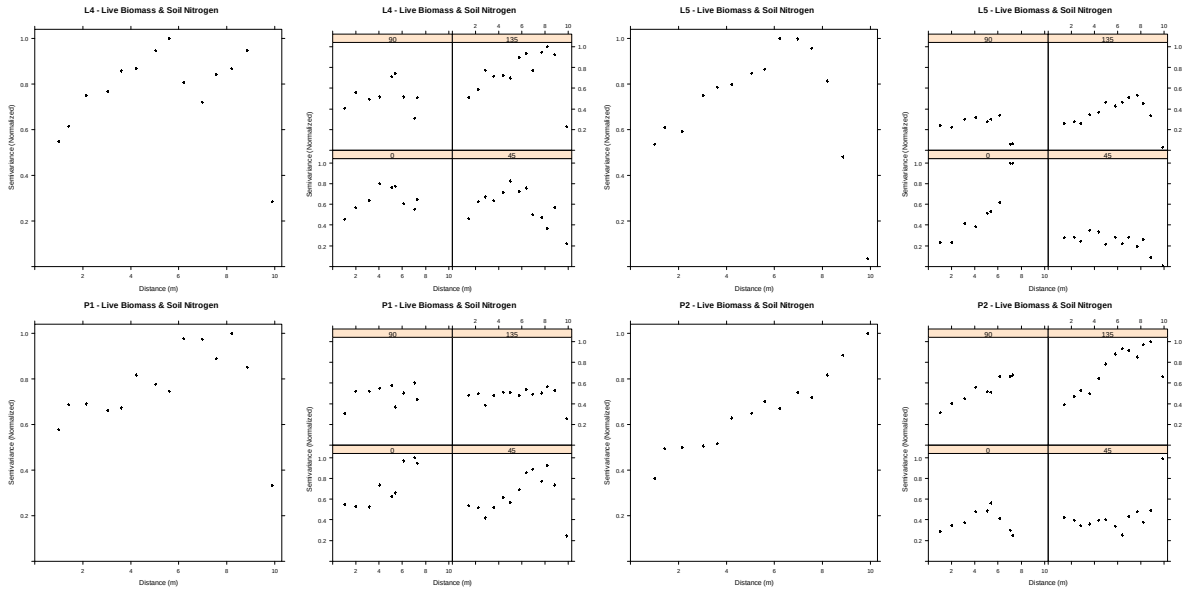


Figure B.23. Normalized semi-variograms of the standardized residuals computed for linear regressions, with log transformed live biomass as the response variable and soil nitrogen as the explanatory variable, for each grid that involved soil sampling (L4, L5, P1 and P2). The second and fourth columns show directional semi-variograms at 0, 45, 90, and 135º.

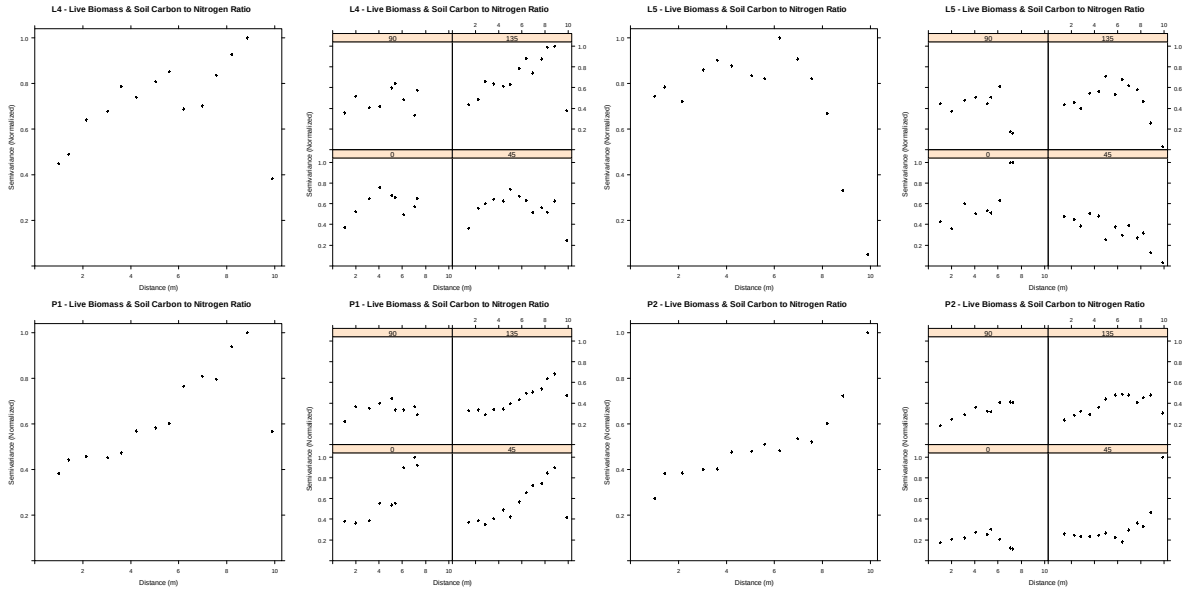


Figure B.24. Normalized semi-variograms of the standardized residuals computed for linear regressions, with log transformed live biomass as the response variable and soil carbon to nitrogen ratio as the explanatory variable, for each grid that involved soil sampling (L4, L5, P1 and P2). The second and fourth columns show directional semi-variograms at 0, 45, 90, and 135º.

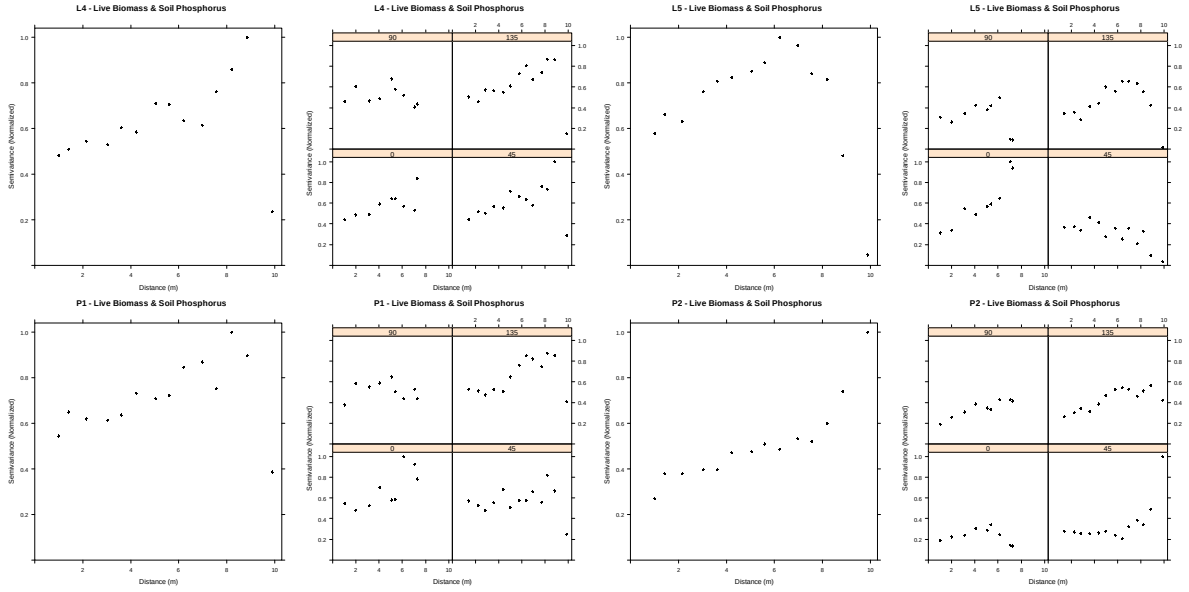


Figure B.25. Normalized semi-variograms of the standardized residuals computed for linear regressions, with log transformed live biomass as the response variable and soil phosphorus as the explanatory variable, for each grid that involved soil sampling (L4, L5, P1 and P2). The second and fourth columns show directional semi-variograms at 0, 45, 90, and 135º.

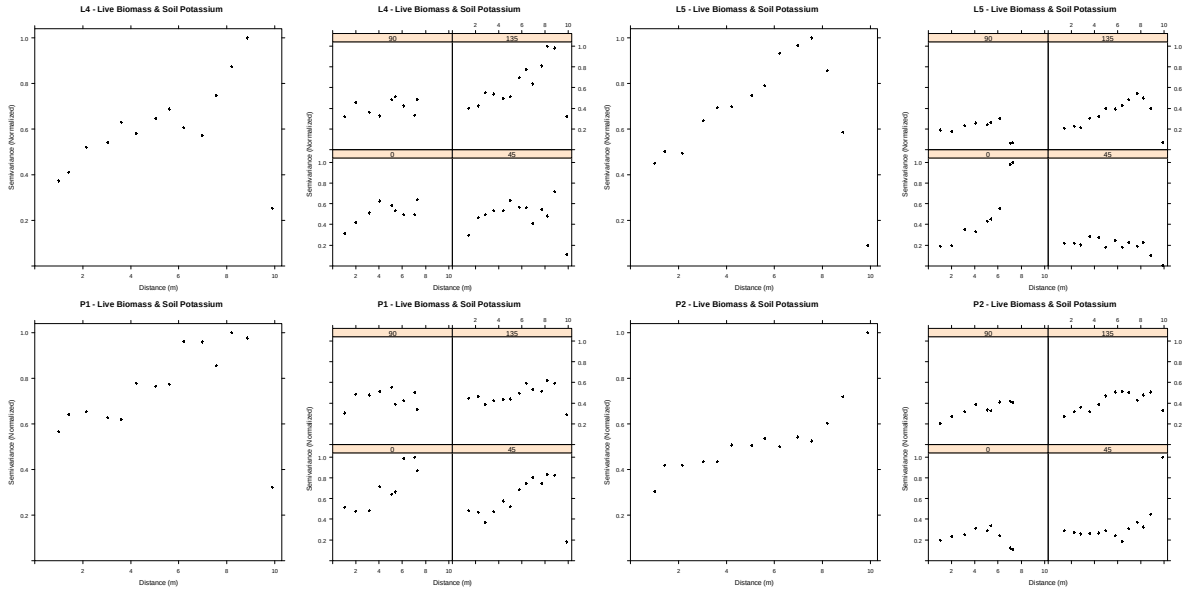


Figure B.26. Normalized semi-variograms of the standardized residuals computed for linear regressions, with log transformed live biomass as the response variable and soil potassium as the explanatory variable, for each grid that involved soil sampling (L4, L5, P1 and P2). The second and fourth columns show directional semi-variograms at 0, 45, 90, and 135º.

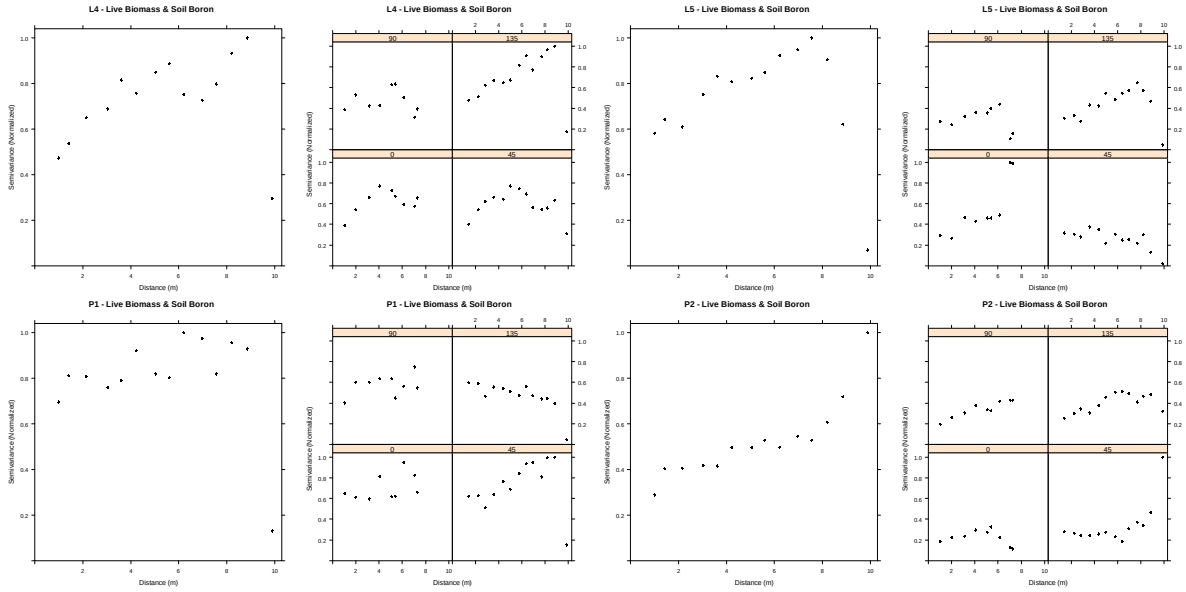


Figure B.27. Normalized semi-variograms of the standardized residuals computed for linear regressions, with log transformed live biomass as the response variable and soil boron as the explanatory variable, for each grid that involved soil sampling (L4, L5, P1 and P2). The second and fourth columns show directional semi-variograms at 0, 45, 90, and 135º.

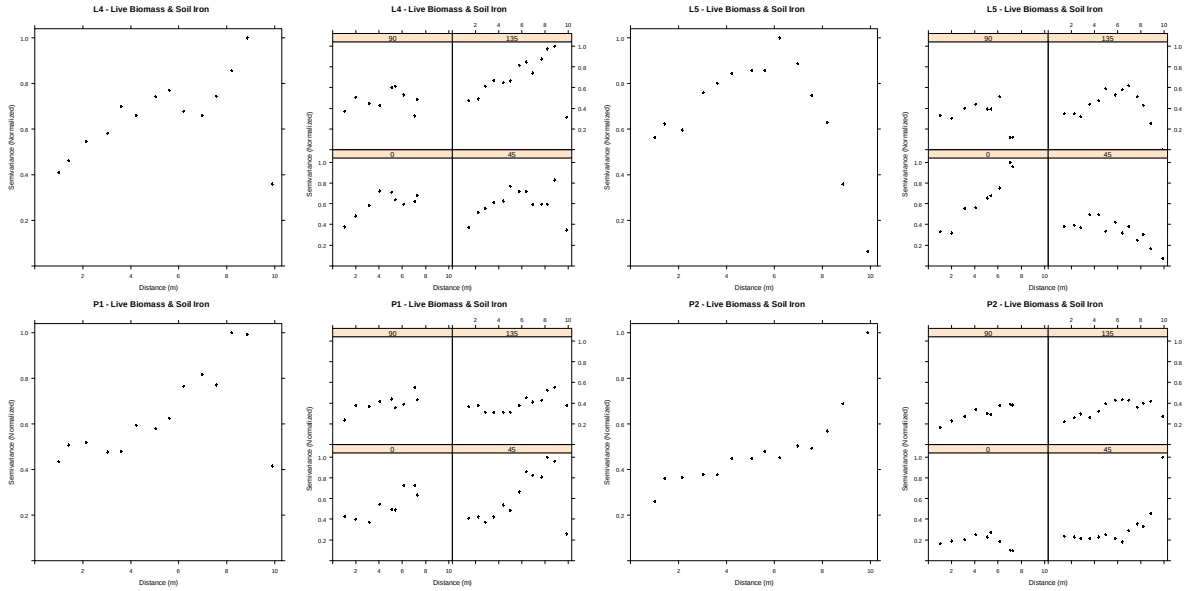


Figure B.28. Normalized semi-variograms of the standardized residuals computed for linear regressions, with log transformed live biomass as the response variable and soil iron as the explanatory variable, for each grid that involved soil sampling (L4, L5, P1 and P2). The second and fourth columns show directional semi-variograms at 0, 45, 90, and 135º.

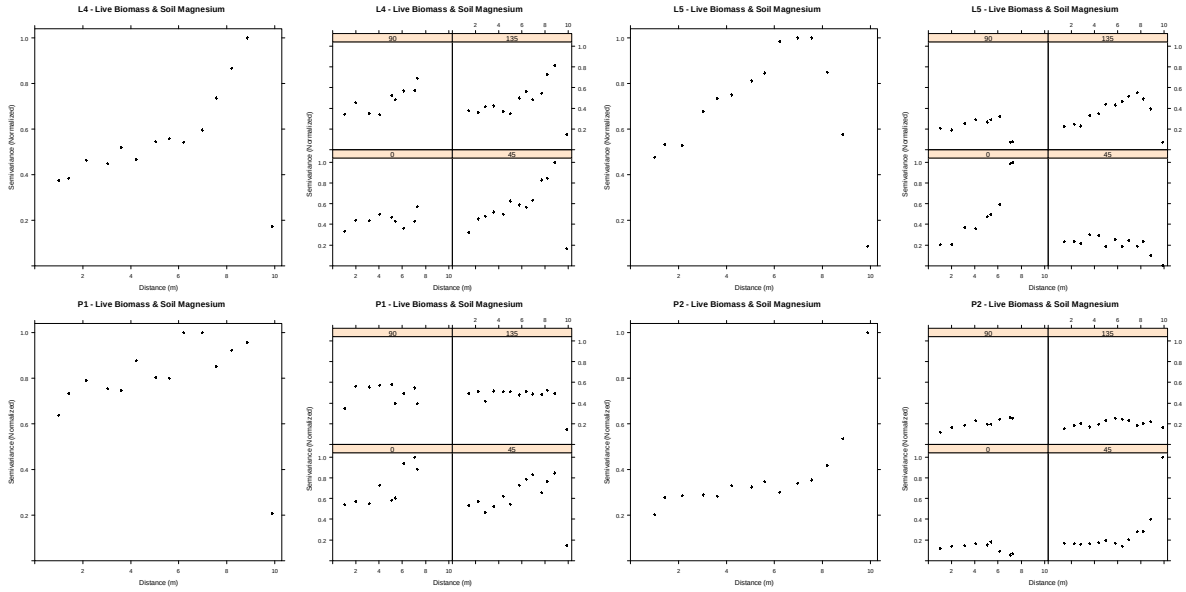


Figure B.29. Normalized semi-variograms of the standardized residuals computed for linear regressions, with log transformed live biomass as the response variable and soil magnesium as the explanatory variable, for each grid that involved soil sampling (L4, L5, P1 and P2). The second and fourth columns show directional semi-variograms at 0, 45, 90, and 135º.

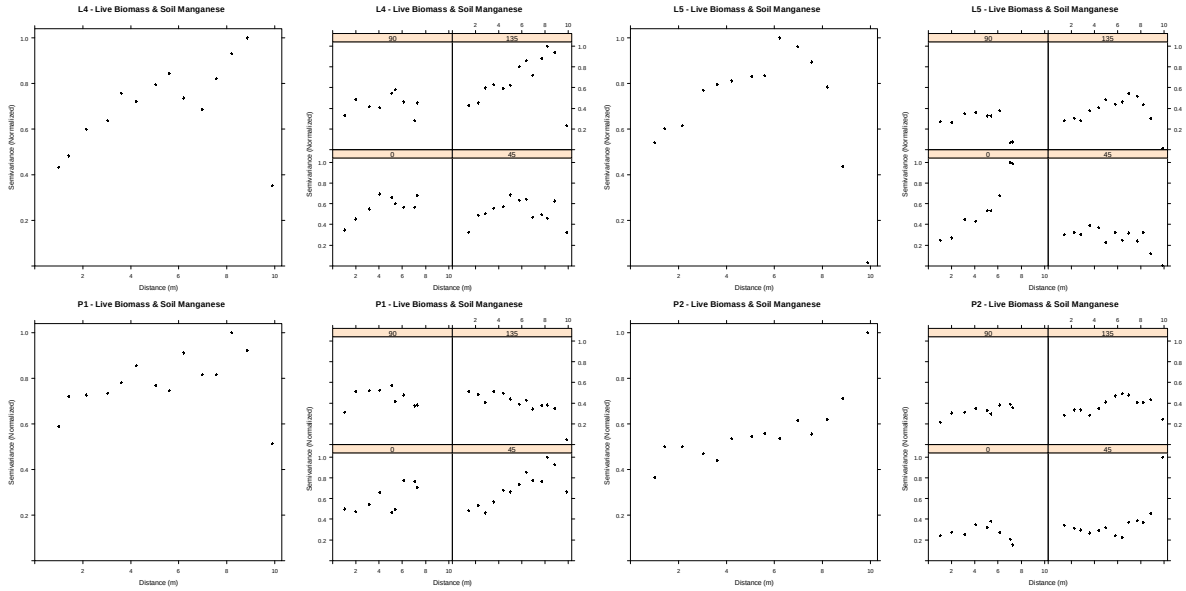


Figure B.30. Normalized semi-variograms of the standardized residuals computed for linear regressions, with log transformed live biomass as the response variable and soil manganese as the explanatory variable, for each grid that involved soil sampling (L4, L5, P1 and P2). The second and fourth columns show directional semi-variograms at 0, 45, 90, and 135º.

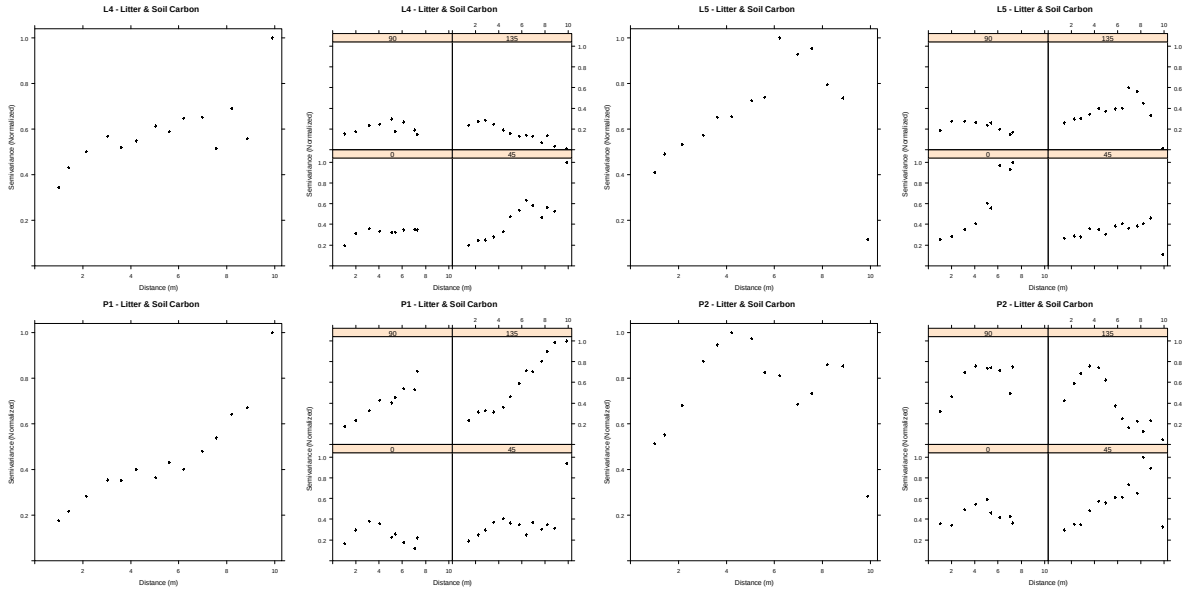


Figure B.31. Normalized semi-variograms of the standardized residuals computed for linear regressions, with log transformed litter as the response variable and soil carbon as the explanatory variable, for each grid that involved soil sampling (L4, L5, P1 and P2). The second and fourth columns show directional semi-variograms at 0, 45, 90, and 135º.

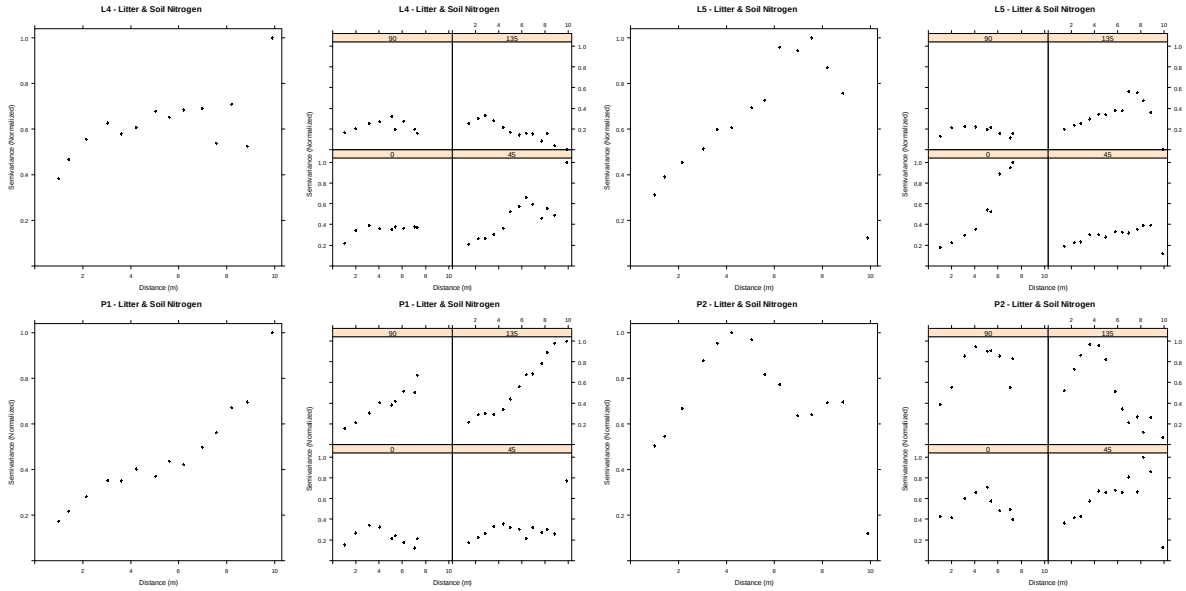


Figure B.32. Normalized semi-variograms of the standardized residuals computed for linear regressions, with log transformed litter as the response variable and soil nitrogen as the explanatory variable, for each grid that involved soil sampling (L4, L5, P1 and P2). The second and fourth columns show directional semi-variograms at 0, 45, 90, and 135º.

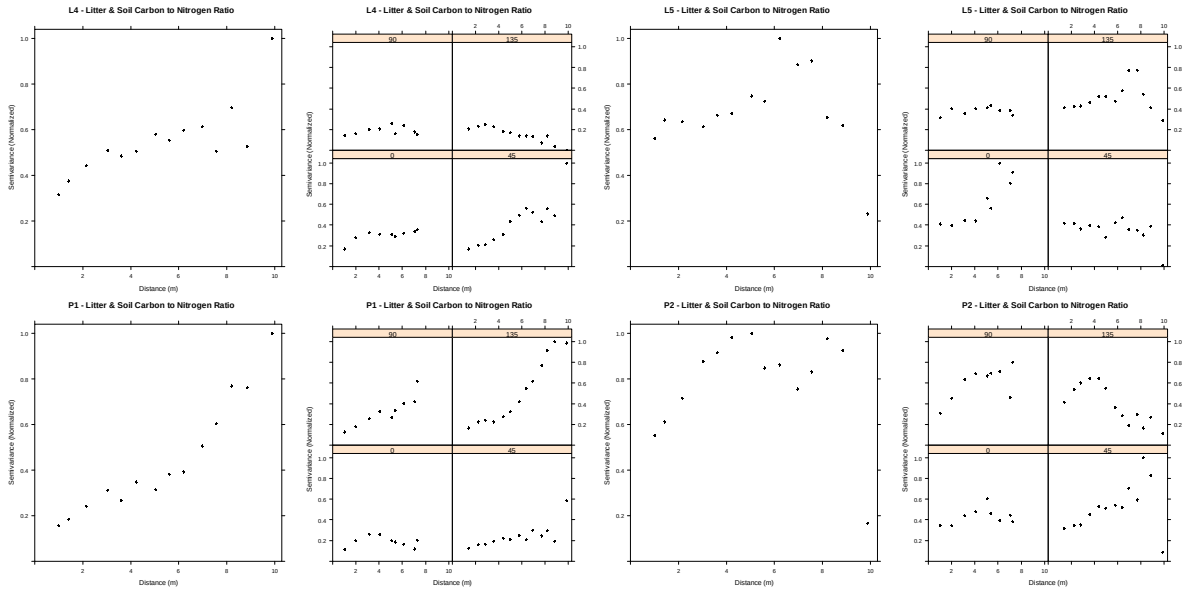


Figure B.33. Normalized semi-variograms of the standardized residuals computed for linear regressions, with log transformed litter as the response variable and soil carbon to nitrogen ratio as the explanatory variable, for each grid that involved soil sampling (L4, L5, P1 and P2). The second and fourth columns show directional semi-variograms at 0, 45, 90, and 135º.

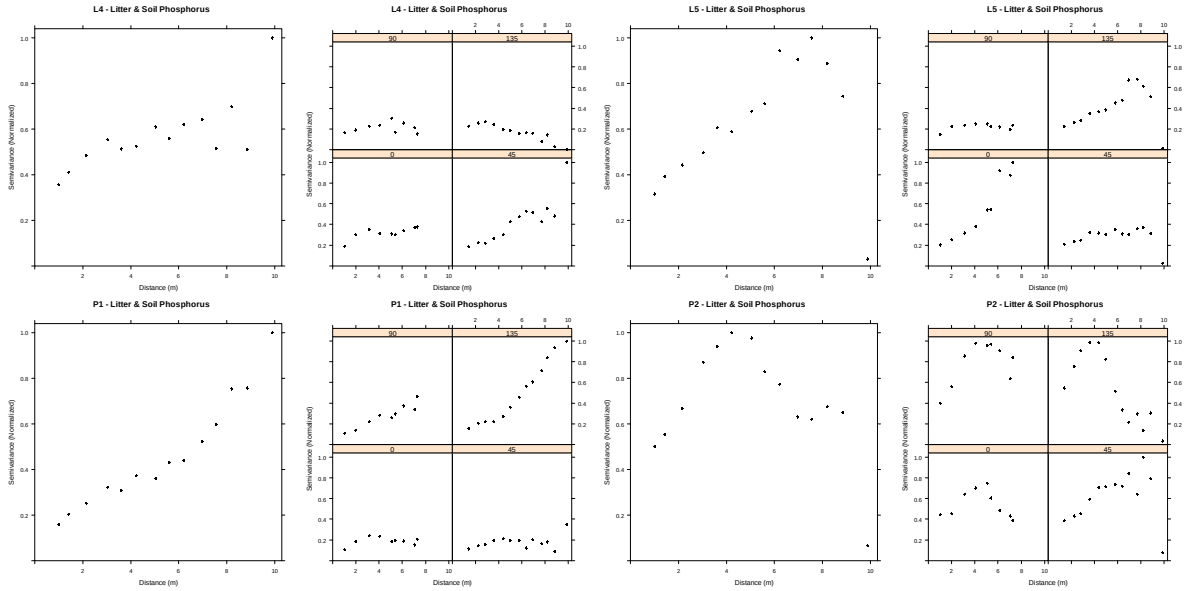


Figure B.34. Normalized semi-variograms of the standardized residuals computed for linear regressions, with log transformed litter as the response variable and soil phosphorus as the explanatory variable, for each grid that involved soil sampling (L4, L5, P1 and P2). The second and fourth columns show directional semi-variograms at 0, 45, 90, and 135º.

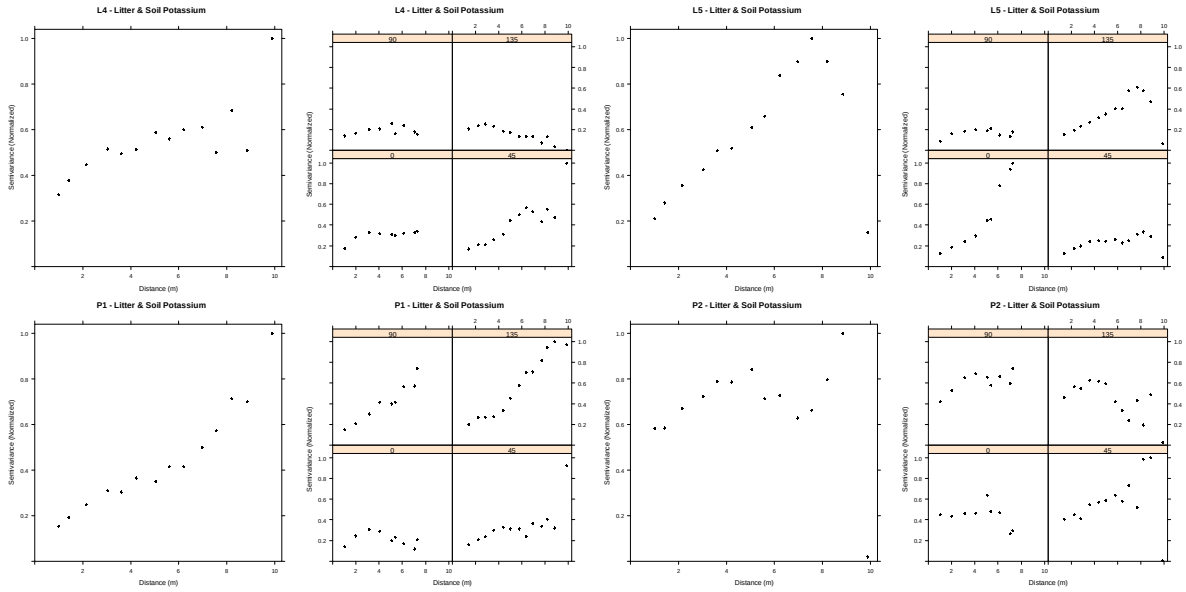


Figure B.35. Normalized semi-variograms of the standardized residuals computed for linear regressions, with log transformed litter as the response variable and soil potassium as the explanatory variable, for each grid that involved soil sampling (L4, L5, P1 and P2). The second and fourth columns show directional semi-variograms at 0, 45, 90, and 135º.

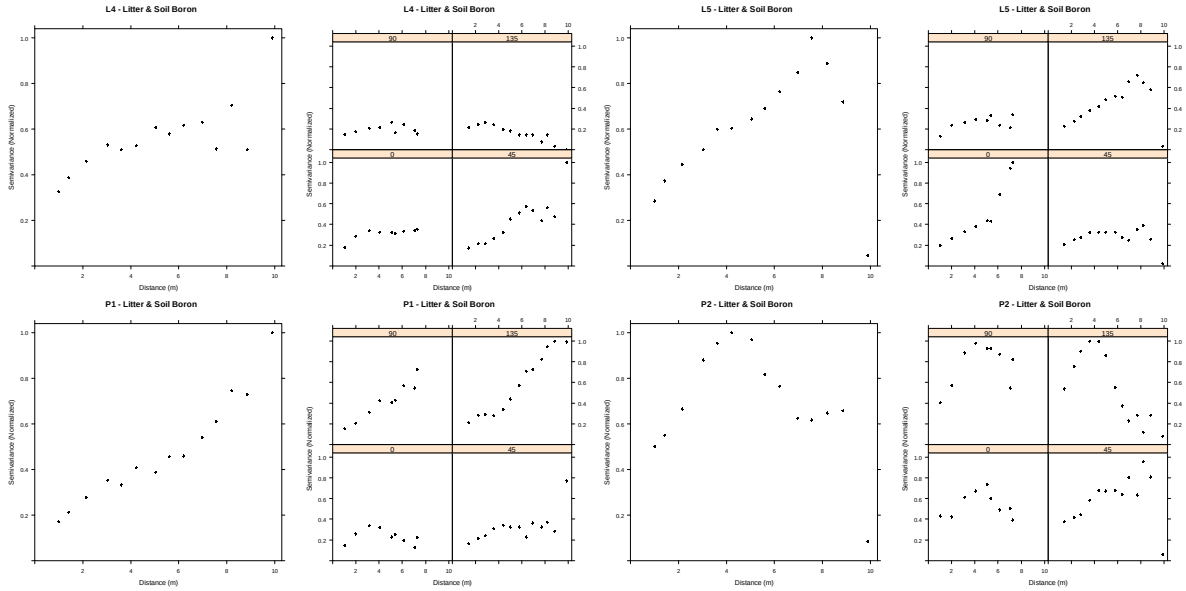


Figure B.36. Normalized semi-variograms of the standardized residuals computed for linear regressions, with log transformed litter as the response variable and soil boron as the explanatory variable, for each grid that involved soil sampling (L4, L5, P1 and P2). The second and fourth columns show directional semi-variograms at 0, 45, 90, and 135º.

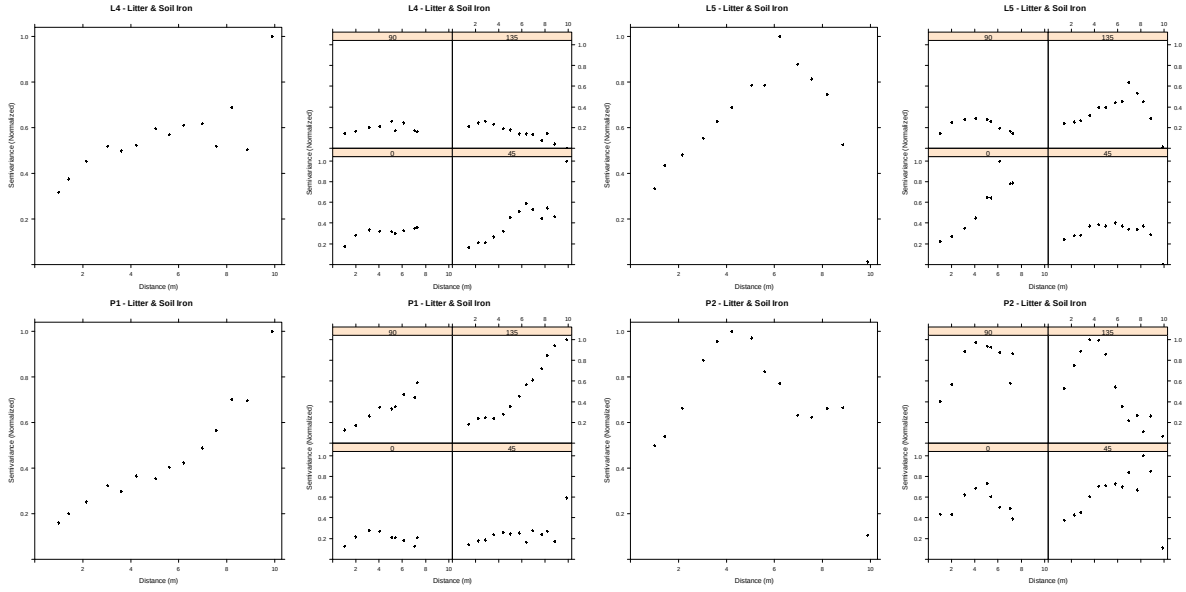


Figure B.37. Normalized semi-variograms of the standardized residuals computed for linear regressions, with log transformed litter as the response variable and soil iron as the explanatory variable, for each grid that involved soil sampling (L4, L5, P1 and P2). The second and fourth columns show directional semi-variograms at 0, 45, 90, and 135º.

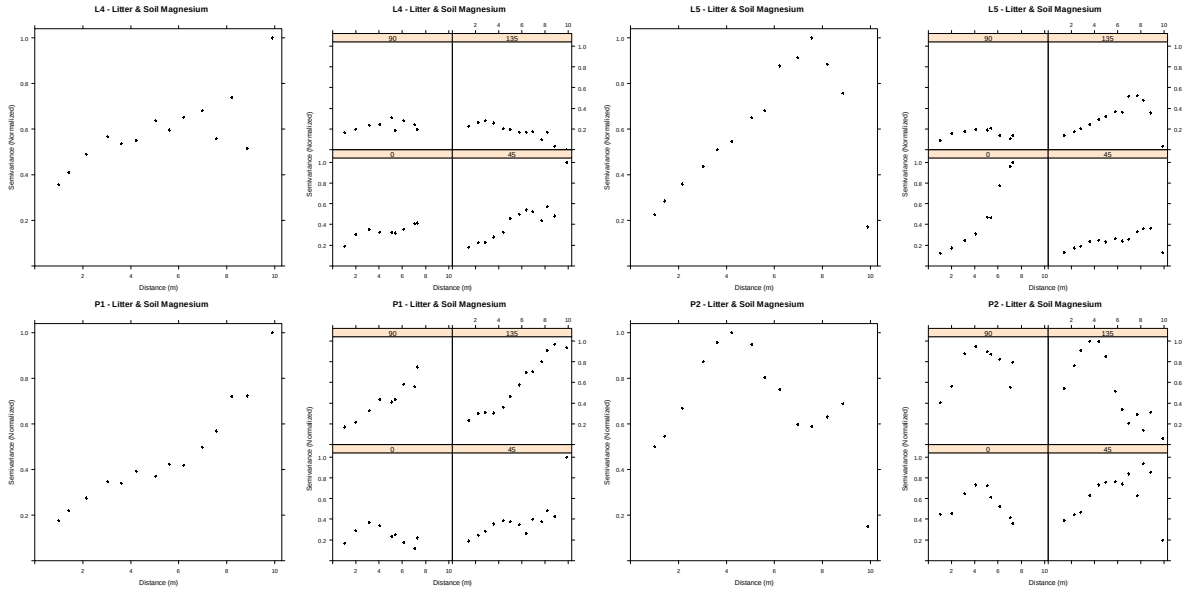


Figure B.38. Normalized semi-variograms of the standardized residuals computed for linear regressions, with log transformed litter as the response variable and soil magnesium as the explanatory variable, for each grid that involved soil sampling (L4, L5, P1 and P2). The second and fourth columns show directional semi-variograms at 0, 45, 90, and 135º.

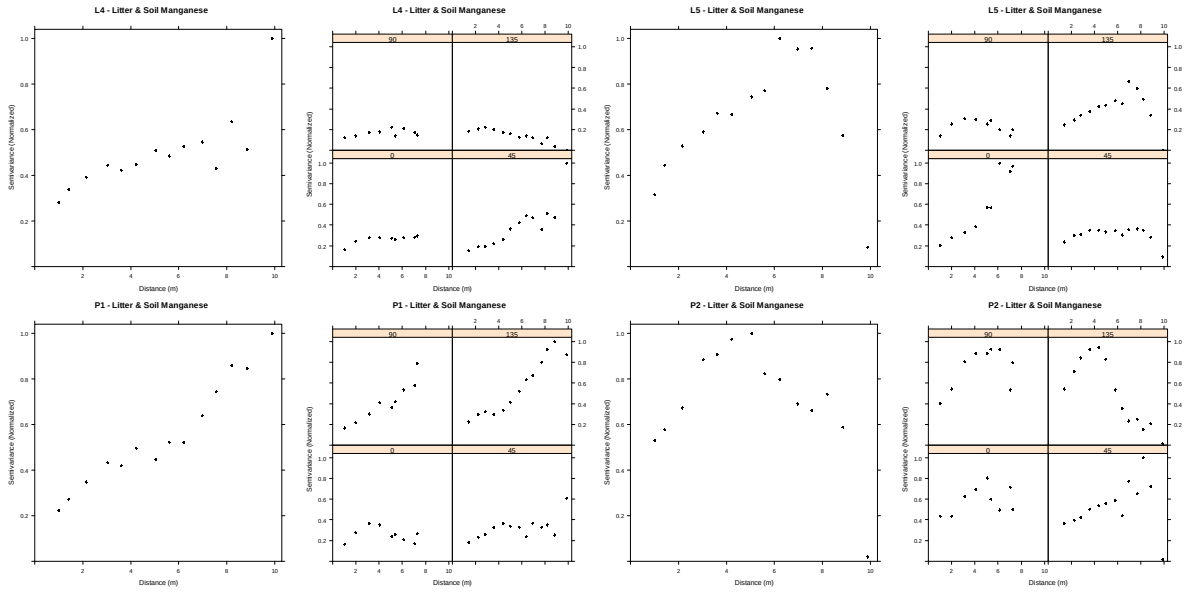


Figure B.39. Normalized semi-variograms of the standardized residuals computed for linear regressions, with log transformed litter as the response variable and soil manganese as the explanatory variable, for each grid that involved soil sampling (L4, L5, P1 and P2). The second and fourth columns show directional semi-variograms at 0, 45, 90, and 135º.

APPENDIX C: POISSON REGRESSIONS

Table C.1. Poisson regressions using data from all 14 grids with species richness as the response variable. Form codes are as follows: CD = concave down quadratic model, CU = concave up quadratic model, POS = positive linear model, and NEG = negative linear model. For quadratic models degrees of freedom for the null and residual deviance respectively are 895 and 893 at 1 m^2, 447 and 445 at 2 m^2, 223 and 221 at 4 m^2, 55 and 53 at 16 m^2, 13 and 11 at 64 m^2; and for linear models are 895 and 894 at 1 m^2, 447 and 446 at 2 m^2, 223 and 222 at 4 m^2, 55 and 54 at 16 m^2, and 13 and 12 at 64 m^2. Grey highlights show regressions at the 1 m^2 scale. Non-significant results are left blank.

Exp. Variable (g) (Log10)	**Scale (m^2)**	**Form**	**Term 1**		**Term 2**		**Model**				
			t Statistic	*p* Value	*t* Statistic	*p* Value	Disp.	Null Dev.	Res. Dev.	Exp. Dev.	AIC
Total Biomass	1	CD	8.41	4.25E-17	-8.69	3.50E-18	0.84	848.27	752.13	11.33	4203.63
	2	CD	7.56	3.91E-14	-7.76	8.40E-15	1.00	519.58	445.32	14.29	2268.35
	4	CD	5.64	1.73E-08	-5.81	6.33E-09	1.11	293.26	245.86	16.16	1205.16
	16	CD	3.37	7.39E-04	-3.45	5.53E-04	1.11	75.85	59.09	22.09	324.24
	64										
Live Biomass	1	NEG	-3.69	2.29E-04			0.93	848.27	834.57	1.61	4284.07
	2	NEG	-3.25	1.17E-03			1.14	519.58	508.93	2.05	2329.96
	4	NEG	-3.39	6.94E-04			1.27	293.26	281.58	3.98	1238.88
	16										
	64										
Litter	1	CD	8.21	2.25E-16	-8.85	9.02E-19	0.84	848.27	746.01	12.05	4197.52
	2	CD	7.79	6.48E-15	-8.16	3.46E-16	0.99	519.58	438.53	15.60	2261.56
	4	CD	5.45	4.91E-08	-5.75	8.98E-09	1.12	293.26	247.06	15.75	1206.36
	16										
	64										

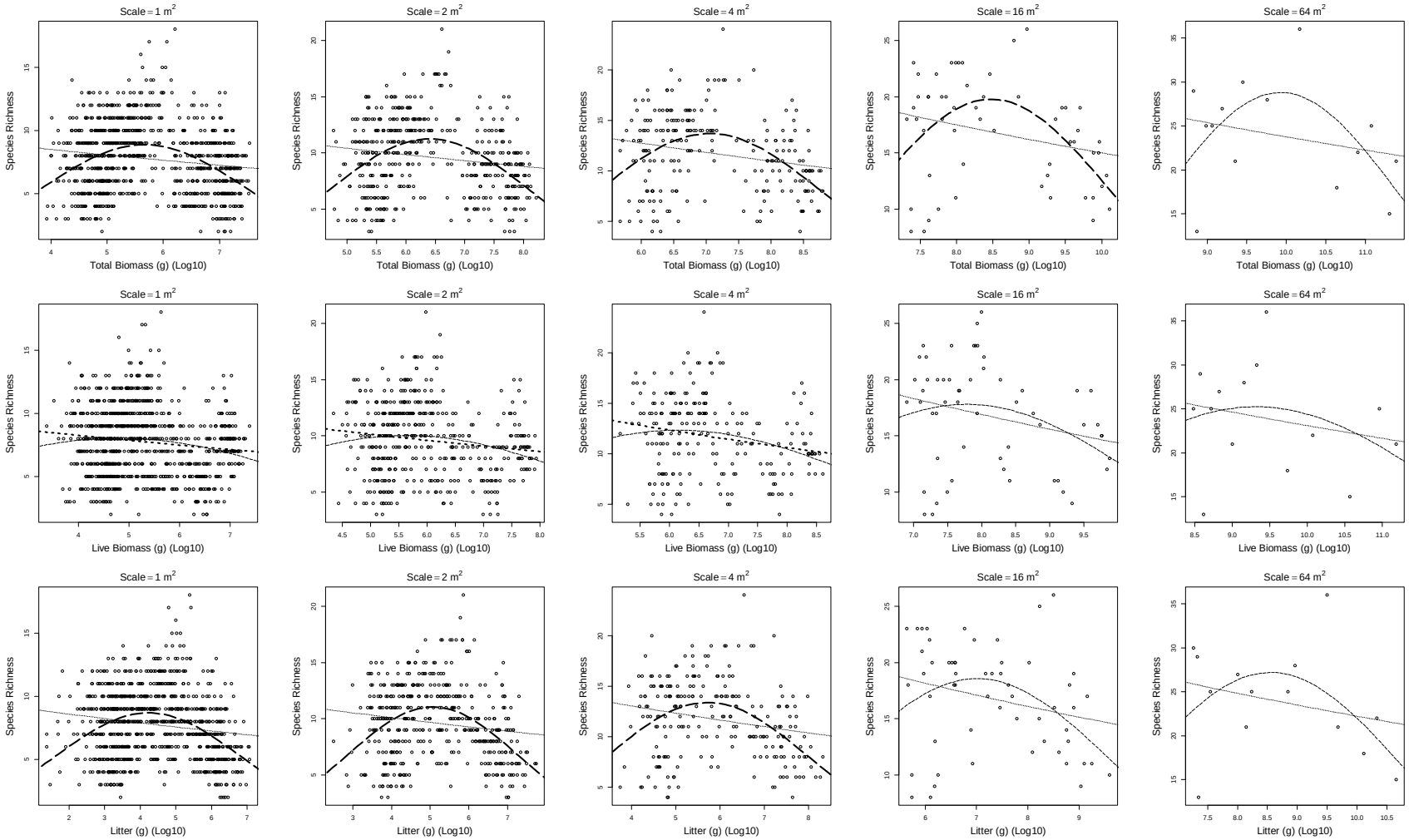


Figure C.1. Linear and quadratic fitted curves from Poisson regressions with species richness as the response variable and log transformed total biomass (top row), live biomass (center row), and litter (bottom row) as the explanatory variables using the 14-grid dataset across scales. The dotted line is the fitted linear model and the dashed line is the fitted quadratic model. The significant model in each plot is shown in bold.

Table C.2. Poisson regressions using data from the four soil grids with species richness as the response variable. Form codes are as follows: CD = concave down quadratic model, CU = concave up quadratic model, POS = positive linear model, and NEG = negative linear model. For quadratic models degrees of freedom for the null and residual deviance respectively are 255 and 253 at 1 m^2, 127 and 125 at 2 m^2, 63 and 61 at 4 m^2, 15 and 13 at 16 m^2, 3 and 1 at 64 m^2; and for linear models are 255 and 254 at 1 m^2, 127 and 126 at 2 m^2, 63 and 62 at 4 m^2, 15 and 16 at 16 m^2, and 3 and 2 at 64 m^2. Grey highlights show regressions at the 1 m^2 scale. Non-significant results are left blank.

Exp. Variable (g) (Log10)	**Scale (m^2)**	**Form**	**Term 1**		**Term 2**		**Model**				
			t Statistic	*p* Value	*t* Statistic	*p* Value	Disp.	Null Dev.	Res. Dev.	Exp. Dev.	AIC
Total Biomass	1	CD	4.88	1.04E-06	-4.99	6.01E-07	0.98	277.75	248.41	10.56	1191.07
	2	CD	4.33	1.52E-05	-4.40	1.10E-05	1.20	172.51	150.10	12.99	652.06
	4	CD	3.94	8.10E-05	-3.98	6.78E-05	1.34	98.98	81.47	17.69	348.23
	16	CD	2.98	2.91E-03	-2.98	2.87E-03	1.26	25.44	16.39	35.59	93.21
	64										
Live Biomass	1	NEG	-3.68	2.34E-04			1.04	277.75	264.18	4.88	1204.85
	2	NEG	-3.11	1.85E-03			1.29	172.51	162.78	5.64	662.74
	4										
	16										
	64										
Litter	1	CD	6.57	5.20E-11	-6.62	3.51E-11	0.91	277.75	229.11	17.51	1171.77
	2	CD	6.81	9.73E-12	-6.84	7.79E-12	0.98	172.51	122.18	29.18	624.14
	4	CD	6.06	1.35E-09	-6.07	1.24E-09	0.97	98.98	59.21	40.18	325.98
	16	CD	3.79	1.49E-04	-3.78	1.55E-04	0.79	25.44	10.31	59.48	87.14
	64										

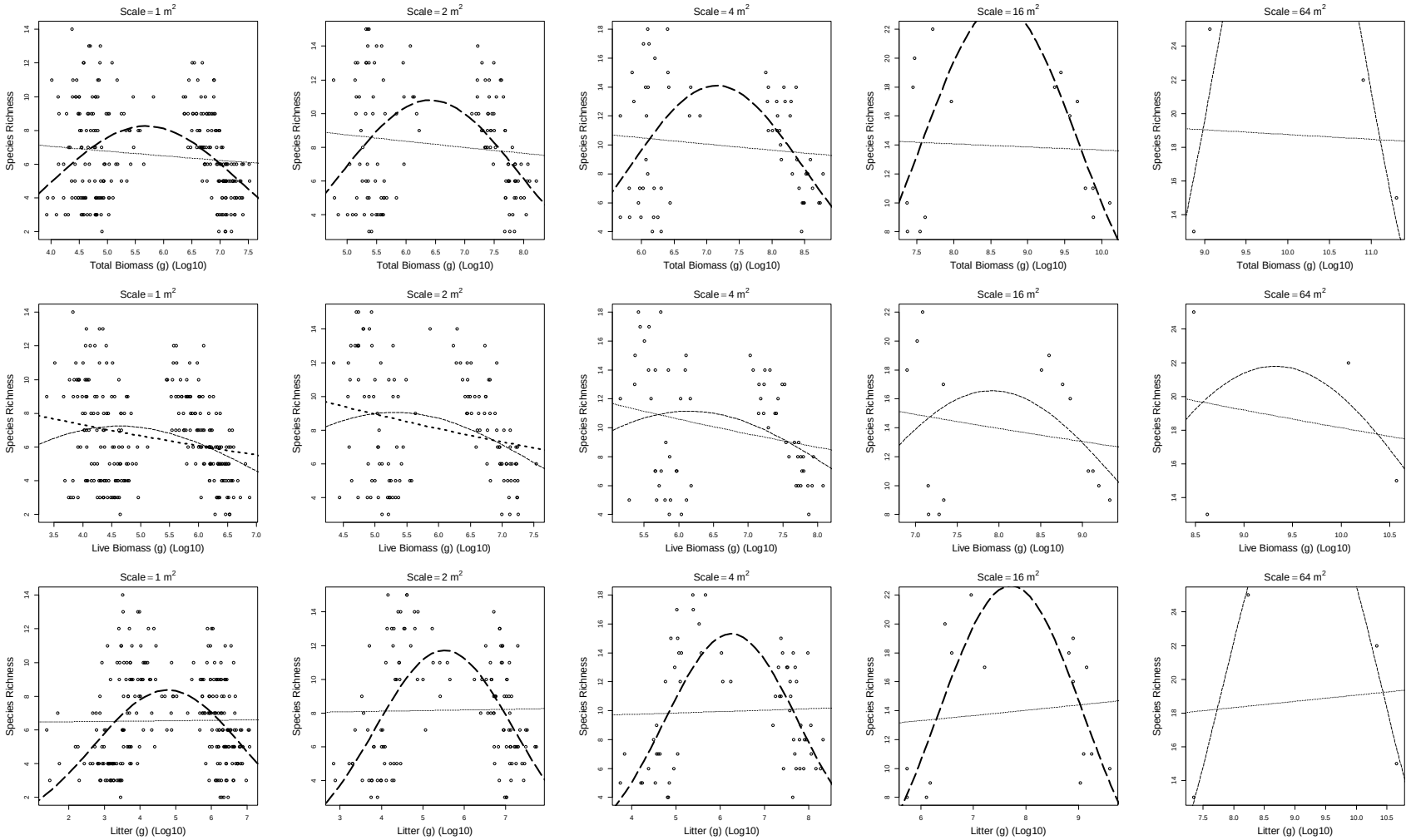


Figure C.2. Linear and quadratic fitted curves from Poisson regressions with species richness as the response variable and log transformed total biomass (top row), live biomass (center row), and litter (bottom row) as the explanatory variables using the four soil grids dataset across scales. The dotted line is the fitted linear model and the dashed line is the fitted quadratic model. The significant model in each plot is shown in bold.

Table C.3. Poisson regressions with soil nutrient PCA axes using data from the four soil grids with species richness as the response variable. Form codes are as follows: CD = concave down quadratic model, CU = concave up quadratic model, POS = positive linear model, and NEG = negative linear model. For quadratic models degrees of freedom for the null and residual deviance respectively are 255 and 253; and for linear models are 255 and 254. Non-significant results are left blank.

Explanatory Variable	**Scale (m^2)**	**Form**	**Term 1**		**Term 2**		**Model**				
			t Statistic	*p* Value	*t* Statistic	*p* Value	Disp.	Null Dev.	Res. Dev.	Exp. Dev.	AIC
PC1	1	CD	2.32	2.02E-02	-9.18	4.17E-20	0.72	277.75	181.47	34.66	1124.14
PC2	1	CD	-9.71	2.63E-22	-3.32	9.04E-04	0.68	277.75	171.74	38.17	1114.40
PC3	1	NEG	-4.45	8.79E-06			1.02	277.75	258.26	7.02	1198.92

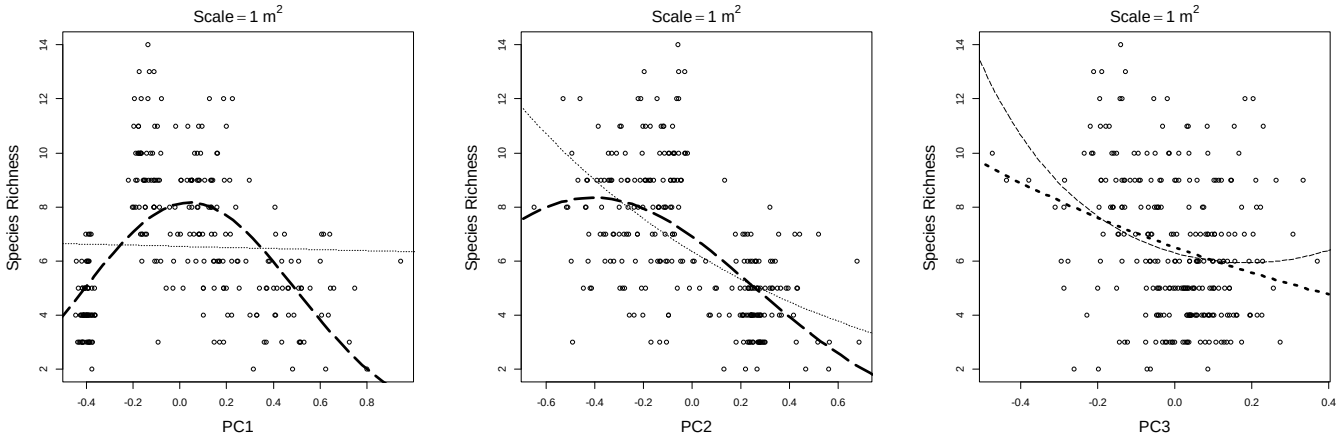


Figure C.3. Linear and quadratic fitted curves from Poisson regressions with species richness as the response variable and PC1, PC2, and PC3 from the soil nutrient PCA. The dotted line is the fitted linear model and the dashed line is the fitted quadratic model. The significant model in each plot is shown in bold.

Table C.4. Poisson regressions of soil nutrients as the explanatory variable with species richness as the response variable. Form codes are as follows: CD = concave down quadratic model, CU = concave up quadratic model, POS = positive linear model, and NEG = negative linear model. For quadratic models degrees of freedom for the null and residual deviance respectively are 255 and 253 at 1 m^2, 127 and 125 at 2 m^2, 63 and 61 at 4 m^2, 15 and 13 at 16 m^2, 3 and 1 at 64 m^2; and for linear models are 255 and 254 at 1 m^2, 127 and 126 at 2 m^2, 63 and 62 at 4 m^2, 15 and 16 at 16 m^2, and 3 and 2 at 64 m^2. Grey highlights show regressions at the 1 m^2 scale. Non-significant results are left blank.

Explanatory Variable	**Scale (m^2)**	**Form**	**Term 1**		**Term 2**		**Model**				
			t Statistic	*p* Value	*t* Statistic	*p* Value	Disp.	Null Dev.	Res. Dev.	Exp. Dev.	AIC
Soil Carbon	1	CD	6.00	2.01E-09	-5.23	1.67E-07	0.93	277.75	234.50	15.57	1177.16
	2	CD	6.00	2.01E-09	-5.23	1.67E-07	0.93	277.75	234.50	15.57	1177.16
	4	CD	5.54	3.11E-08	-4.94	7.95E-07	1.09	172.51	136.51	20.87	638.47
	16	CD	4.59	4.43E-06	-4.12	3.80E-05	1.22	98.98	74.22	25.01	340.99
	64										
Soil Nitrogen	1	CD	5.75	9.19E-09	-5.08	3.68E-07	0.94	277.75	237.55	14.47	1180.22
	2	CD	5.30	1.16E-07	-4.80	1.62E-06	1.12	172.51	139.54	19.11	641.50
	4	CD	4.35	1.38E-05	-3.95	7.68E-05	1.26	98.98	76.80	22.41	343.56
	16										
	64										
Soil C:N	1	CD	4.85	1.21E-06	-4.54	5.66E-06	0.81	277.75	205.86	25.88	1148.52
	2	CD	3.79	1.51E-04	-3.51	4.45E-04	0.93	172.51	115.97	32.78	617.93
	4	POS	5.52	3.30E-08			1.05	98.98	65.37	33.95	330.14
	16	POS	3.04	2.38E-03			1.09	25.44	15.19	40.28	90.02
	64										
Soil Phosphorus	1	CD	4.03	5.62E-05	-3.23	1.22E-03	0.77	277.75	194.44	29.99	1137.11
	2	CD	3.71	2.10E-04	-3.08	2.09E-03	0.85	172.51	106.12	38.48	608.08
	4	POS	6.16	7.30E-10			0.97	98.98	60.41	38.97	325.17

	16	POS	3.67	2.39E-04			0.78	25.44	10.97	56.90	85.79
	64										
Soil Potassium	1	NEG	-6.14	8.41E-10			0.93	277.75	237.28	14.57	1177.94
	2	NEG	-5.28	1.32E-07			1.13	172.51	142.30	17.51	642.26
	4	NEG	-4.19	2.73E-05			1.28	98.98	79.64	19.54	344.41
	16										
	64										
Soil Boron	1	CU	-4.78	1.74E-06	3.77	1.61E-04	0.90	277.75	226.92	18.30	1169.58
	2	CU	-4.47	7.91E-06	3.64	2.70E-04	1.05	172.51	130.93	24.10	632.89
	4	CU	-3.55	3.81E-04	2.93	3.42E-03	1.18	98.98	72.22	27.03	338.99
	16										
	64										
Soil Iron	1	CD	8.55	1.19E-17	-8.72	2.85E-18	0.76	277.75	193.39	30.37	1136.06
	2	CD	8.05	8.05E-16	-8.18	2.92E-16	0.80	172.51	100.14	41.95	602.10
	4	CD	6.83	8.79E-12	-6.92	4.49E-12	0.78	98.98	47.74	51.76	314.51
	16	CD	3.80	1.46E-04	-3.87	1.10E-04	0.68	25.44	8.83	65.30	85.65
	64										
Soil Magnesium	1	CU	-7.02	2.26E-12	5.33	1.01E-07	0.55	277.75	139.69	49.71	1082.35
	2	CU	-6.06	1.35E-09	4.87	1.12E-06	0.55	172.51	68.61	60.23	570.57
	4	CU	-4.74	2.09E-06	3.94	8.26E-05	0.47	98.98	28.87	70.83	295.63
	16	NEG	-3.98	6.89E-05			0.59	25.44	8.21	67.72	83.04
	64										
Soil Manganese	1	CD	3.48	4.98E-04	-3.12	1.80E-03	0.80	277.75	202.50	27.09	1145.16
	2	CD	3.39	6.94E-04	-3.09	1.99E-03	0.83	172.51	103.42	40.05	605.38
	4	CD	3.04	2.39E-03	-2.79	5.28E-03	0.75	98.98	45.68	53.85	312.45
	16	POS	3.84	1.23E-04			0.76	25.44	10.58	58.40	85.41
	64										

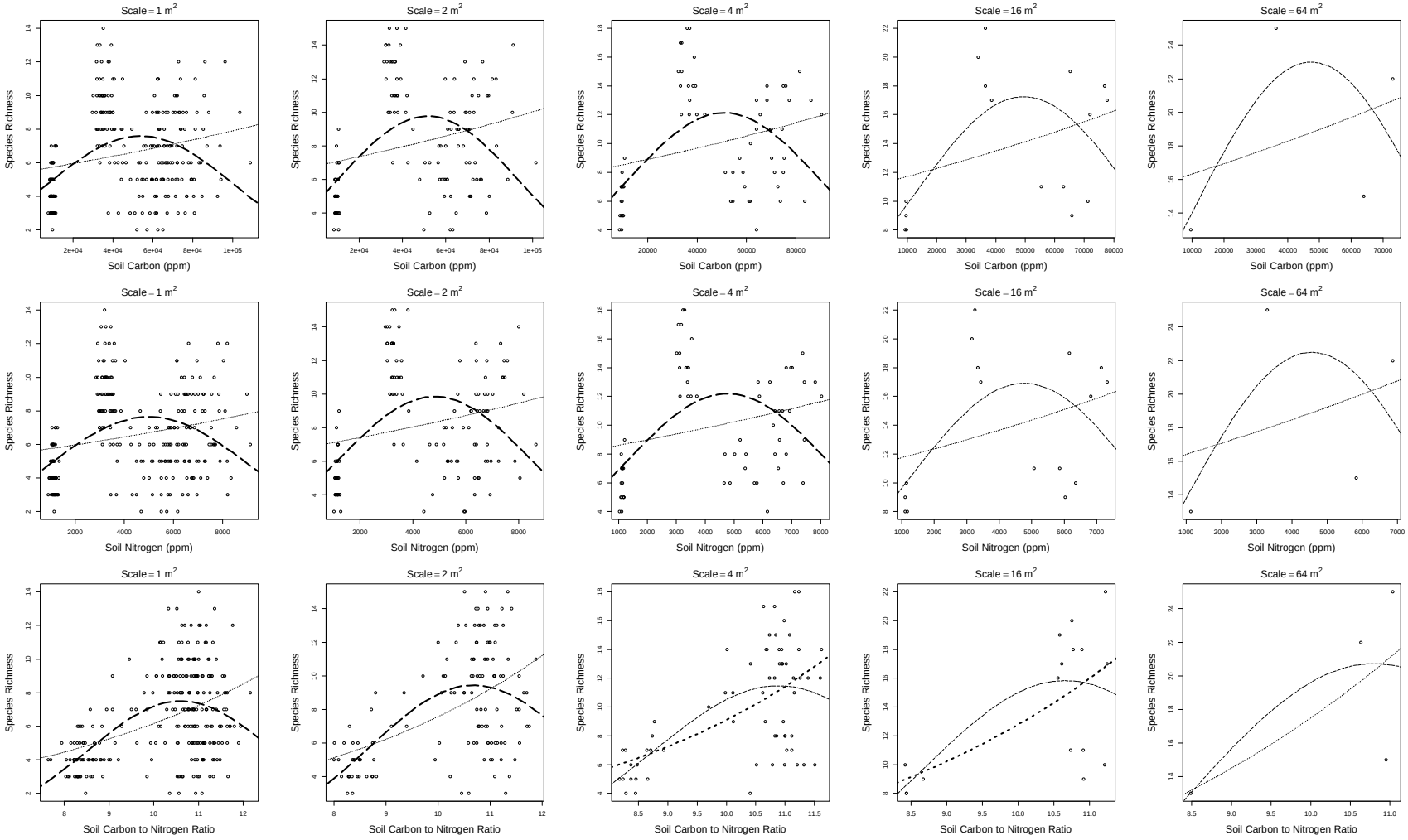


Figure C.4. Linear and quadratic fitted curves from Poisson regressions with species richness as the response variable and soil carbon (top row), soil nitrogen (center row), and soil carbon to nitrogen ratio (bottom row) as the explanatory variables using the four soil grids dataset across scales. The dotted line is the fitted linear model and the dashed line is the fitted quadratic model. The significant model in each plot is shown in bold.

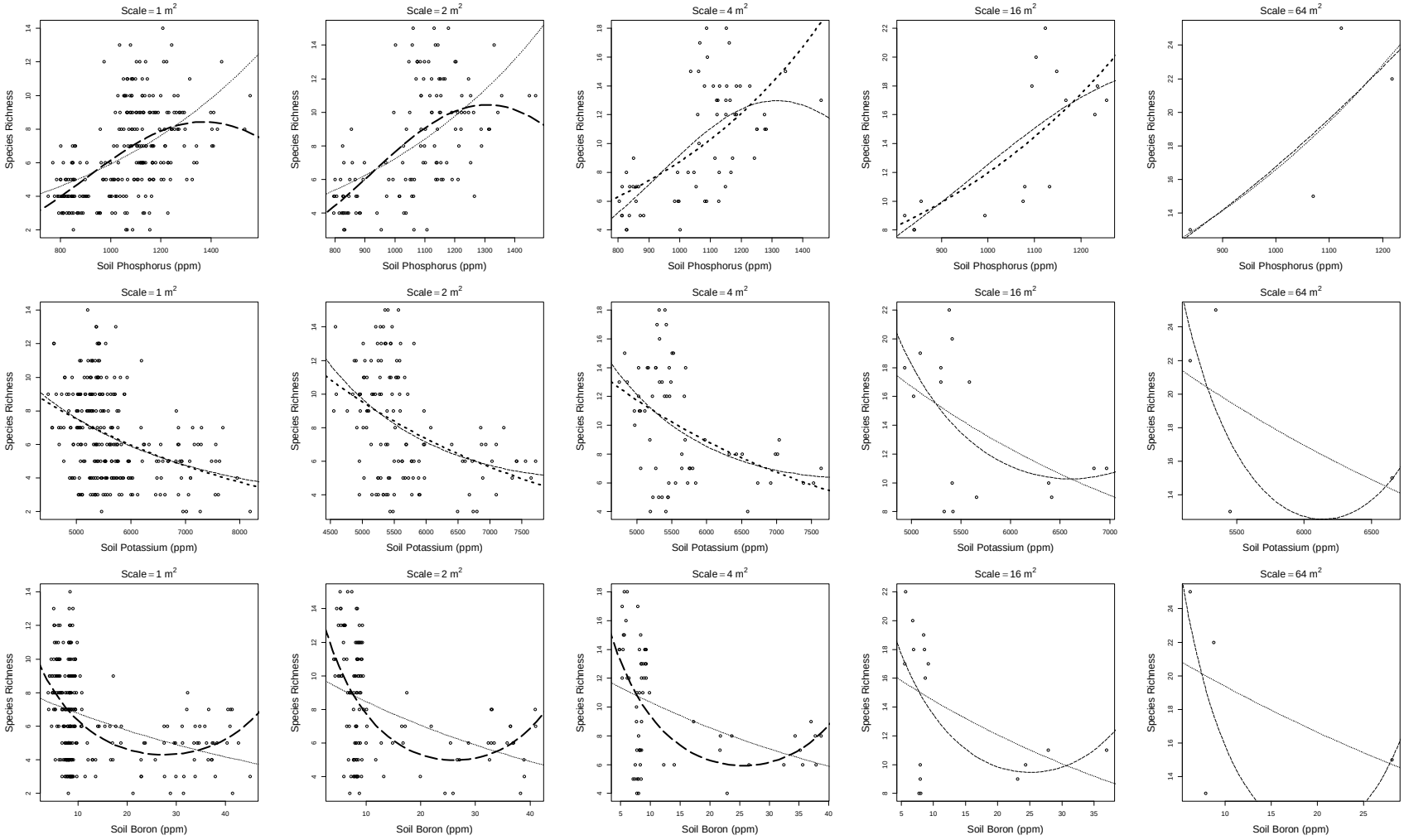


Figure C.5. Linear and quadratic fitted curves from Poisson regressions with species richness as the response variable and soil phosphorus (top row), soil potassium (center row), and soil boron (bottom row) as the explanatory variables using the four soil grids dataset across scales. The dotted line is the fitted linear model and the dashed line is the fitted quadratic model. The significant model in each plot is shown in bold.

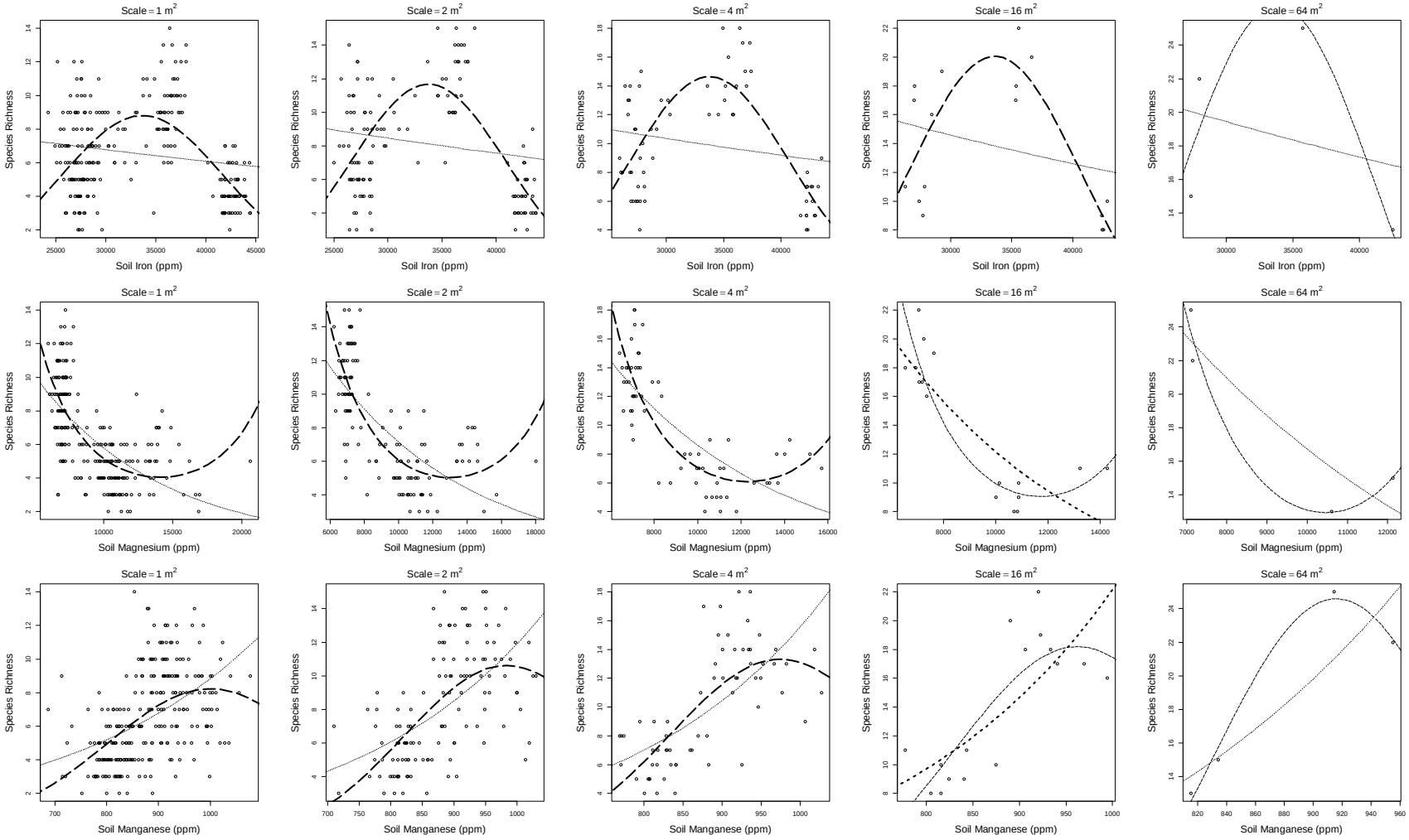


Figure C.6. Linear and quadratic fitted curves from Poisson regressions with species richness as the response variable and soil iron (top row), soil magnesium (center row), and soil manganese (bottom row) as the explanatory variables using the four soil grids dataset across scales. The dotted line is the fitted linear model and the dashed line is the fitted quadratic model. The significant model in each plot is shown in bold.

Table C.5. Poisson regressions with axes from the PCA of all soil and leaf nutrients as the explanatory variables and species richness as the response variable. Form codes are as follows: CD = concave down quadratic model, CU = concave up quadratic model, POS = positive linear model, and NEG = negative linear model. For quadratic models degrees of freedom for the null and residual deviance respectively are 35 and 33, and for linear models are 35 and 34. Non-significant results are left blank.

Explanatory Variable	**Scale (m^2)**	**Form**	**Term 1**		**Term 2**		**Model**				
			t Statistic	*p* Value	*t* Statistic	*p* Value	Disp.	Null Dev.	Res. Dev.	Exp. Dev.	AIC
PC1	1	CD	-0.54	5.88E-01	-2.77	5.53E-03	0.89	38.70	29.39	24.05	166.27
PC2	1	NEG	-3.41	6.53E-04			0.76	38.70	26.01	32.81	160.88
PC3	1										

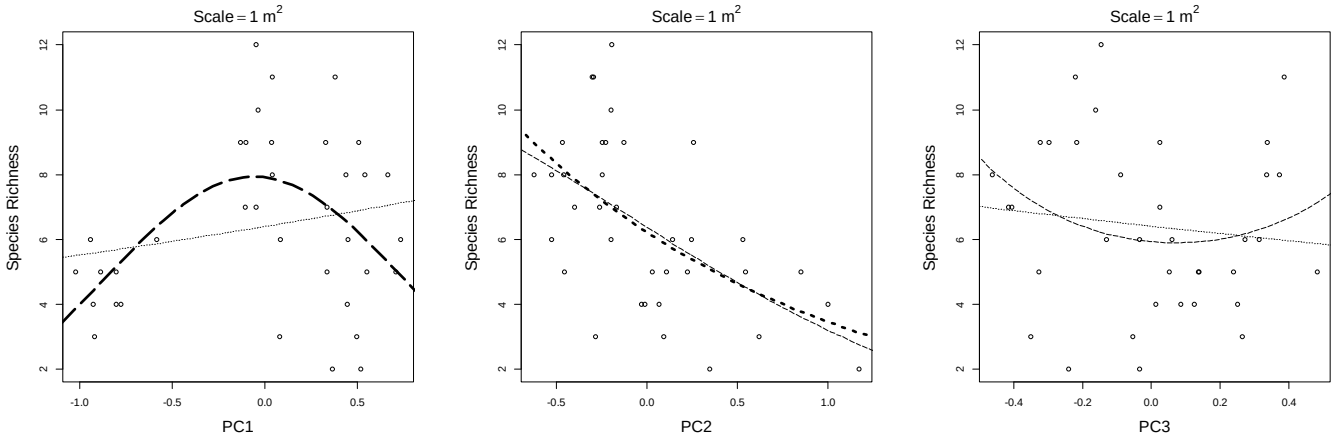


Figure C.7. Linear and quadratic fitted curves from Poisson regressions with species richness as the response variable and PC1, PC2, and PC3 from the soil and leaf nutrient PCA. The dotted line is the fitted linear model and the dashed line is the fitted quadratic model. The significant model in each plot is shown in bold.

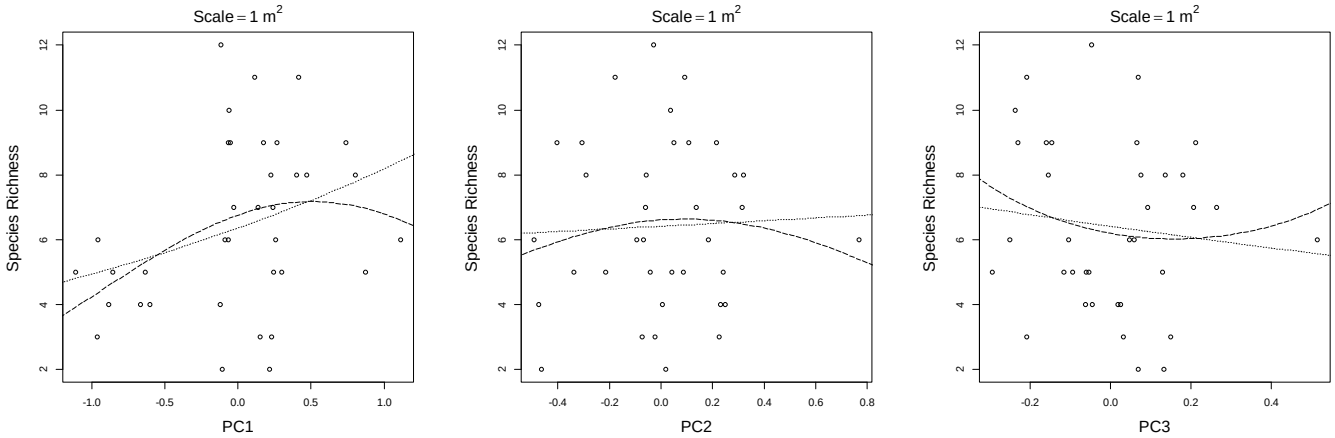


Figure C.8. Linear and quadratic fitted curves from Poisson regressions with species richness as the response variable and PC1, PC2, and PC3 from the PCA of only soil carbon, nitrogen and carbon to nitrogen ratio and leaf carbon, nitrogen and carbon to nitrogen ratio. The dotted line is the fitted linear model and the dashed line is the fitted quadratic model. The significant model in each plot is shown in bold.

APPENDIX D: SPECIES RICHNESS AND BIOMASS - SCALED REGRESSIONS

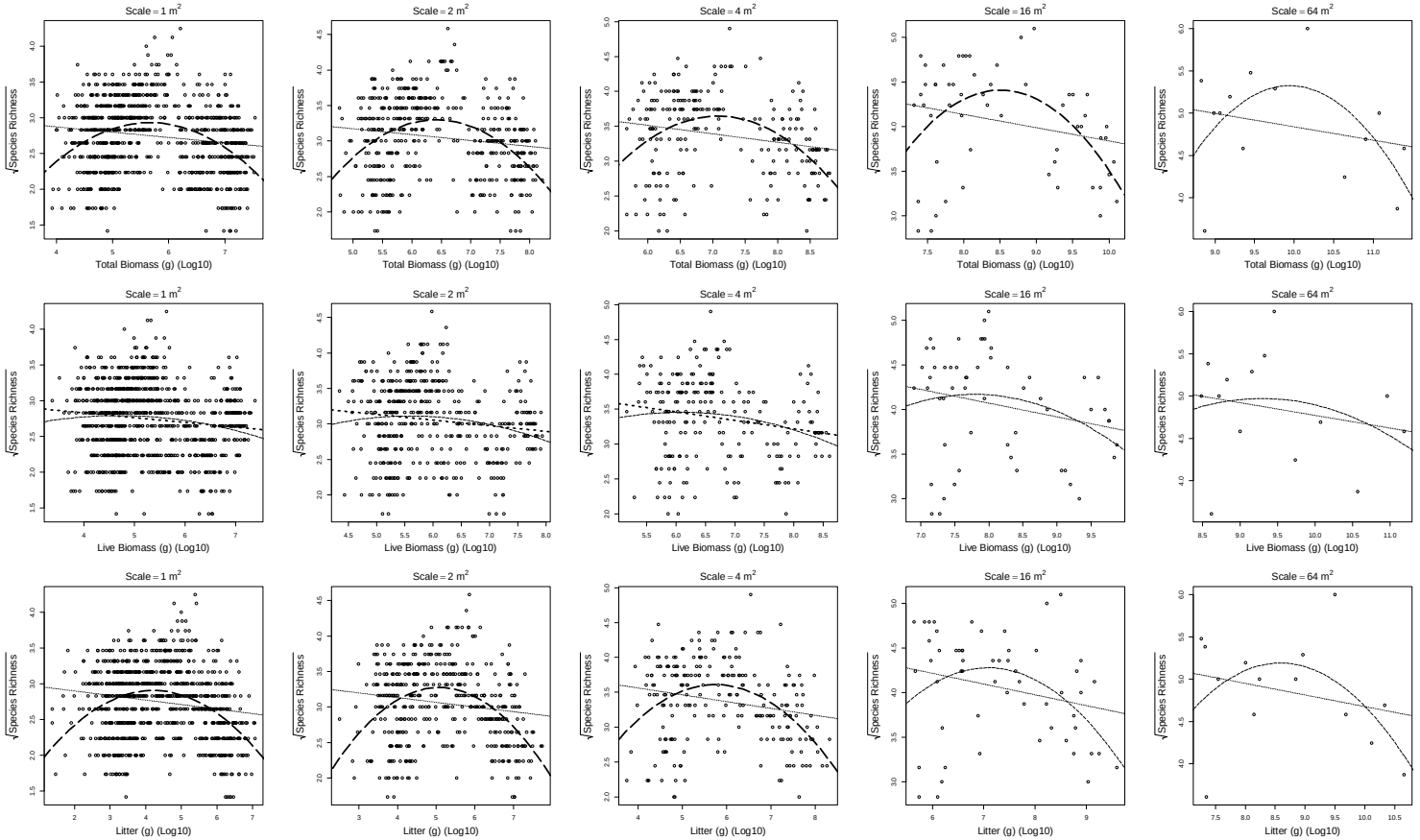


Figure D.1. Square root transformed species richness with fitted curves from linear regression models with log transformed total biomass (top row) and log transformed live biomass (center panels) and log transformed litter (bottom panels) as the explanatory variables, across scales, using the 14-grid dataset. The dotted line is the fitted linear model and the dashed line is the fitted quadratic model. The significant model in each plot is shown in bold.

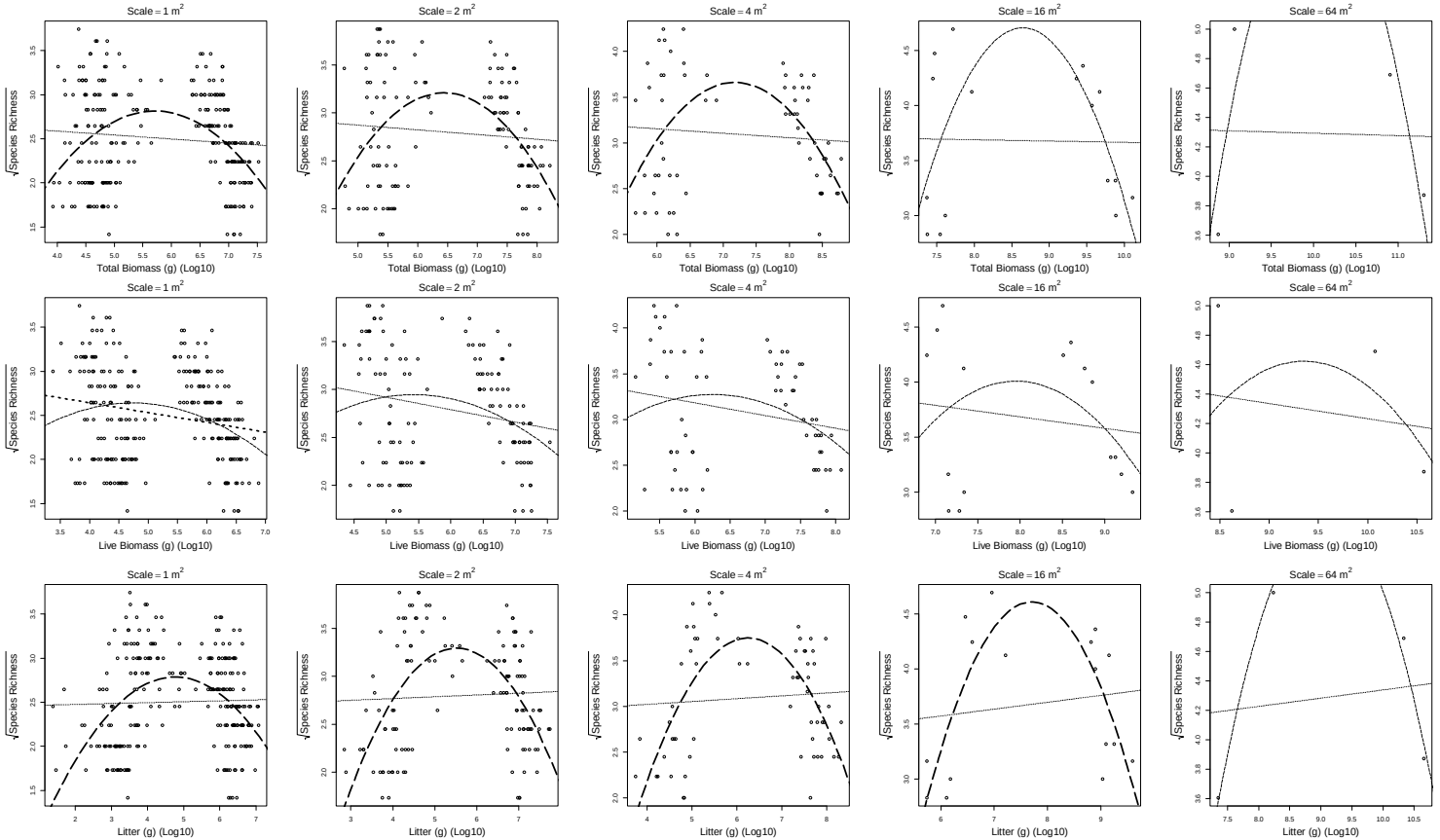


Figure D.2. Square root transformed species richness with fitted curves from linear regression models with log transformed total biomass (top row) and log transformed live biomass (center panels) and log transformed litter (bottom panels) as the explanatory variables, across scales, using the 4-grid dataset. The dotted line is the fitted linear model and the dashed line is the fitted quadratic model. The significant model in each plot is shown in bold.

APPENDIX E: KAISER-GUTTMAN AND PC3 BIPLOTS

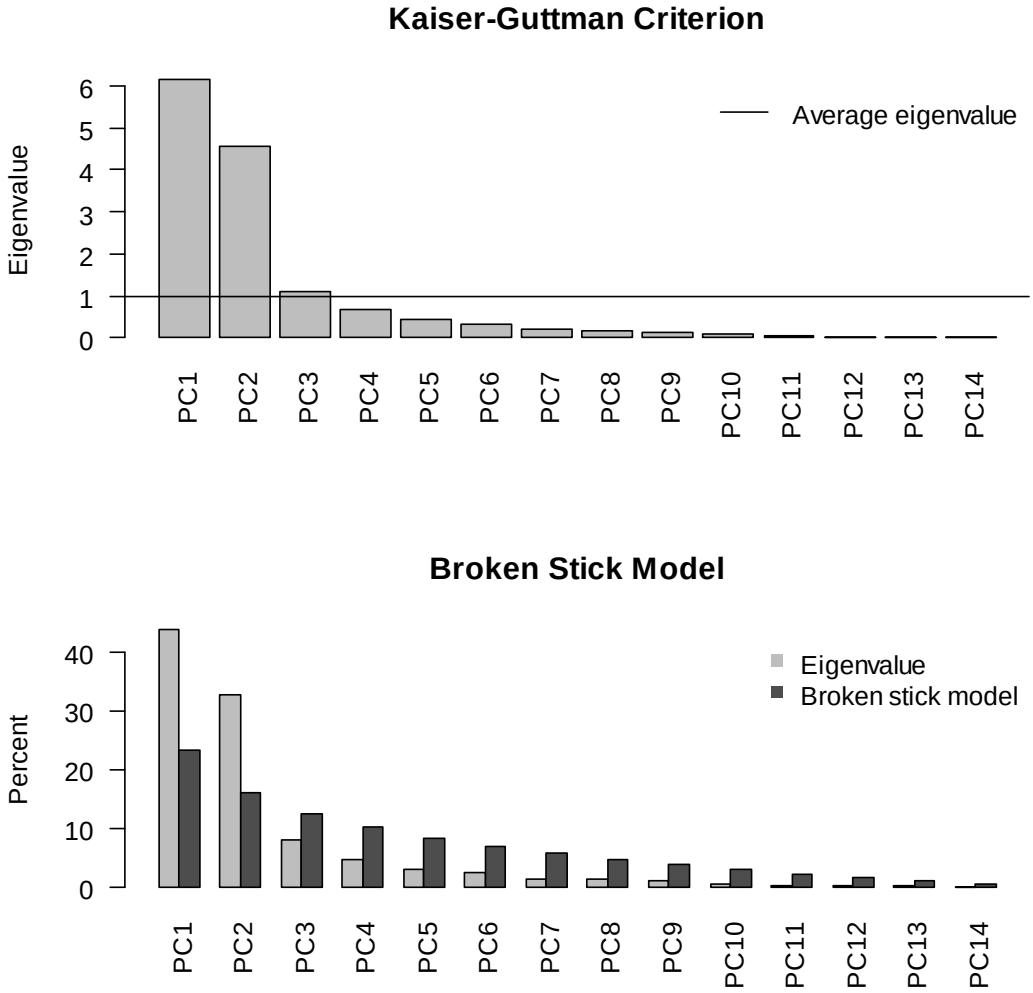


Figure E.1. Kaiser-Guttman criterion (upper panel) and broken stick model (lower panel) evaluation of the PCA axes on the soil nutrient data.

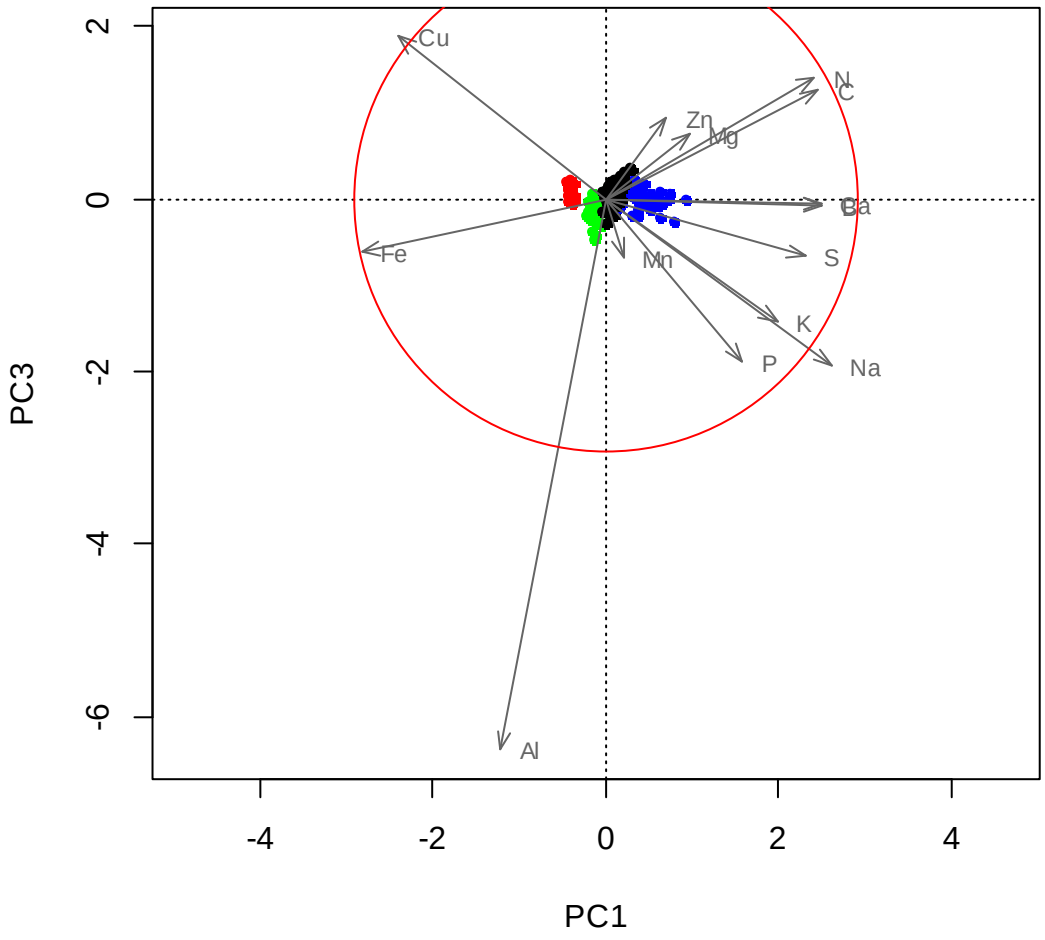


Figure E.2. Distance biplot of PC1 and PC3 from the PCA of the soil nutrient data. Each grid is indicated by points of a certain colour. The L4 (red points) and L5 (green points) grids were lower biomass grids while the P1 (blue points) and P2 (black points) grids were higher biomass grids.

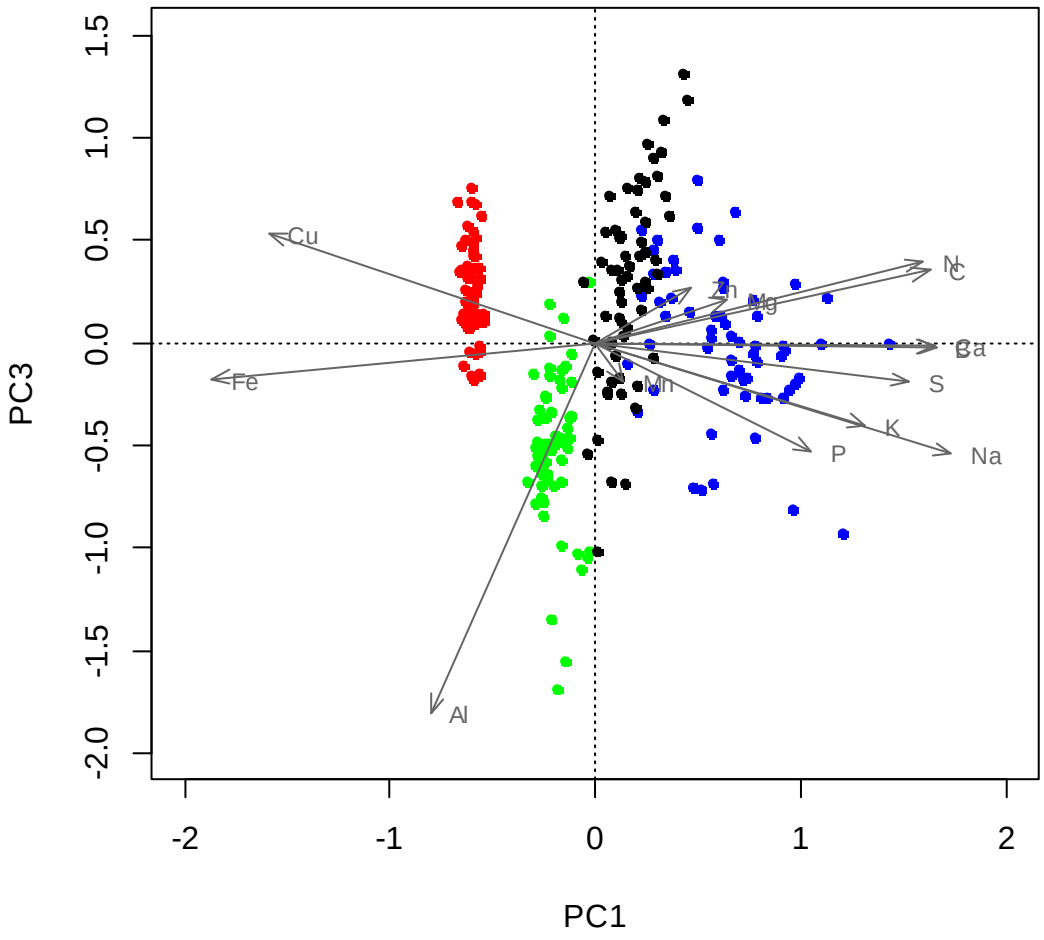


Figure E.3. Correlation biplot of PC1 and PC3 from the PCA on the soil nutrient data. Each grid is indicated by points of a certain colour. The L4 (red points) and L5 (green points) grids were lower biomass grids while the P1 (blue points) and P2 (black points) grids were higher biomass grids.

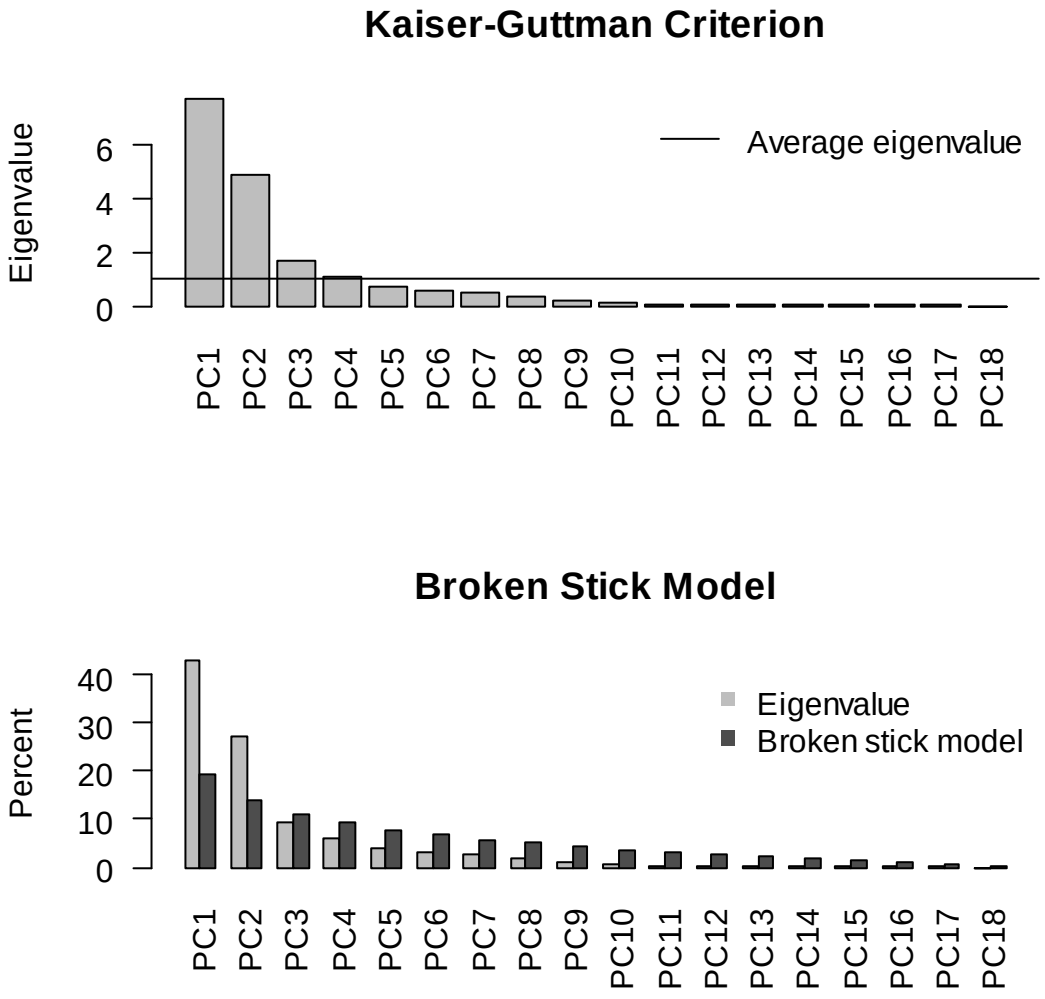


Figure E.4. Plots of the Kaiser-Guttman criterion and broken stick models of the PCA on the soil and leaf nutrient data. The Kaiser-Guttman plot shows the first four principal component axes contain relevant information while the more conservative broken stick model indicates only two axes need be considered.

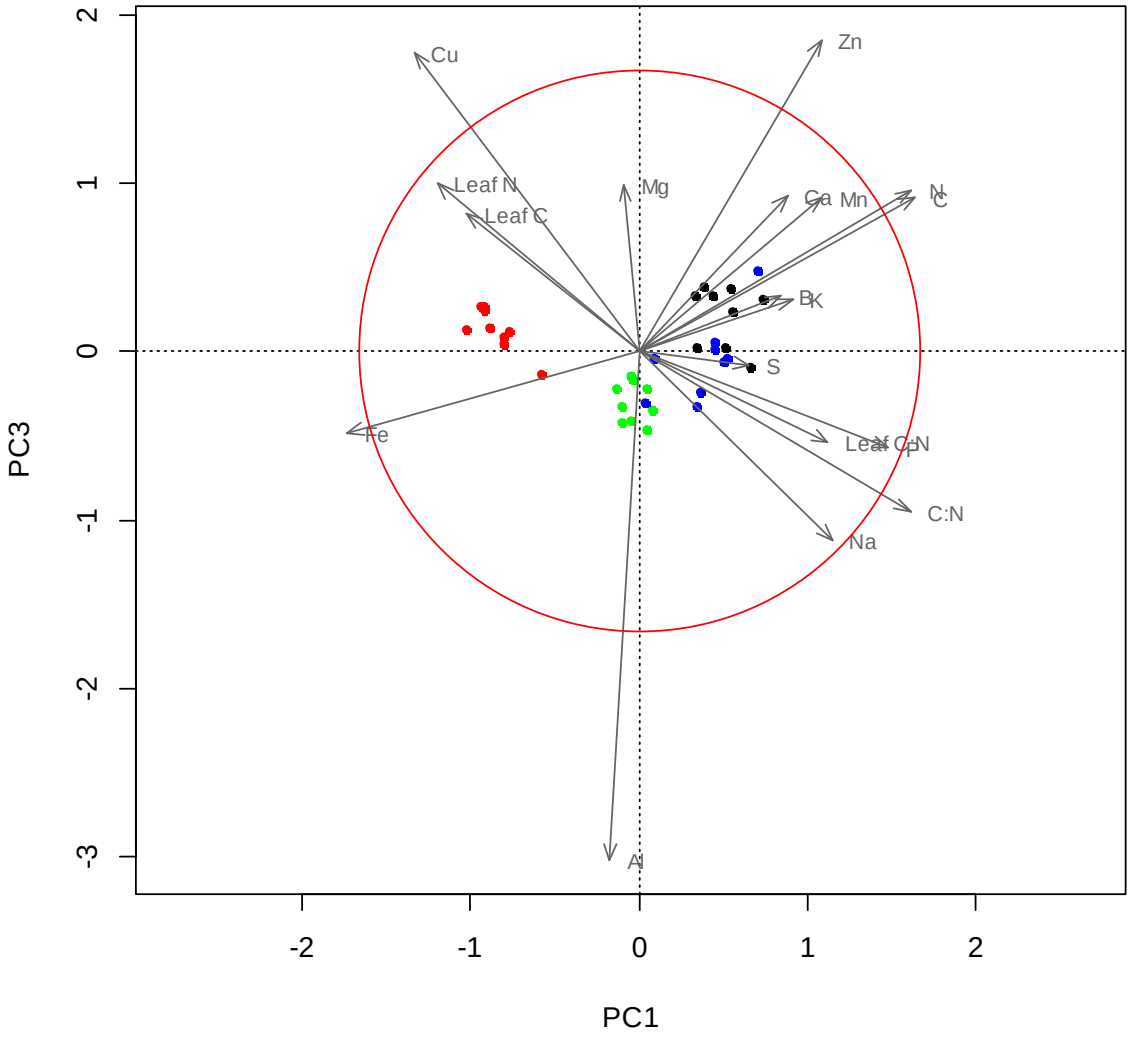


Figure E.5. Distance biplot of PC1 and PC3 from the PCA on the soil and leaf nutrient data. Each grid is indicated by points of a certain colour. The L4 (red points) and L5 (green points) grids were lower biomass grids while the P1 (blue points) and P2 (black points) grids were higher biomass grids.

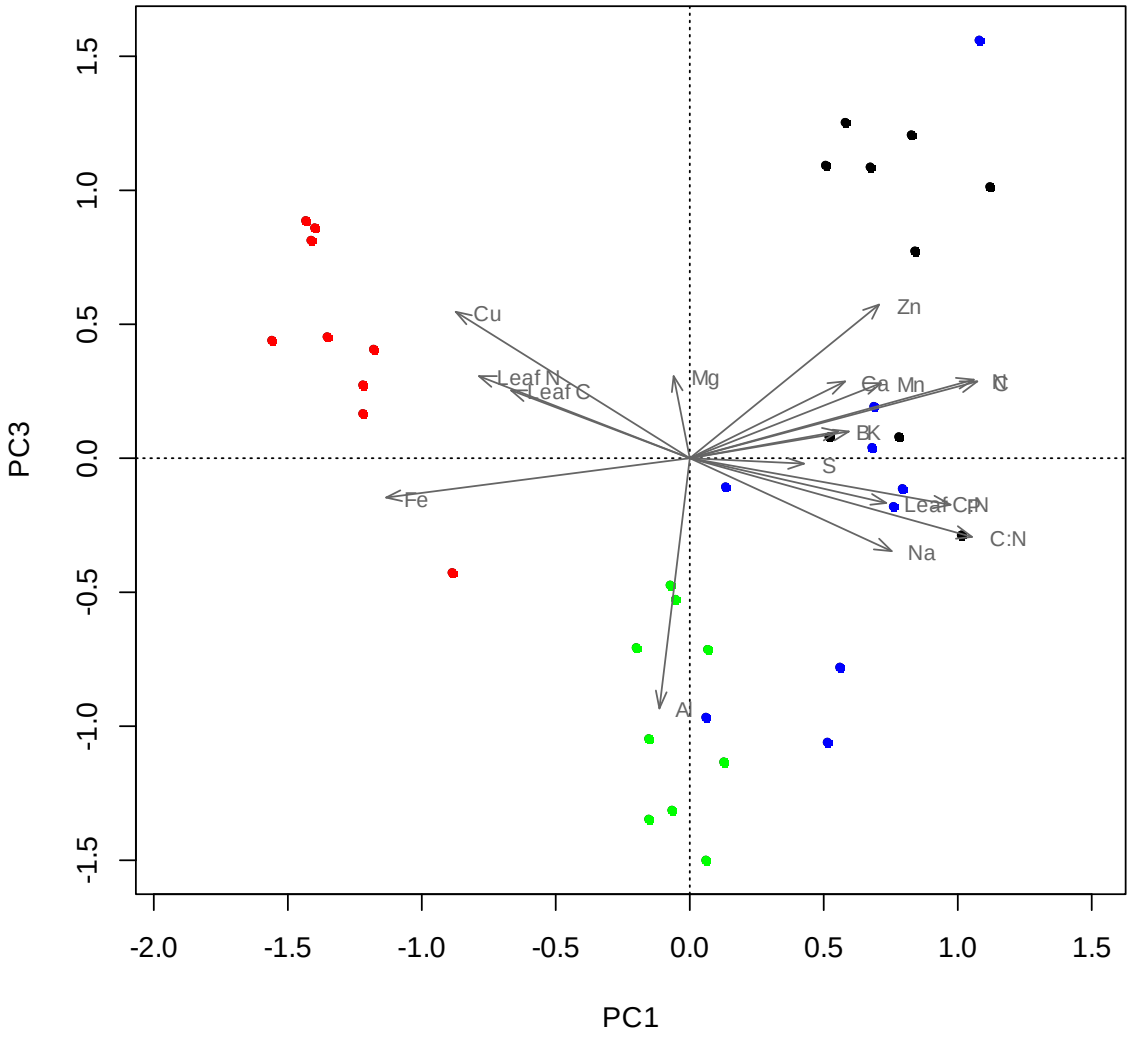


Figure E.6. Correlation biplot of PC1 and PC3 from the PCA on the soil and leaf nutrient data. Each grid is indicated by points of a certain colour. The L4 (red points) and L5 (green) grids were lower biomass grids while the P1 (blue points) and P2 (black points) grids were higher biomass grids.

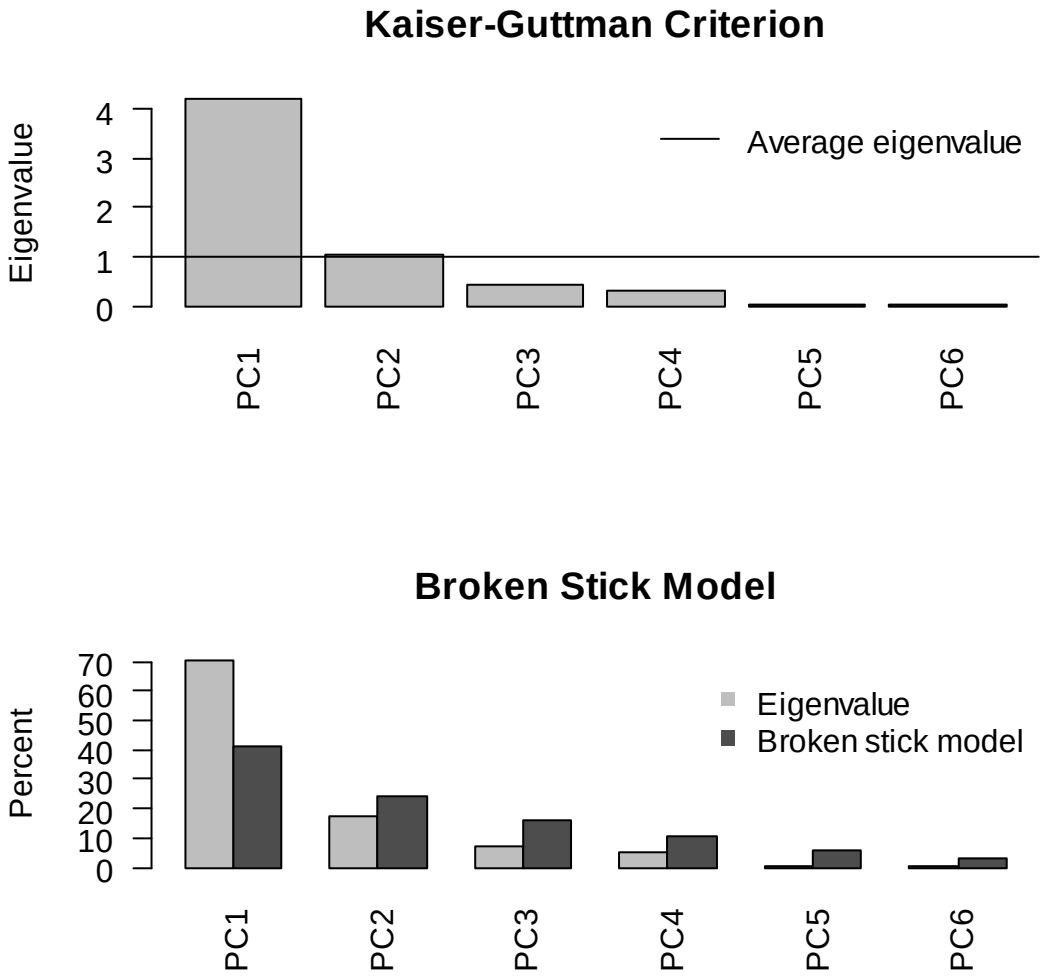


Figure E.7. Plots of the Kaiser-Guttman criterion and broken stick models of the PCA on the soil and leaf carbon, nitrogen and carbon to nitrogen ratio nutrient data. The Kaiser-Guttman plot suggests the first two PCA axes contain relevant information while the more conservative broken stick model indicates only PC1 need be considered.

APPENDIX F: PCA REGRESSIONS

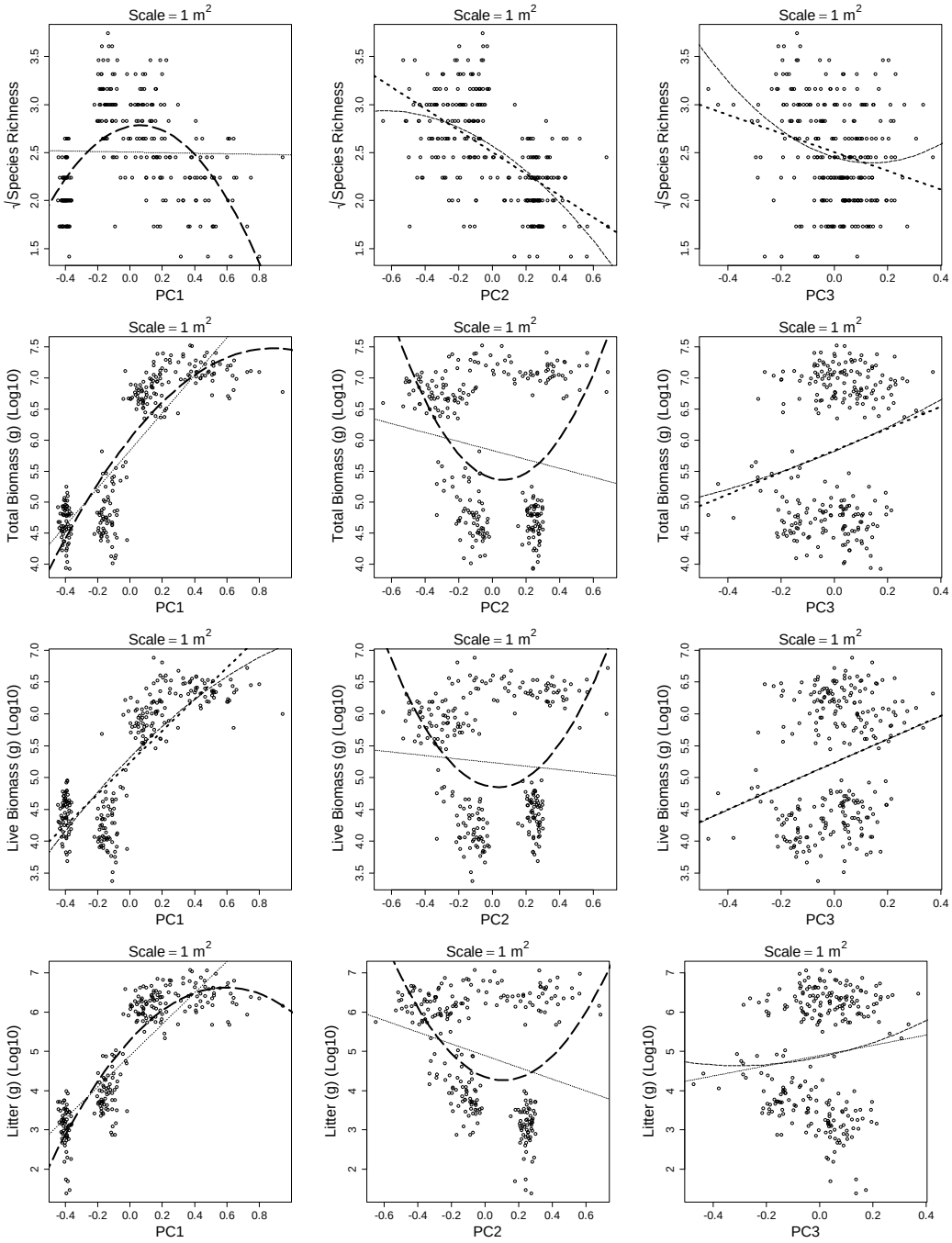


Figure F.1. Square root transformed species richness, log transformed total biomass, log transformed live biomass, and log transformed litter with the soil nutrient PCA axes. Fitted curves from linear regression models at 1 m^2 having PC1 (left panels) PC2 (center panels) and PC3 (right panels) as the explanatory variables are shown. The dotted line is the fitted linear model and the dashed line is the fitted quadratic model. The significant model in each plot is shown in bold.

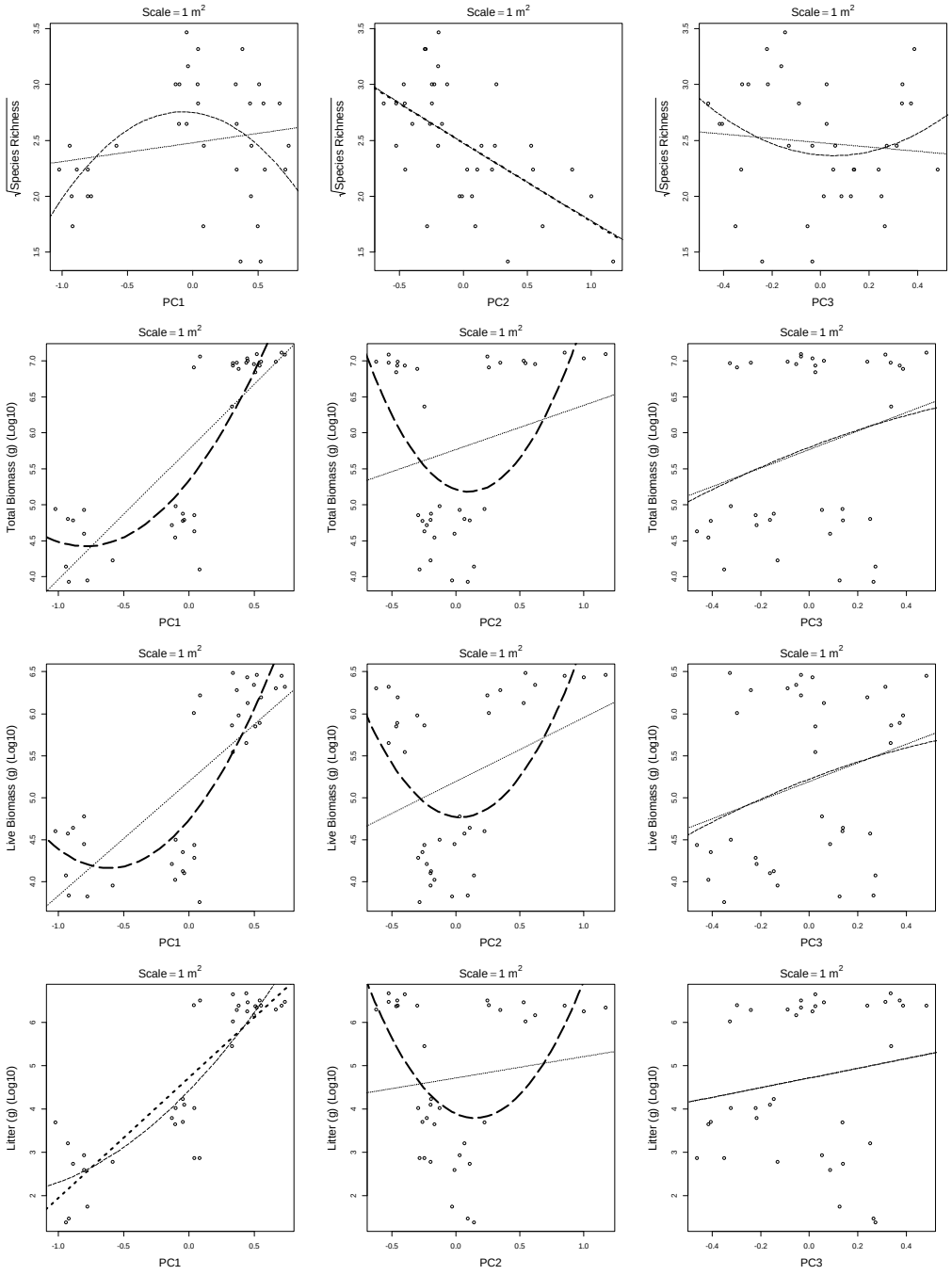


Figure F.2. Square root transformed species richness, log transformed total biomass, log transformed live biomass, and log transformed litter with the soil and leaf nutrient PCA axes. Fitted curves from linear regression models at 1 m^2 having PC1 (left panels) PC2 (center panels) and PC3 (right panels) as the explanatory variables are shown. The dotted line is the fitted linear model and the dashed line is the fitted quadratic model. The significant model in each plot is shown in bold.

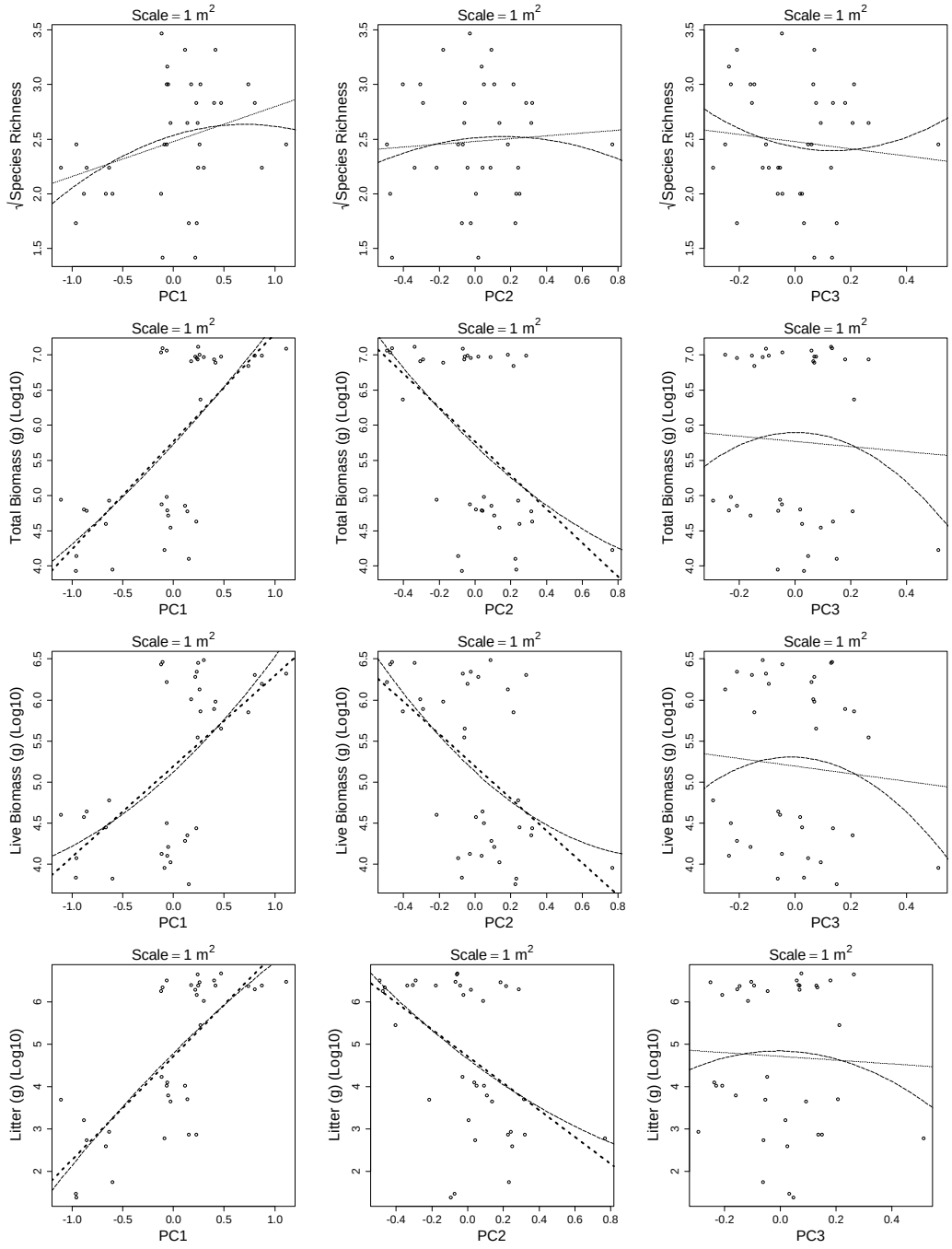


Figure F.3. Square root transformed species richness, log transformed total biomass, log transformed live biomass, and log transformed litter with the soil and leaf carbon, nitrogen and carbon to nitrogen ratio PCA axes. Fitted curves from linear regression models at 1 m^2 having PC1 (left panels) PC2 (center panels) and PC3 (right panels) as the explanatory variables are shown. The dotted line is the fitted linear model and the dashed line is the fitted quadratic model. The significant model in each plot is shown in bold.

APPENDIX G: SOIL NUTRIENTS - SCALED REGRESSIONS

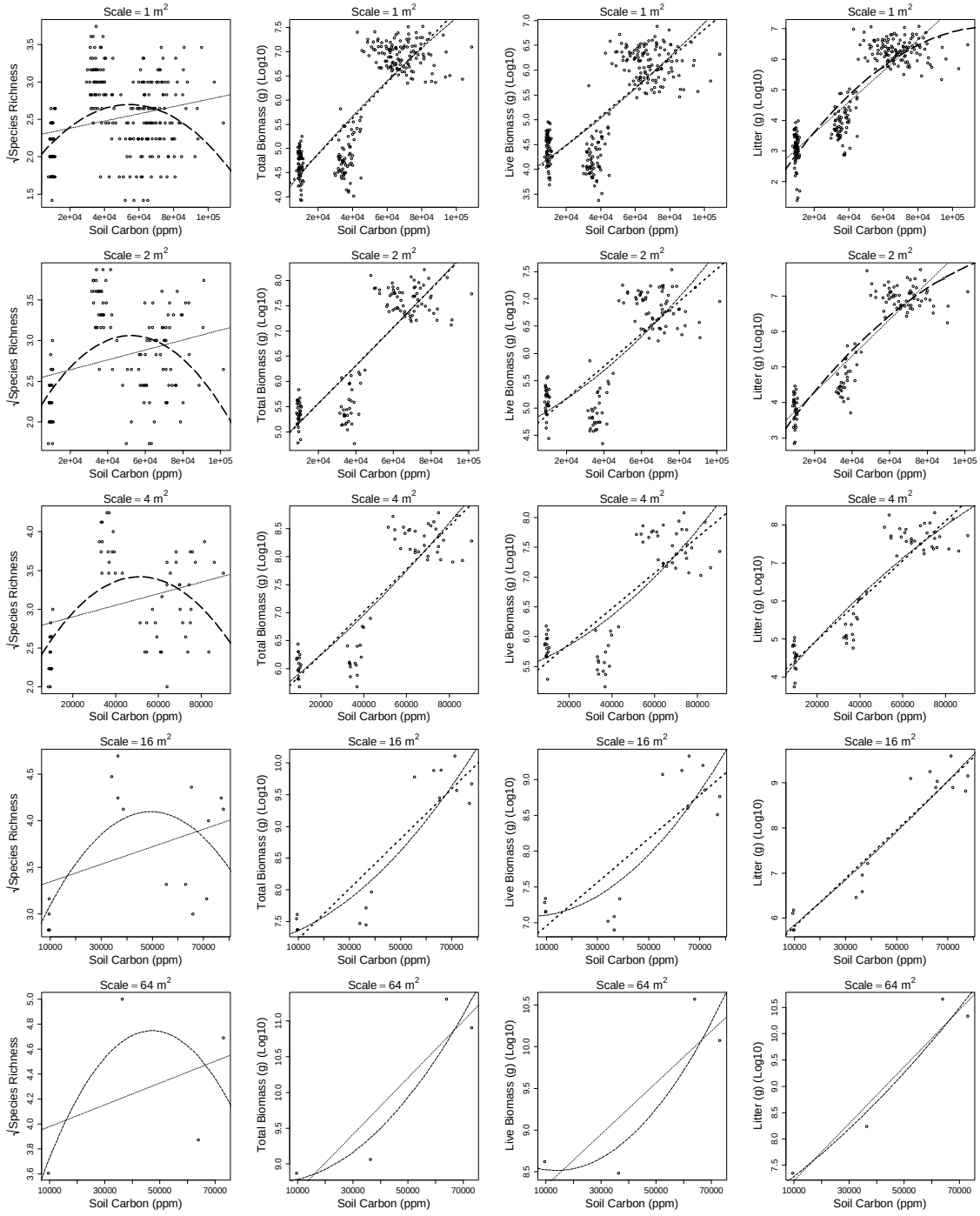


Figure G.1. Fitted curves from linear regressions with soil carbon as the explanatory variable and square root transformed species richness (first column), log transformed total biomass (second column), log transformed live biomass (third column) and log transformed litter (fourth column) as response variables across scales. The dotted line is the fitted linear model and the dashed line is the fitted quadratic model. The significant model in each plot is shown in bold.

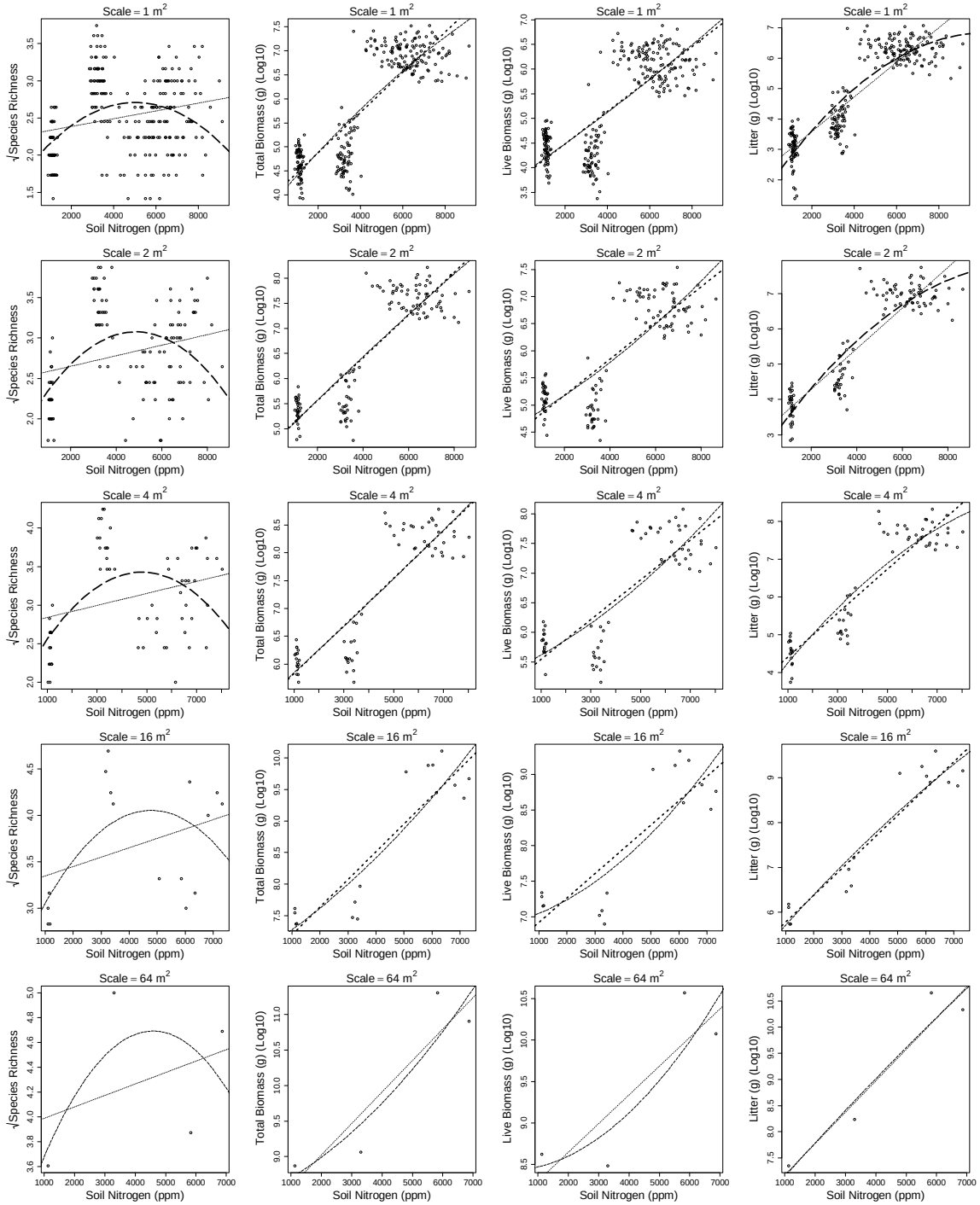


Figure G.2. Fitted curves from linear regressions with soil nitrogen as the explanatory variable and square root transformed species richness (first column), log transformed total biomass (second column), log transformed live biomass (third column) and log transformed litter (fourth column) as response variables across scales. The dotted line is the fitted linear model and the dashed line is the fitted quadratic model. The significant model in each plot is shown in bold.

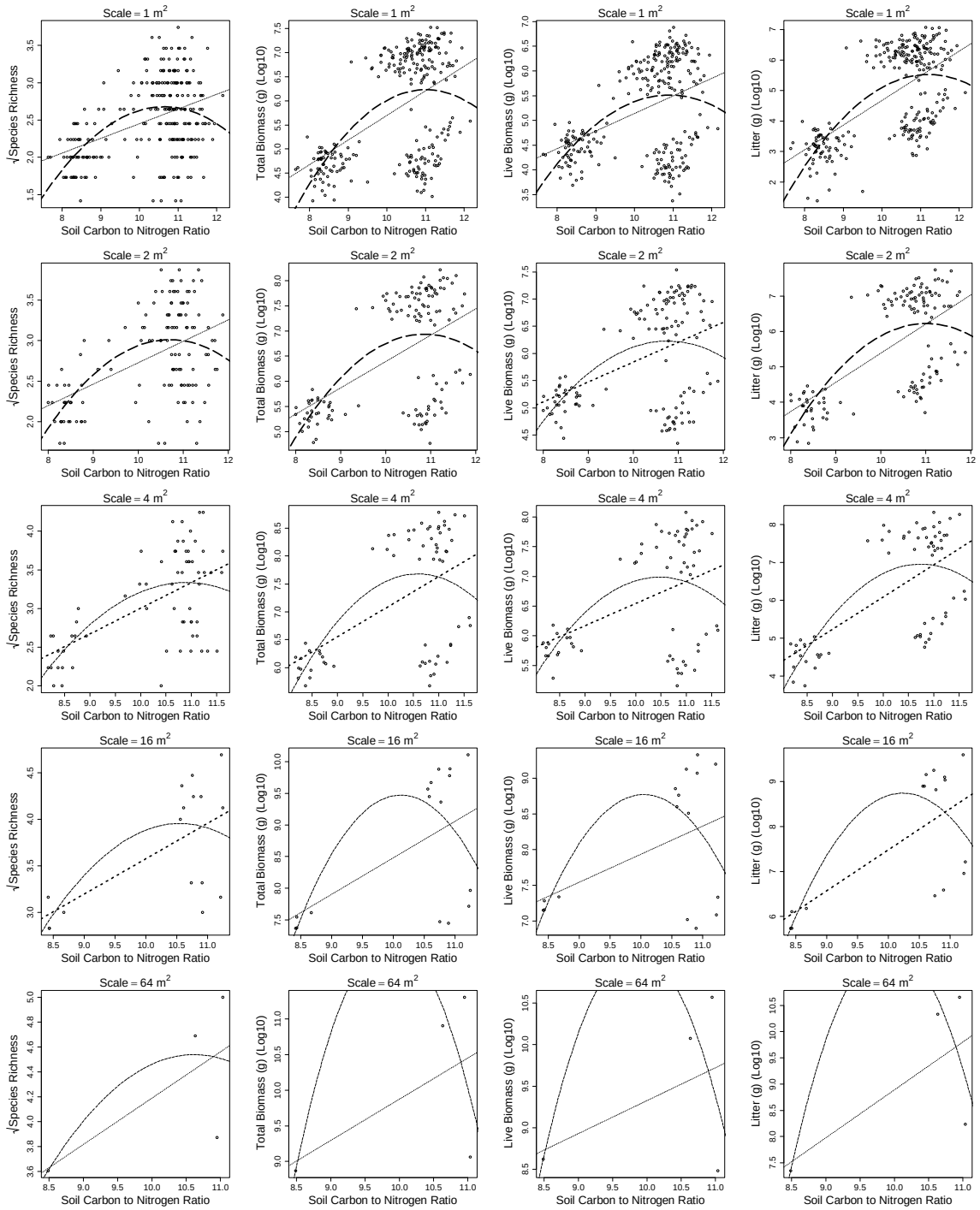


Figure G.3. Fitted curves from linear regressions with soil carbon to nitrogen ratio as the explanatory variable and square root transformed species richness (first column), log transformed total biomass (second column), log transformed live biomass (third column) and log transformed litter (fourth column) as response variables across scales. The dotted line is the fitted linear model and the dashed line is the fitted quadratic model. The significant model in each plot is shown in bold.

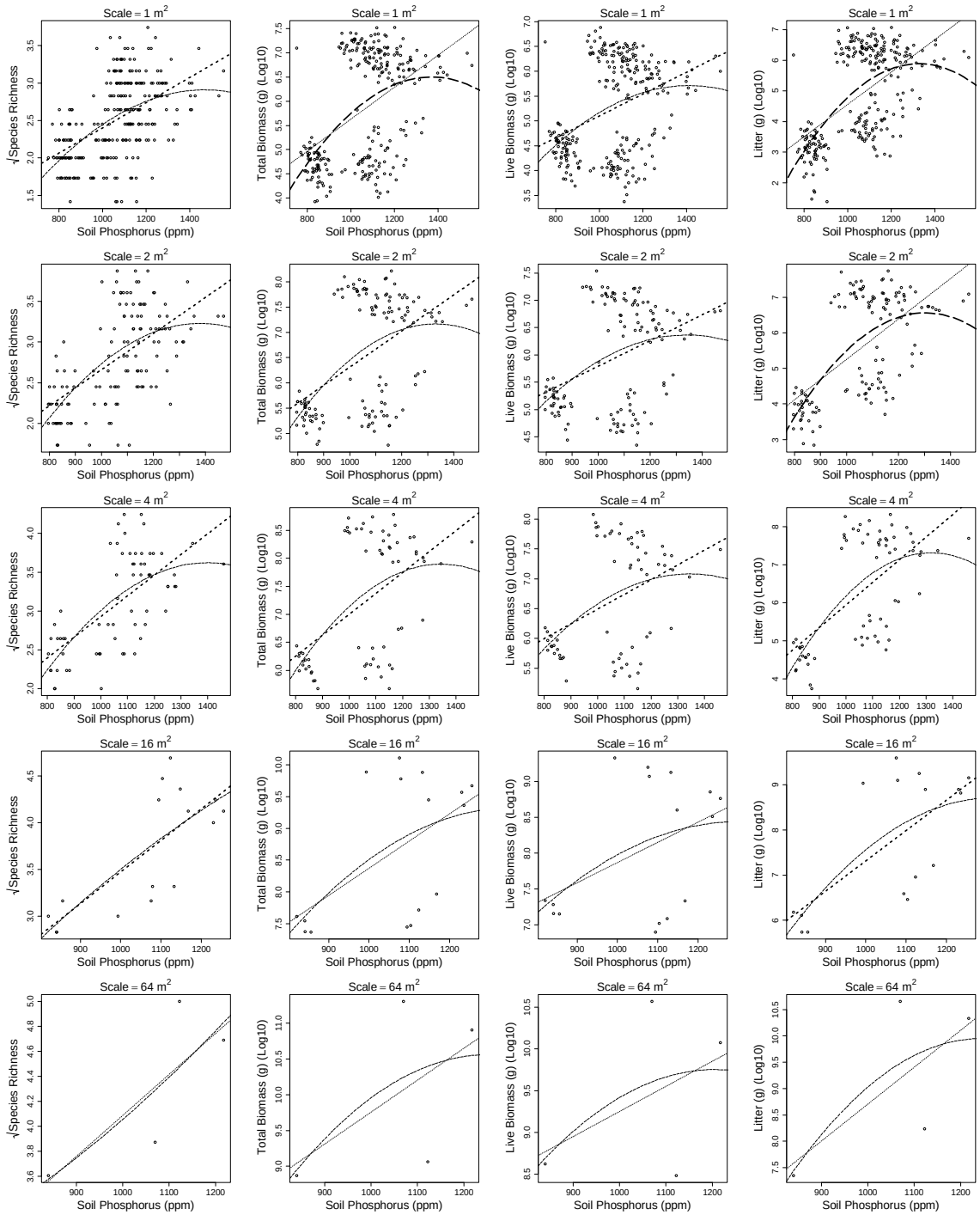


Figure G.4. Fitted curves from linear regressions with soil phosphorus as the explanatory variable and square root transformed species richness (first column), log transformed total biomass (second column), log transformed live biomass (third column) and log transformed litter (fourth column) as response variables across scales. The dotted line is the fitted linear model and the dashed line is the fitted quadratic model. The significant model in each plot is shown in bold.

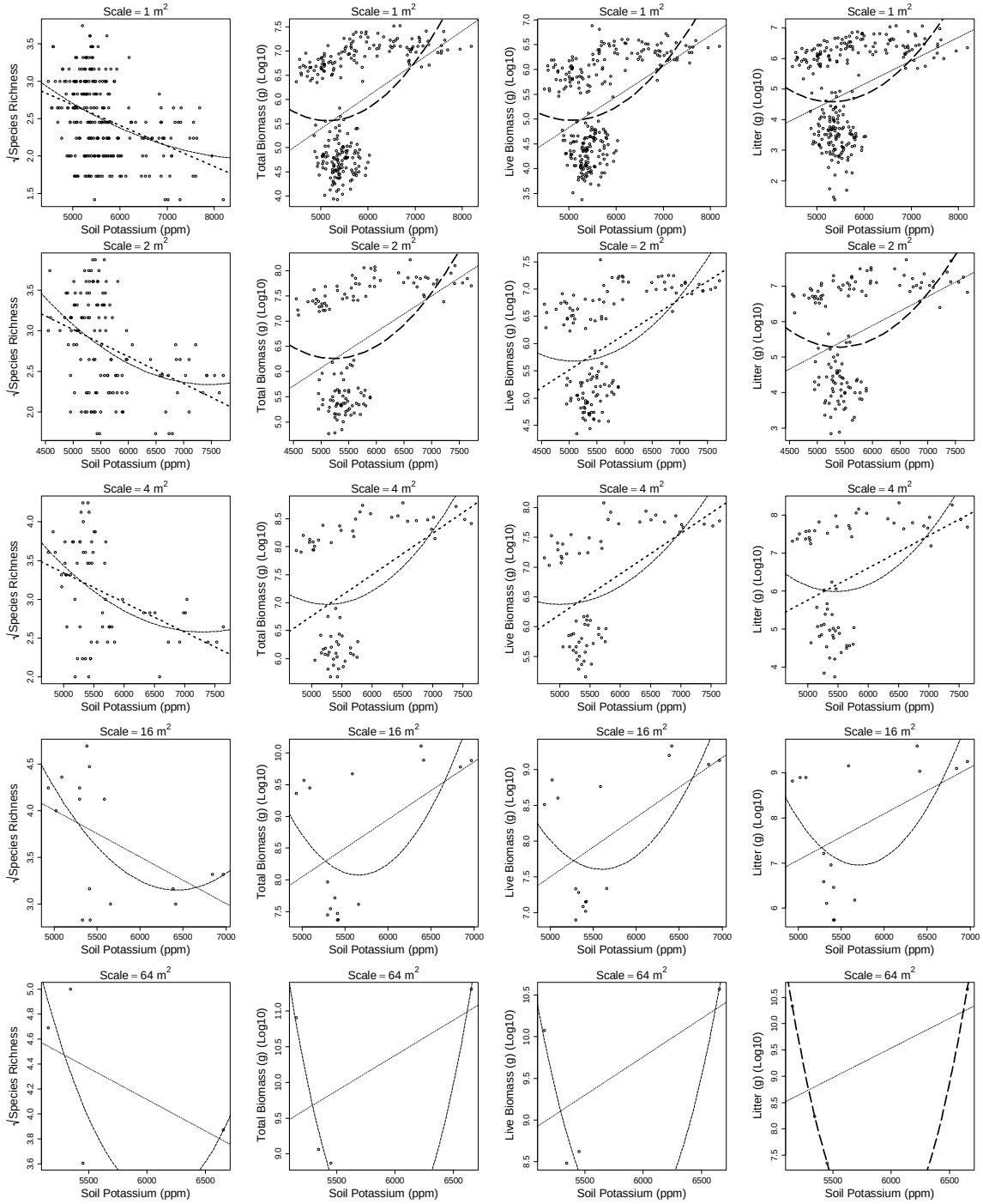


Figure G.5. Fitted curves from linear regressions with soil potassium as the explanatory variable and square root transformed species richness (first column), log transformed total biomass (second column), log transformed live biomass (third column) and log transformed litter (fourth column) as response variables across scales. The dotted line is the fitted linear model and the dashed line is the fitted quadratic model. The significant model in each plot is shown in bold.

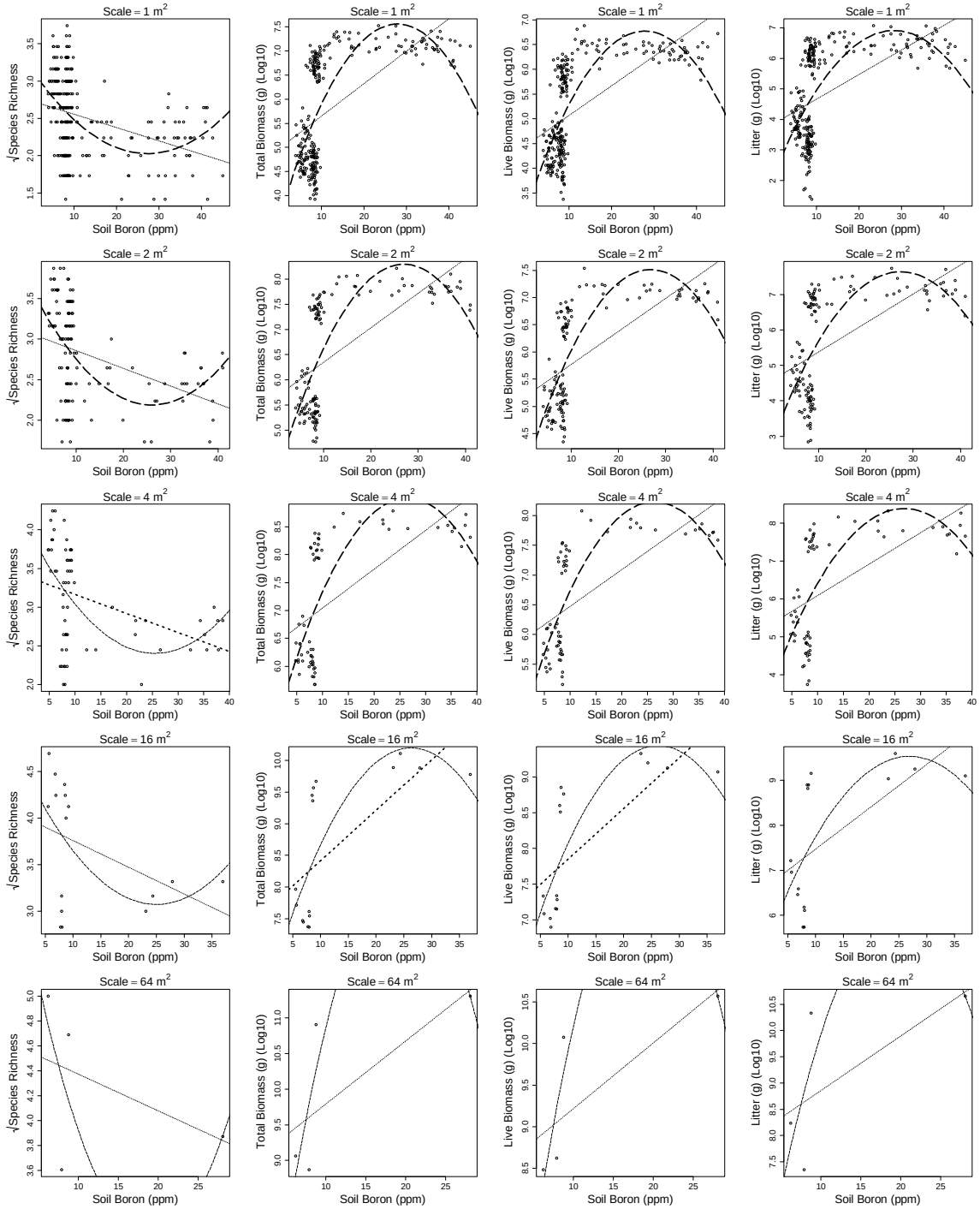


Figure G.6. Fitted curves from linear regressions with soil boron as the explanatory variable and square root transformed species richness (first column), log transformed total biomass (second column), log transformed live biomass (third column) and log transformed litter (fourth column) as response variables across scales. The dotted line is the fitted linear model and the dashed line is the fitted quadratic model. The significant model in each plot is shown in bold.

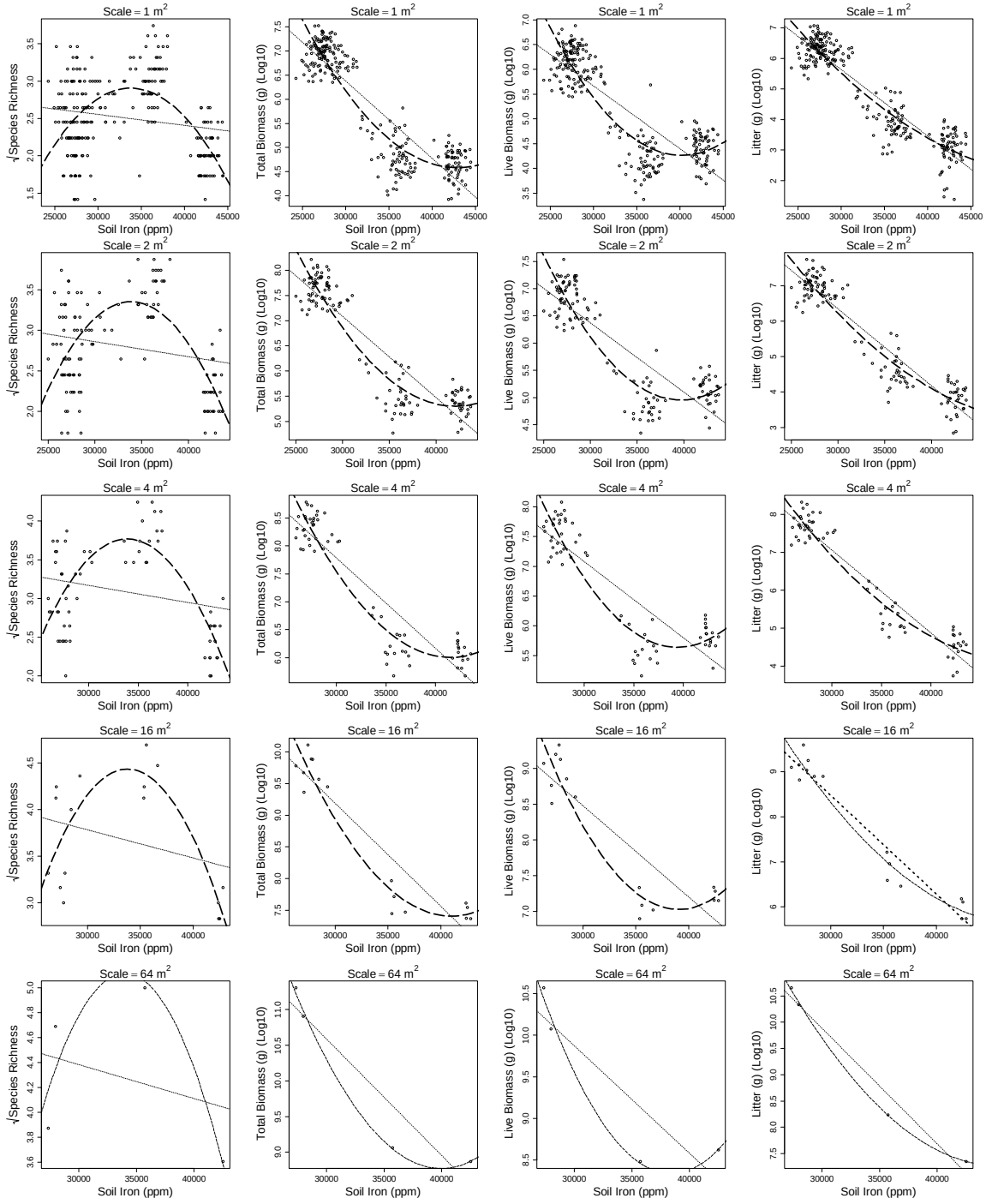


Figure G.7. Fitted curves from linear regressions with soil iron as the explanatory variable and square root transformed species richness (first column), log transformed total biomass (second column), log transformed live biomass (third column) and log transformed litter (fourth column) as response variables across scales. The dotted line is the fitted linear model and the dashed line is the fitted quadratic model. The significant model in each plot is shown in bold.

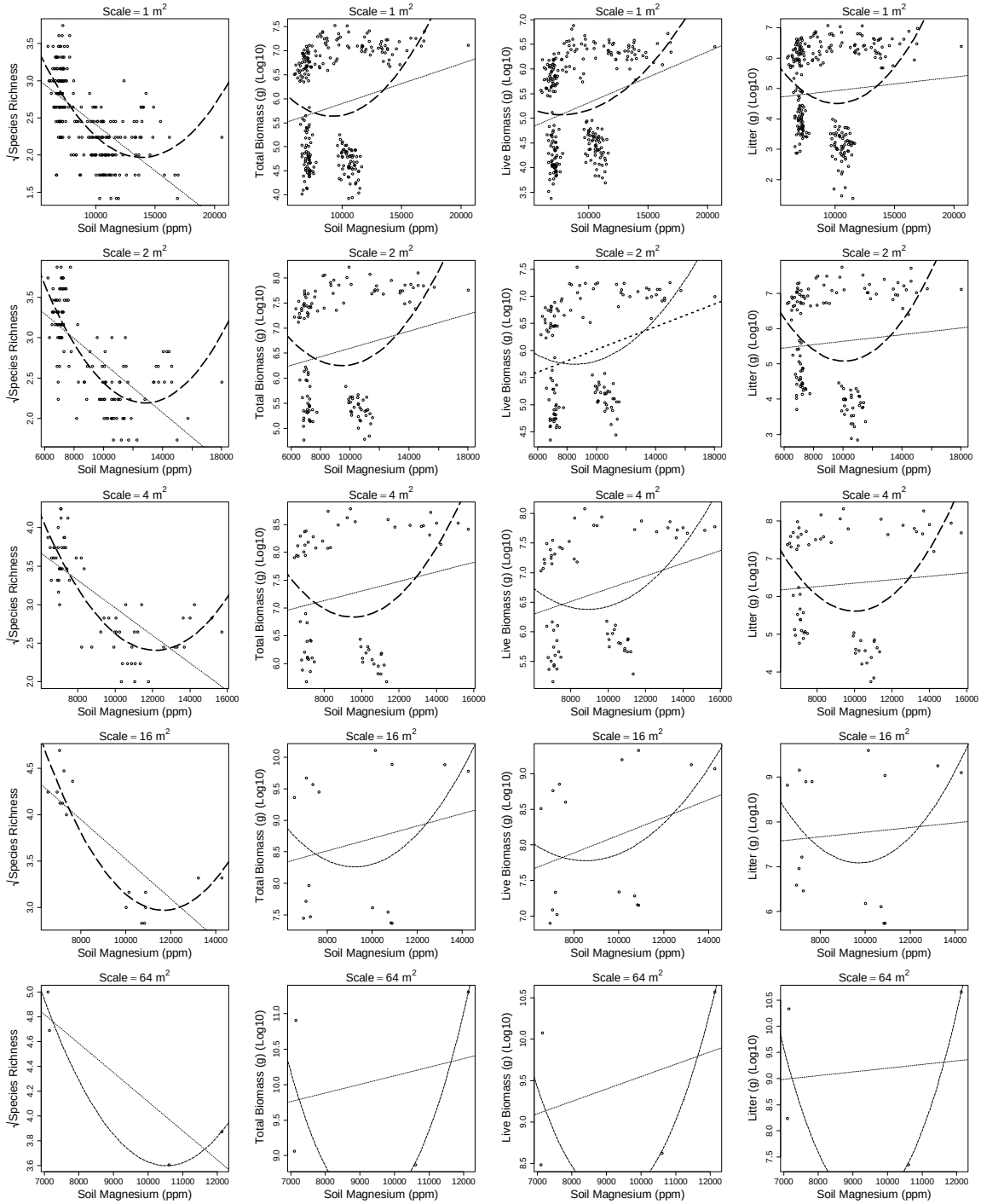


Figure G.8. Fitted curves from linear regressions with soil magnesium as the explanatory variable and square root transformed species richness (first column), log transformed total biomass (second column), log transformed live biomass (third column) and log transformed litter (fourth column) as response variables across scales. The dotted line is the fitted linear model and the dashed line is the fitted quadratic model. The significant model in each plot is shown in bold.

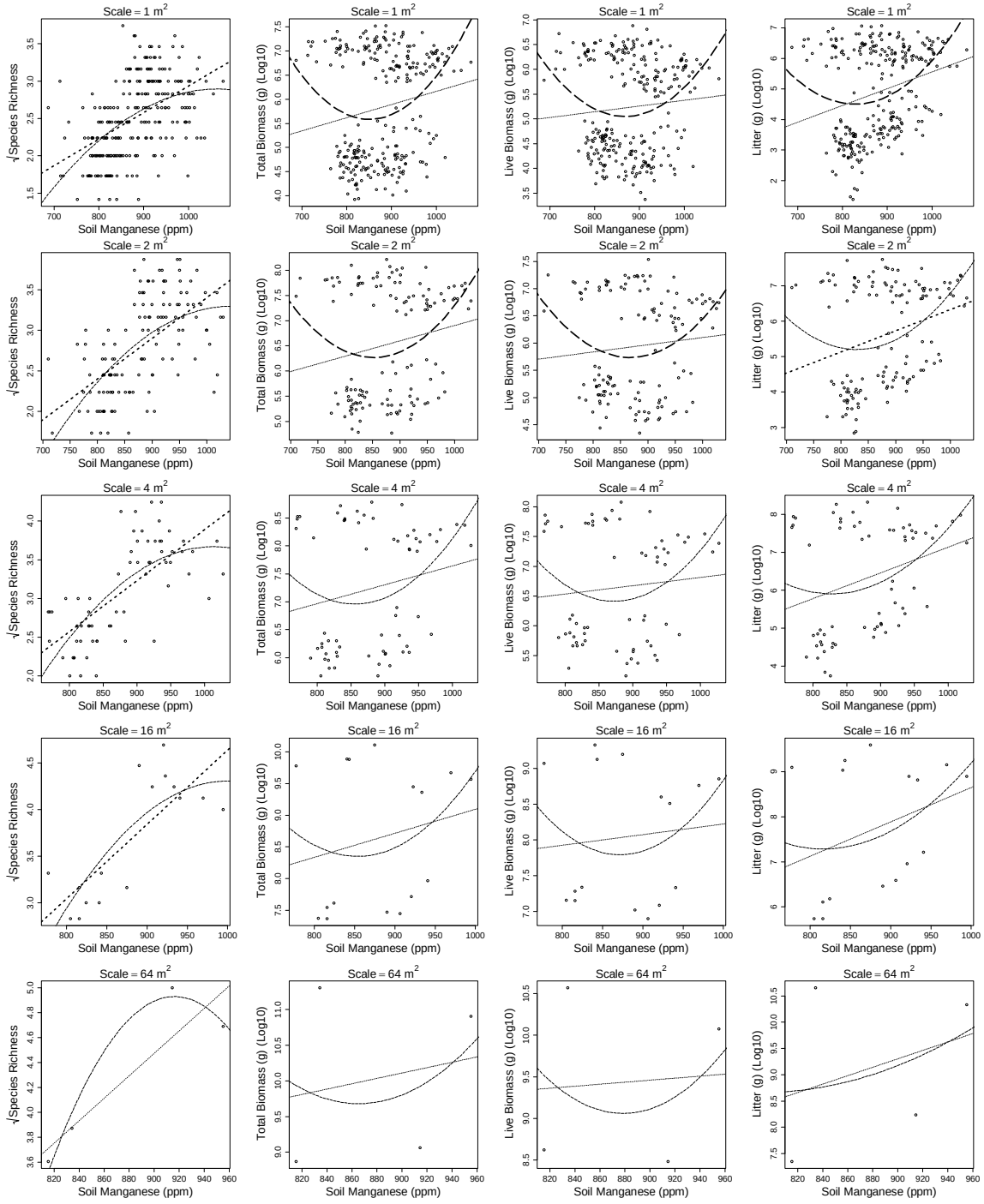


Figure G.9. Fitted curves from linear regressions with soil manganese as the explanatory variable and square root transformed species richness (first column), log transformed total biomass (second column), log transformed live biomass (third column) and log transformed litter (fourth column) as response variables across scales. The dotted line is the fitted linear model and the dashed line is the fitted quadratic model. The significant model in each plot is shown in bold.

APPENDIX H: SPECIES IDENTIFIED

Table H.1. Plant species occurring in the study plots. Species presence in a grid (L1-5, U1-5, P1-4) is indicated by and "X". There were 41 species that could not be identified, not shown here.

Species	L1	L2	L3	L4	L5	U1	U2	U3	U4	U5	P1	P2	P3	P4
Achillea millefolium	X	X	X		X	X	X	X	X	X	X	X		
Achnatherum nelsonii					X				X					
Achnatherum occidentale	X	X	X				X	X						
Achnatherum richardsonii	X					X	X			X				
Agoseris glauca var. *dasycephala*									X	X				
Agropyron cristatum				X							X			
Agrostis gigantea													X	X
Antennaria microphylla	X	X	X			X	X	X						
Antennaria umbrinella					X				X	X				
Arabis holboellii		X	X		X			X	X					
Artemisia frigida		X	X	X	X			X						
Astragalus collinus						X			X					
Astragalus miser	X	X	X			X	X	X				X		
Balsamorhiza sagittata														
Bromus squarrosus			X		X			X	X					
Bromus tectorum		X		X										
Campanula rotundifolia						X				X	X	X		
Cardamine pensylvanica													X	X
Carex petasata										X				
Carex praticola									X					
Carex utriculata													X	
Castilleja thompsonii	X	X	X		X		X	X	X					

	(L1	*L2*	*L3*	*L4*	*L5*	*U1*	*U2*	*U3*	*U4*	*U5*	*P1*	*P2*	*P3*	*P4)*
Centaurea diffusa	X													
Centaurea stoebe ssp. *micranthos*						X	X							
Cerastium arvense			X				X							
Chenopodium album											X			
Collinsia parviflora			X											
Comandra umbellata	X													
Crepis atribarba	X	X				X								
Danthonia intermedia										X				
Delphinium nuttallianum							X							
Lescurainia sophia											X			
Eleocharis palustris													X	
Elymus glaucus						X								
Elymus repens											X	X	X	X
Elymus trachycaulus ssp. *subsecundus*										X				
Epilobium ciliatum													X	
Equisetum arvense													X	
Erigeron compositus														
Erigeron corymbosus	X		X		X	X	X					X		
Erigeron filifolius var. *filifolius*				X	X									
Erigeron flagellaris		X												
Erigeron linearis		X	X											
Erigeron pumilus var. *intermedius*					X									
Eriogonum heracleoides					X	X		X						
Festuca campestris		X	X			X	X		X	X		X		
Linum lewisii ssp. *lewisii*			X					X						
Fritillaria pudica	X					X	X							
Gaillardia aristata	X				X									

	(L1	*L2*	*L3*	*L4*	*L5*	*U1*	*U2*	*U3*	*U4*	*U5*	*P1*	*P2*	*P3*	*P4)*
Galium boreale												X		
Galium trifidum ssp. *subbiflorum*													X	
Geranium viscosissimum var. *viscosissimum*										X				
Geum triflorum						X	X		X					
Symphyotrichum pilosum var. *pilosum*						X								
Hesperostipa comata	X	X	X	X	X		X	X	X	X				
Juncus balticus	X				X	X			X		X	X	X	
Koeleria macrantha	X	X	X		X	X	X	X	X	X				
Lactuca serriola											X	X		
Linaria genistifolia ssp. *dalmatica*									X					
Lithospermum ruderale	X		X				X		X	X		X		
Lomatium macrocarpum				X										
Lomatium dissectum	X													
Lotus denticulatus									X					
Medicago lupulina	X		X			X		X			X	X		
Medicago sativa								X				X		
Melilotus alba											X	X		
Moehringia lateriflora													X	X
Muhlenbergia asperifolia											X			
Opuntia fragilis				X	X									
Orthocarpus luteus							X		X					
Oxytropis campestris						X								
Penstemon procerus						X	X					X		
Phalaris arundinacea													X	X
Phleum pratense														X
Plantago major													X	X
Plantago patagonica					X									

	(L1	*L2*	*L3*	*L4*	*L5*	*U1*	*U2*	*U3*	*U4*	*U5*	*P1*	*P2*	*P3*	*P4)*
Poa palustris													X	X
Poa pratensis	X		X		X	X	X	X	X	X	X	X		X
Poa secunda	X	X	X	X	X	X		X	X					
Polygonum douglasii	X		X		X	X	X	X	X					
Potentilla gracilis							X	X						
Pseudoroegneria spicata	X	X	X	X	X	X	X	X	X			X		
Rhinanthus minor							X							
Rumex crispus													X	
Schoenocrambe linifolia				X										
Scirpus microcarpus													X	
Scutellaria galericulata														X
Sium suave													X	
Sonchus arvensis											X			
Sporobolus cryptandrus				X										
Symphyotrichum ericoides											X			
Taraxacum officinale	X	X			X	X	X	X	X	X	X	X	X	X
Tragopogon dubius	X	X	X		X	X	X	X	X	X		X		X
Trifolium pratense														X
Triglochin maritima													X	
Verbascum thapsus										X				
Vicia americana														X
Zigadenus venenosus	X	X	X			X	X	X						