The Biodiversity-Ecosystem Function Relationship in Natural Grassland Communities at Silwood Park

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"The scientific theorist is not to be envied. For Nature, or more precisely experiment, is an exorable and not very friendly judge of his work. It never says "Yes" to a theory. In the most favorable cases it says "Maybe," and in the great majority of cases simply "No." If an experiment agrees with a theory it means for the latter "Maybe," and if it does not agree it means "No." Probably every theory will some day experience its "No" - most theories, soon after conception."

Albert Einstein

Abstract

Biodiversity is a central concept in ecology, fundamental to how we conceive of the natural world, measure human impacts on it, and orient conservation efforts to protect it. When species are lost, their links are lost, and functions for which they are responsible can be lost as a result. There is evidence of an intuitive link between diversity and function, where more diverse systems should generally include a greater number of functions with a greater amount of redundancy built into them, but defining this link has proven difficult. This is an important challenge in ecology, however, because the function and stabilizing role of biodiversity is one of the most important arguments for its preservation. This thesis examines the role of biodiversity in ecosystem function and community stability grassland communities across Silwood Park. The experiment uses natural gradients in plant diversity, measured in a number of alternative ways.

Species richness can be an imperfect metric for investigating the link between diversity and ecosystem functioning but can be used as a proxy for more complex diversity measures in grassland communities at Silwood Park. There was no general relationship between plant species richness and plant biomass, and a negative relationship between plant richness and soil mesofaunal biomass. An extreme flooding event negatively impacted some soil mesofauna and not others whilst increasing biomass yield during the following year. Plant biomass stability was independent of species richness and soil mesofaunal biomass varied with either plant richness or plant biomass depending on the definition of stability being used. The inclusion of relative abundance and phylogenetic information allows us more predictive power when looking at the biodiversity-ecosystem function relationship for both primary and secondary production. Experiments such as DExtER are vital to understanding the role of diversity in natural communities.

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Declaration:

I confirm that all of the written work within this thesis is my own. Collembola and plant biomass data was partially collected by Gerlinde Schaeffter, Mattison Peters, Barbara Szabo, and Menelik Lee. The rest of the data collection and all analyses are my own work.

Signed: Kathryn Luckett

Date: 21st October 2015

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Chapter 1

A general introduction to the evidence for biodiversity–function and biodiversity–stability relationships, and directions for future investigation

1.1 The biodiversity-ecosystem function relationship

Since Darwin's formulation that, ""If a plot of ground be sown with one species of grass, and a similar plot be sown with several distinct genera, a greater number of plants and a greater weight of dry herbage can thus be raised" (1859), we have understood that diversity should affect the outputs of the many life processes that take place in ecosystems. Changes in diversity affect the structure of ecological networks and, presumably, the number of functional attributes present in those networks, and this comes with implications for resource use, carbon and nutrient cycles, and a range of other community properties and ecosystem functions. Diversity has been proposed or demonstrated to affect levels of primary and secondary production (Tilman *et al.* 1996), nutrient cycling (Hooper & Vitousek 1998), and resistance to invasion (Levine 2000, Naeem *et al.* 2000, Kennedy *et al.* 2002).

Grime (1973) initially posited that the relationship between diversity and production would be humped-shaped, however opposing results emerged from empirical studies indicating a generally saturating positive correlation (Tilman *et al.* 2006). Working at the Cedar Creek Natural History Area in Minnesota, USA Tilman and colleagues seeded and maintained species diversity at 1, 2, 4, 8 or 16 species to test how species diversity and functional group diversity influence stability, nutrient dynamics and productivity (Tilman *et al.* 2001). Evidence from this experiment spanning more than 15 years showed that diversity of species and functional groups has strong positive effects on productivity at lower levels of diversity that level off at higher levels (Figure 1.1).

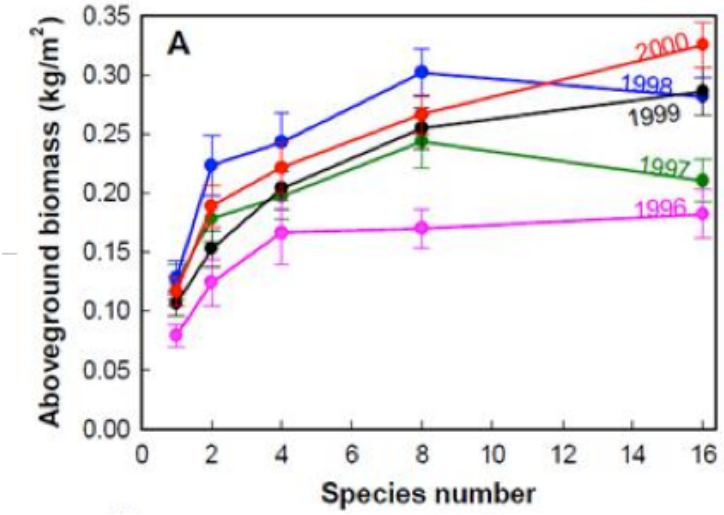


Figure 1.1 Species-richness-biomass relationships over six consecutive years in experimentally sown communities at the Cedar Creek Natural History Area (from Tilman 2001).

To try and remove the effects of environmental factors a series of experiments were carried out at the Ecotron facility at Imperial College, London. The controlled environment facility allowed researchers to singly manipulate diversity and try and elucidate the diversity-function relationship with fewer confounding factors. A key result published in Nature in 1994 showed that a reduction in biodiversity lead to a reduction in community productivity (Naeem *et al.* 1994). This echoed the results of earlier studies and lead to a series of theories to explain this relationship, which will be discussed later in this chapter.

A pan-European effort to test the relationship between plant diversity and production, BIODEPTH, replicated experimental tests across seven countries and found that productivity generally increased with higher species richness, although the strength of this relationship varied among study sites (Hector *et al.* 1999) (Figure 1.2). A still more comprehensive test of this relationship comes from the NutNet research program (see Adler *et al.* 2011), where productivity-diversity relationships from over 40 different grasslands across five continents revealed no consistent trend in direction (Figure 1.3). A meta-analysis that steps back still further, comparing biomass responses to diversity manipulations in more than 300 experiments spanning terrestrial, marine and freshwater ecosystems, revealed a general trend toward asymptotic positive relationships (Cardinale *et al.* 2006).

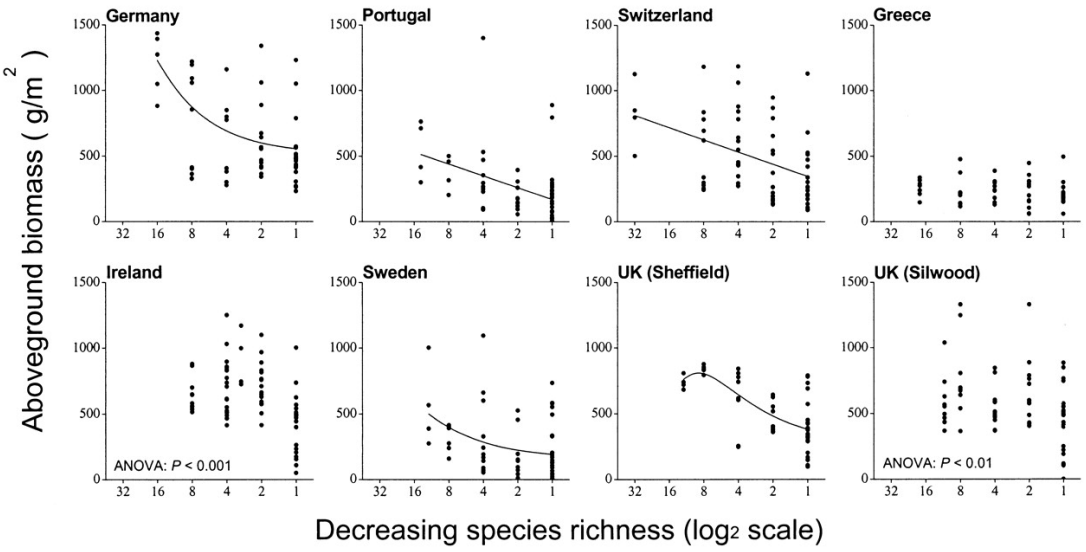


Figure 1.2 Species richness-biomass relationships in Biodepth experiments across eight sites in seven countries in Europe (from Hector et al. 1999).

To explain a causal relationship between species diversity and ecosystem function, two mechanisms have been suggested - niche complementarity and sampling effects (Huston 1979, Loreau & Hector 2001). Under niche complementarity, if species exploit different resources (e.g. by having differing phenologies, physiologies or nutrient use strategies), an increase in species richness would mean more comprehensive use of community resources overall, and therefore increased productivity. Similarly, with increasing recognition of the prevalence of mutualistic relationships in nature (Bruno *et al.* 2003, Bertness and Leonard 1997, Kareiva and Bertness 1997), facilitation may lead to complementarity effects, as species improve resource use of co-occurring species.

Under niche complementarity effects, as the number of species increases the number of unused resources should decline. This has been seen empirically, where increased plant species richness led to a decrease in available soil nitrogen and total dissolved nitrogen in experimental plant systems in Germany (Oelmann *et al.* 2007); and in a recent meta-analysis, Cardinale *et al.* (2011) showed that more diverse polycultures resulted in reduced nutrient concentrations in underlying soils.

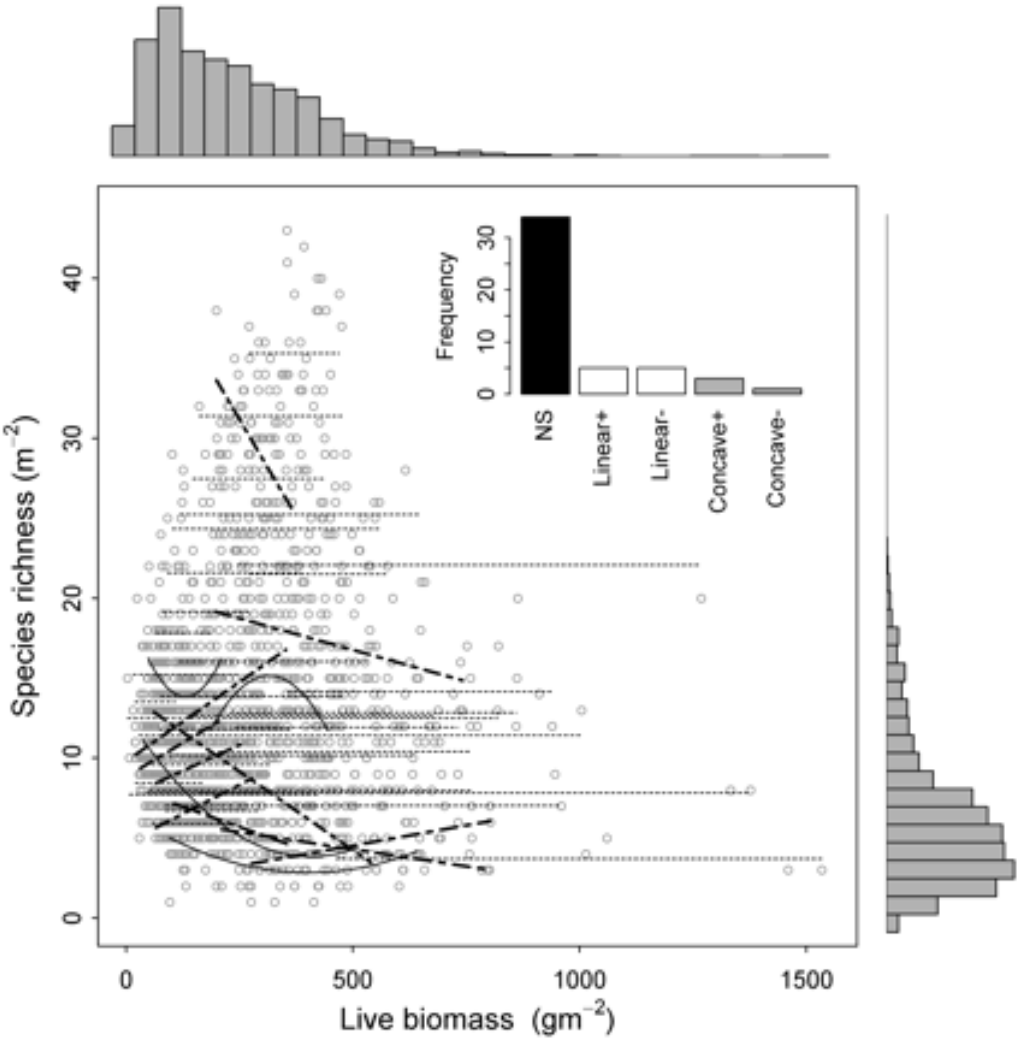


Figure 1.3 With-in site species richness-biomass relationships in NUTNET experiments spread globally across 40 sites (from Adler et al. 2011). Relationships that were non-significant are illustrated with thin dashed lines, positive or negative linear relationships are thick dashed lines and concave relationships are shown by solid curves. The inset shows the frequencies of each relationship type.

Under sampling effects, on the other hand, a community with more total number of species is simply more likely by chance to contain those species capable of higher productivity. An issue with this particular theory is the assumption that communities are randomly assembled in terms of the productivity being measured. The importance of sampling effect as a mechanism to describe the biodiversity-function relationship rather than being an artifact of experimental design is still contested and requires further development. This is unlikely to be a case of one explanation being right and the other being wrong in all cases; instead, evidence points toward system age as the deciding factor between the two

mechanisms (Cardinale *et al.* 2007, Fargoine *et al.* 2007, Marquard *et al.* 2009). In the early stages of experiments where new communities are establishing, sampling effects tend to drive higher biomass production in more species-rich communities; however as experimental communities mature we see a shift to niche complementarity effects (Tilman *et al.* 2001, Marquard *et al.* 2009).

Considering this relationship from point of view of biodiversity loss leads to reduction in ecosystem function, in terms of what level of decline in species richness a system could experience before a loss in function was detectable, some empirical evidence thus suggests a threshold (see asymptotes in Figure 1.1). Under such a threshold, ecosystem function is not impacted by species losses until a system-specific threshold is crossed, where further losses lead to measurable declines in functional output. Two hypotheses have been proposed to explain this pattern – the redundancy hypothesis and the rivet hypothesis. The redundancy hypothesis states that more than one species is capable of performing a given role, and thus a system is able to lose small numbers of species while maintaining most functions (Walker 1992). The rivet hypothesis likens species to the rivets holding a plane's wing together; if a few are lost the overall loss of function is negligible, however once enough are lost the system collapses (Lawton 1994). Field studies have tended to support the redundancy hypothesis (Grime 1997, Tilman 2001) whilst evidence from Naeem *et al.*'s (1995) ECOTRON microcosm experiment shows more species-specific functional specialism in support of the rivet hypothesis.

Despite the plethora of field, laboratory and observational studies ecologists cannot agree on the nature of the biodiversity-function relationships nor the underlying mechanisms that govern them.

1.2 The biodiversity-stability relationship

Greater numbers of species will generally entail not just a greater number of traits and related functions, but a greater redundancy in those traits and functions as well. Thus there is a corollary to the longstanding idea that biodiversity affects the levels of outputs of ecological processes in ecosystems, and that is that biodiversity influences the stability of outputs of ecological processes in ecosystems as well. To clarify in a more diverse

community it is likely there will be more than one species capable of fulfilling the same niche or role therefore if the community can maintain the overall production (thus remain stable) should species drop out. A hundred years after Darwin offered his simple formulation of the Biodiversity-Ecosystem Function relationship, Charles Elton offered a simple formulation for this corollary: "The balance of relatively simple communities of plants and animals is more easily upset than that of richer ones" (1958)

Odum Lack, and MacArthur initially investigated stability in terms of overall constancy or general lack of change (Odum 1953, Lack 1954, MacArthur 1955). MacArthur proposed that it is not the sheer number of species in an ecosystem that is relevant to the stability of ecosystem functions, but the number of connections among them, such that a large number of specialist species or a small number of generalist species may confer comparable levels of stability (MacArthur 1955).

Theoretical work by Robert May in the early 1970s challenged the conventional wisdom of a positive relationship between diversity and stability (1972, 1973). Using randomly constructed model communities, May and other ecologists since have shown that as complexity increases stability decreases (May 1972, Pimm & Lawton 1978, Pimm 1982). May (1972) constructed community networks of species, species interactions and interaction strengths, and found that as any one of these parameters increased overall network stability decreased. The random assembly processes and arbitrary interspecific interactions of these theoretical communities make them ecologically unrealistic; however more recent work attempting to simulate realistic assembly processes by adding one species at a time (Post & Pimm 1983, Law & Morton 1996) or by incorporating ecological clustering of species has supported May's initial findings (Sinha 2005, Sinha & Sinha 2006).

The contradiction between these theoretical results and the natural history intuition of Elton and many others spurred a great deal of empirical research into questions of the relationship between diversity and stability. Many large-scale experiments (e.g. Cedar Creek, Jena, Biodepth) have tested the diversity-stability relationship in the decades following May's work, and these have generally found it to be positive to negligible, but not negative (Tilman 1996, Naeem & Li 1997, Hector *et al.* 1999, Tilman *et al.* 2001, Proulx *et al.* 2010).

Surveying the field and its contradictions in a 1975 review, Goodman prophesied that hypotheses over the diversity-stability relationship would "vanish in light of discordant facts". Since then the contradictions have prompted a large research effort on both empirical and theoretical sides attempting to reconcile empirical and theoretical findings. Various reviews of empirical results have concluded that more species rich communities are more stable in their annual biomass production and other community-level outputs, but perhaps less stable in the abundance and presence-absence of individual populations (MCCann 2000, Worm & Duffy 2003). Working in a theoretical framework, Wilmers *et al.* 2002 proposed a different sort of resolution to some of the apparent contradictions, showing that stronger interaction strengths and increases in connectivity tend to produce communities with fewer species, but that diverse systems with greater connectivity are more stable. Also Levine, taking a landscape-scale approach to experimentation into the question, showed that while diversity itself increases stability, the most diverse communities may commonly be the least stable due to the action of external factors that co-vary with diversity and can overwhelm its effects on stability (Levine 2000).

With both function and stability, some of the confusion underlying different results and interpretations could stem simply from the definitional ambiguity with which we talk about these concepts. We call a 'lot' of different things—presumably driven by a lot of different processes—stability (Table 1.1). Since MacArthur's early work framing stability as a simple absence of change, there has been a great deal of ambiguity surrounding how best to define the concept, and the term has oscillated among a number of different meanings. A comprehensive review in the late 90s found 25 definitions of stability, 5 for constancy, 9 for resistance and 17 for resilience (Grimm & Wissel 1997). From a simple absence of change (constancy), the term evolved into the concept of persistence or resistance - the continued existence of an individuals or species in the face of some external forcing (Margalef 1968). For a definition that relied on absence of change, ecologists would need to determine the exact amount of variation that can be accommodated in a community or population that is stable. One solution was Holling's idea of ecological resilience: the amount of disturbance a system can withstand before changing into a different stable state (Holling 1973). But this definition has given way to an alternative meaning of resilience – one that complements the concept of "resistance" in making up the two components of stability. Here, resilience

(referred to as "engineering resilience" by Holling) is defined as the time taken for a system to return to equilibrium or its stable state following perturbation by an external forcing (1996). Resilience has now taken on many meanings – those discussed and another widely used ones (Table 1.1) therefore 'resilience' has become an ambiguous term. Lastly, resistance is now widely accepted and used as the degree to which a system changes from its equilibrium or stable state in response to that external forcing.

Few studies have looked at more than one measure of stability, and due to the lack of standardised definitions or measures; it is hard to draw cross-study comparisons. Do communities differ in their ability to remain constant, resist changes and recover from said changes? In an effort to disentangle the effects of diversity on different definitions of stability, van Ruijen *et al.* (2010) used the response of experimental plants communities to a natural drought – initially it appeared resistance to drought decreased as species richness increased but once differences in biomass were accounted for this relationship disappeared. Alternatively (using van Ruijen *et al.*'s definitions) recovery was strongly positively correlated with species richness and resilience was the same regardless of diversity. Recent theoretical work has shown that resilience and resistance illicit opposite trends and may in fact operate independently from each other (Vallina & Le Quere 2011). This research showed that resistance rather than resilience might govern the overall stability of complex food webs. Depending on one's definition of stability, one may therefore find a wide range of diversity-stability relationships. Given the variety of ways an ecosystem may respond to a perturbation, to focus on one single definition of stability risks underestimating or overestimating the consequences of perturbations. For example, a community may resist significant changes in the short term while being pushed into a trajectory of lagged longer-term change. Alternatively, a community may be substantively perturbed from some pre-disturbance state but recover quickly and fully without any apparent legacy of the disturbance.

There may not be one best measurement of stability, nor one best output or function to measure the stability of. Therefore the best approach to understanding the diversity-stability relationship may be to consider multiple forms of stability in multiple community attributes or functions. The studies discussed so far have tended to look at functional outputs of biodiversity, such as production or nutrient use in testing stability, but we could

step back and measure changes in diversity itself as a kind of stability. Before looking at how diversity influences various ecosystem functions, it may be useful to understand how diversity itself fluctuates, and whether the degree of fluctuation scales with the starting level of diversity. Characterizing variation in diversity through space and time can shed light on the processes governing patterns of diversity on the landscape, and is an important precursor to testing functional outputs of diversity.

Table 1.1: Terms used to described community or population stability

Stability Term	Definition	Used by:
Constancy	Extent of change in a community through time. Ability to remain unchanged through time.	Connel & Sousa (1983) Lewontin (1969) Harrison (1979)
Resistance/Persistence	Extent of change in the face of an external disturbance	Allen (1983) Connell & Sousa (1983) Steinman *et al.* (1991) Odum (1989)
Recovery/Elasticity	Speed of return to initial state following external. disturbance.	Connell & Sousa (1983) Westman (1978)
Resilience	Capacity of the system to resist and recover from a disturbance whilst maintaining function and structure. Resilience is used interchangeably in the literature to mean either resistance or recovery.	Walker *et al.* 2004 Harrison (1979) Leps *et al.* (1982) Westman (1978)

Work has shown that the nature of any diversity-variability relationship is subject to a number of influences, including environmental conditions (Shurin *et al.* 2007, Adler *et al.* 2006), trophic complexity and interactions (Amaresekare 2003, Whiles & Charlton 2006, Rzanny & Voigt 2012), and soil properties (Laakso & Setala 1999, Wardle *et al.* 2004). Experimentation in sown (i.e. artificially-assembled) communities provides researchers greater control over these covarying influences, enabling the clearest look into the fundamental process of how diversity affects function and stability, the general organizing principles in operation. Work in natural communities, on the other hand, show how these processes play out amid the spectrum of covarying influences that characterize nature.

1.3 Teasing apart different aspects of stability

Given the many definitions of stability, it is critical when working in this area to clarify exactly what that stability is in reference to. Under ambient conditions, relative change in communities through time may best represent the idea of 'constancy'. To focus on stability as 'resistance' or 'recovery', some external perturbation is needed. This can be a chance natural event, as in Tilman's work following a prolonged drought at the Cedar Creek study site (Tilman & Dowling 1994), or a simulated weather extreme. Due to the unpredictable, abrupt and idiosyncratic nature of extreme weather events, most species are not adapted to them, such that extreme events can cause local extinctions dramatically alter community structure (Bengtsson 2002 Miriti *et al.* 2007, Thibault & Brown 2008). Given the rate of recent climate change (Mann *et al.* 2008), research into ecological responses to weather extremes takes on added importance, particularly how changes will affect community functioning and stability. Climate change is increasingly the focus of ecological studies, mainly in terms of long-term trends such as increasing temperature or changing rainfall and how these will affect biodiversity (Chapin *et al.* 2000, Thomas *et al.* 2004, Butchart *et al.* 2010, Harley 2011). What is currently lacking is understanding the emphasis on the ecological consequences of extreme weather events (EWE) and the relatively low number of experiments testing them (Jentsch *et al.* 2007, Jentsch & Beierkuhnlein 2008).

Climate change is generally perceived as long-term directional changes in climatic conditions, such as the 2-4˚C increases in temperature expected over the next hundred years (IPCC 2007). Extreme climatic events, such as increased rainfall events or droughts, are also predicted to increase in frequency and magnitude (Easterling *et al.* 2000, IPCC 2011), and by several measures these increases are already apparent (Hansen *et al.* 2012). Summer heat waves are occurring more frequently, some with temperatures up to three standard deviations higher than long-term means, and flooding episodes in the UK are more likely to occur with an increase in magnitude and recurrence of North Atlantic atmospheric rivers (Lavers *et al.* 2013).

Extreme weather events are emerging as an important emerging area of research into climate change. Recent EWEs illustrated the wide-ranging repercussions for human wellbeing and increased disease transmission (Patz *et al.* 2005). The 2003 heat waves in

France and Russia claimed nearly 15,000 and 56,000 lives, respectively (Robine *et al.* 2008). More frequent extreme rainfall events may be similarly damaging, resulting in flooding and increases in water-borne diseases and disease vectors (Kondo *et al.* 2002, Koelle *et al.* 2005). Beyond the immediate effects, droughts, heat waves and floods have caused longer-term food shortages (FAO UN food price increases) throughout the world.

Extreme events can also alter ecosystem functioning and structure, and the provisioning of ecosystem services (e.g. Reichstein *et al.* 2007, Jentsch & Bierkuhnlein 2008). Yet how they do this and what factors make ecosystems more or less susceptible to extreme weather events, are not well understood, in part because most evidence has so far come from observational research without a strong experimental counterpart.

1.4 Alternative metrics for diversity to describe biodiversity-ecosystem function relationships

The range of ways to characterize "diversity" may further introduce confusion into our understanding and application of diversity-function and diversity-stability relationships. We need to ask whether one measure is more appropriate or relevant than another, and to what extent this might depend on the specific functions under consideration. For example, the extent of dominance apparent in the species composition of a community—whether species are mixed in roughly equal numbers, or the abundance distribution is skewed toward showing a few highly abundant species and many rare species—may be a better predictor of ecosystem function and stability than the raw number of species (Smith & Knapp 2003). There are several metrics available that account for differences in relative abundances of species, all of which can be rightly said to express "diversity".

Species Richness is simply the number of species present within a given area, and is therefore the most straightforward measure of diversity and the one most widely used in studies into diversity, function, and stability. Major advantages of this measure are the ease with which it can be calculated and that it conveys the taxonomic variety present in an area in easy to interpret terms. There are however many potential drawbacks associated with equally weighting rare and common species if our interest is in the functional output or stability of the whole collection of species (i.e. the community), because highly abundant

and rare species would be expected to contribute differently. To account for this there are many measures that emphasize different aspects of the dominance or evenness of the community. These include the Simpson index - weighted towards most abundant species; the Shannon-Weiner diversity index – emphasizing evenness, or the likelihood that one species has an equal probably of being represented in a random sample as all other species; and the Berger-Parker index - emphasizing dominance, or the proportional importance of the most abundant species. A comprehensive review of taxonomic diversity measures is provided by Magurran (2010). All of these metrics are commonly used in ecological research, and there may be pros and cons to each one in evaluating diversity-function and diversity-stability relationships. Since all accurately represent some kind of "diversity", however, it is important to understand how they relate to each other in describing diversity-function and diversity-stability relationships.

We must also note that measures based on taxonomic variety are not the only measures of diversity available in ecology, and may not be the most relevant ones for evaluating diversity-function and diversity-stability relationships. Since it is the functional traits of species that ultimately account for ecosystem functions, and likely are important influences on stability as well, measures of diversity at the trait level may be most relevant to this field of research. Functional diversity provides a measure that accounts for such variety at the trait level. Species richness may not be a reliable proxy for functional diversity: because of the functional redundancy and disparity among species, it may not be the case that adding a species to a community increases the diversity of traits present in that community, and when it does, it may not do so linearly. Ecologists working with functional diversity instead estimate a logarithmic relationship between species richness and trait richness (Balvanera *et al.* 2006, Cardinale *et al.* 2006, Worm *et al.* 2006).

Functional diversity quantifies the variety of biological traits present within a community. It is considered by some most informative in understanding the relationship between diversity and ecosystem functioning (Tilman *et al.* 1996, Diaz & Cabido 2001). It is not a new concept, as early as 1982 Leps and colleagues posited functional attributes rather than the number of species governed community-level processes present. In a set of experimental plant communities in Northern England responses to frost, drought and

burning were predictable using the functional traits of dominant plants and were independent of plant diversity (MacGillivray *et al.* 1995).

Functional trait data can be obtained from direct measurements in the field and greenhouses, databases or literature sources (Hill *et al.* 1999, Kleye *et al.* 2008, Royal Botanic Gardens, Kew 2008, Kattge *et al.* 2010). There are challenges with this measure, however, and many obstacles to its use. First and foremost is the lack of comprehensive data on functional and physiological traits. The quality of functional trait data can be highly variable with many trait ranges being acquired in greenhouses or in considerably different environments to the study system being used. Moreover, the extent of intraspecific variability in traits is not well understood in this context. There are a number of sources for the evaluation of the links between trait and processes, indicating root depth and density, nitrogen fixing capacity, specific leaf area (SLA), leaf size, leaf dry matter content (LDMC) and leaf nitrogen are correlated with nutrient cycling and biomass production (e.g. Klumpp & Soussana 2009, de Bello *et al.* 2010). Due to the general scarcity of detailed information on traits and the difficulty in acquiring this, studies that use functional diversity tend to incorporate only those traits that are associated with the particular function being measured, but this makes a lot of a priori assumptions about the comprehensiveness of our understanding of functions and the traits underlying them.

Treating species richness as a proxy for functional diversity (FD) implies that with each added species, FD increases by a similar amount. This is most likely not the case, as there is a certain level of functional redundancy within communities we would expect the relationship to be logarithmic (Balvanera *et al.* 2006, Cardinale *et al.* 2006, Worm *et al.* 2006). Identifying functional redundancy within communities would highlight thresholds and natural buffering. How many species can a community afford to lose before function is affected?

As with species richness metrics, there are functional diversity measures that incorporate abundances and dominance to account for evenness and rare species, such as functional evenness (Table 1.2). Functional group diversity has been used to explore diversity-function relationships (e.g. Tilman 1996), but this tends to be so broad a grouping that relationships revealed may not be very informative. Despite the numerous studies and a

shift from species-based to trait-based measures, there is no general consensus on the apposite measure of functional diversity (Petchey *et al.* 2004, Mason *et al.* 2005, Villeger *et al.* 2008, Schleuter *et al.* 2010, Meisser *et al.* 2010)

Table 1.2 Examples of comparable taxonomic, phylogenetic and functional diversity metrics

	Taxonomic	Phylogenetic *- adding relatedness*	Functional *- adding functional trait information*
Presence	Species Richness **(S)**	Phylogenetic Diversity (Faith's **PD**) (Faith 1992)	Functional Diversity (**FD**) (Petchey and Gaston 2002)
Presence and Abundance	Shannon-Weiner Index (**H**) (Shannon 1948)	Phylogenetic Entropy ($\mathbf{H_P}$) (Allen *et al.* 2009)	
	Simpsons Index (**D**) (Simpson 1949)	Quadratic Diversity (**Q**) (Rao 1982)	Functional trait diversity ($\mathbf{FD_Q}$) (Botta-Dukat 2005)
Abundance	Evenness ($\mathbf{E_{var}}$) (Smith & Wilson 1996))	Phylogenetic-Abundance-Evenness (**PAE**) (Cadotte *et al.* 2010)	Functional Evenness ($\mathbf{F_{EVE}}$) (Villeger *et al.* 2008)
	Berger-Parker Dominance Index (**BPD**) (Parker & Berger 1970)		Community weighted means for individual traits (**CWM**) (Garnier *et al.* 2004)

Phylogenetic diversity may provide a 'happy' medium between taxonomic and functional measures (Swenson & Enquist 2009, Pavoine *et al.* 2010), integrating evolutionary history and patterns of relatedness (and by extension sharing of traits) into our understanding of diversity. Measuring phylogenetic diversity relies upon the creation or availability of phylogenetic trees (which in itself is not a trivial exercise), and as with taxonomic and functional diversity, there are a variety of measures of phylogenetic diversity, each incorporating different aspects of phylogenies but with no consensus on best application among these measures (Table 1.2). Usefully, some taxonomic measures have been adapted to incorporate relatedness (Allen *et al.* 2009), providing for direct comparability between measures of taxonomic diversity and phylogenetic diversity. Thus Faith's PD measure is the counterpart to species richness; Rao's quadratic diversity (Q) the counterpart to Simpsons

index (D); phylogenetic entropy (H_P) the counterpart to the Shannon-Weiner index (H); and Phylogenetic-abundance-evenness (PAE) the counterpart to Evenness (E). By testing each phylogenetic measure against its taxonomic counterpart we can identify the importance of relatedness in biodiversity-ecosystem function relationships. Moreover, as we do not comprehensively understand which traits are most important for many functions, phylogenetic diversity allows us to compensate by including much of the functional trait variation within a community implicitly (Cadotte *et al.* 2008, Cadotte *et al.* 2009).

Many ecologists working with diversity have shifted towards functional and phylogenetic diversity rather than species number alone (Diaz & Cabido 2001, Lavorel & Garnier 2002, Petchey & Gaston 2006, Cadotte *et al.* 2011, Grigulis *et al.* 2013). Similarly to functional diversity, phylogenetic diversity has proven to be a useful predictor of ecosystem function (Conolly et at 2011, Flynn *et al.* 2011, Pavoine & Bonsall 2011, Cadotte *et al.* 2012), with one direct comparison showing comparable predictive power (Flynn *et al.* 2011). Yet still, relationships of species, functional, and phylogenetic richness to ecosystem function are poorly understood for natural systems (Naeem 2002).

Are there broad relationships between the diversity measures, such that one can be used reliably as a proxy for another? Phylogenetic diversity has been found to correlate with species richness, and species richness to affect functional diversity (Cadotte *et al.* 2008, Cadotte *et al.* 2011), but the strength and robustness of these relationships are not clear. Nor is it understood how these measures compare in assessing the biodiversity-function and biodiversity-stability relationships. Does the appropriateness of a given metric vary based on the function we are examining? Our understanding of how biodiversity affects function and stability is drawn from the specific ways we've defined our terms, and may not convey an inherent "true" relationship between these variables more broadly considered.

1.5 Lessons from natural communities

All of the studies discussed so far use artificially created and maintained communities. Whilst this is an essential first step in understanding the relationship between diversity, function, and stability (e.g. there are fewer confounding factors) it is important to relate

these findings to real communities and evaluate how the relevant mechanisms play out against the very real, very many confounding factors that exist in any real ecosystem.

Grace *et al.* (2007) investigated species diversity-biomass relationships in 12 natural grasslands ranging widely in type and location (e.g. Utah (USA) mountain grasslands, Indian tropical savannas, Finish meadows, Minnesota (USA) prairie). In these established, mature ecological communities, species richness either had weak to negligible correlation to biomass, with five of the sites showing no significant relationship. Threes sites showed non-linear negative relationships between production and richness, negative linear relationships were found in all other sites. The only significant relationships identified were negative (increased diversity correlated with decreased function) over at least part of its span, contradicting the strongly positive relationships found in BIODEPTH and other studies with sown communities (Hector *et al.* 1999). Furthermore, the biodiversity-ecosystem function relationship at Grace's Minnesota prairie site was non-significant while in Tilman's sown Minnesota communities it was significantly positive (Tilman 1996). The sites in this study were spread worldwide, and therefore differ markedly in numerous abiotic and biotic conditions. Yet biotic and abiotic variation exists at smaller scales and well, so it is essential that test relationships and mechanisms uncovered in experimental work with sown communities in the context of natural communities even at site-specific and landscape scales.

As with research into the relationship between biodiversity and ecosystem function, most empirical research into relationships between biodiversity and stability has used artificially assembled communities where species composition and richness are defined *a priori*. Experimentally sown and naturally assembled communities can exhibit different relationships even within the same experiment: using both sown and self-assembled communities, Bezemer and van der Putten (2007) looked at temporal stability in biomass production. Long term positive relationships between richness and stability were seen in sown plots not subsequently maintained by weeding, echoing evidence from other studies with sown communities that were weeded to maintain treatments, whereas the natural plots showed the opposite relationship – more species rich plots were more temporally unstable. Only two diversity levels were used in this study (high diversity – 15 species; and low diversity – 4 species). It is worth considering the extent to which our understanding of

the BEF relationship and the role of biodiversity in stabilising communities may be biased by the carefully controlled and heavily manipulated structure of our research.

Typical community assembly may explain differences in stability between mature and immature communities (Wilson 1969), with implications for research into how diversity relates to stability. Ecological communities first form with a non-interactive phase characterized by rapid colonisation of available space. The colonising species then undergo an interactive phase where the number of species is limited through competition. Ecological or assortative arranging then occurs resulting in combinations of coexisting species better able to cohabit the same area. It is at this stage that the diversity/composition "stabilises". When testing the overall stability of communities, it makes sense to start at a relatively stable state and then perturb.

1.6 The importance of spatial scale with respect to biodiversity relationships

Most of the biodiversity-function and biodiversity-stability relationships considered above have been documented using small spatial scale studies, making translation to more conservation-relevant scales of landscapes potentially challenging. Species losses and invasions are particular concerns associated with global change, so it is imperative we understand relationships between species diversity, and the function and stability of ecosystems at landscape scales. We can begin addressing this issue by asking whether the patterns identified at the scale of plots within a single study site are consistent with those identified at the scale of different sites across the landscape.

A few studies have examined patterns in diversity-function relationships at landscape scales or across multiple scales, asking how scaling up from alpha diversity (local species richness) to gamma diversity (landscape unique species richness) affects the biodiversity-ecosystem function relationship (Anderson *et al.* 2009, Aragon *et al.* 2011, Maestre *et al.* 2012, Pasari *et al.* 2012). The Jena Experiment, set up in Germany where plant diversity is manipulated at different spatial scales, found a similar species diversity-productivity relationship from scales of small plots measuring 12.25m^2 up to scales of large plots measuring plots 400m^2 (Roscher *et al.* 2005). A landscape-scale study with Pampean grasslands and Patagonian meadows showed that increasing diversity at the landscape level could either have positive

or no effect on the stability of ecosystem functioning (Aragon *et al.* 2011). The two landscapes varied considerably in mean annual temperature and mean annual precipitation, which may account for the different results - there was a positive relationship between landscape-level species richness and stability in pampas grasslands, with no such trend found in the Patagonian meadows. In a separate study, national-scale biodiversity and ecosystem variables were compared in the UK at two different scales of resolution: 100km^2 and 4km^2 (Anderson *et al.* 2009). The relationships between biodiversity and ecosystem functioning varied based on the spatial scale under focus used and were found to be regionally dependent. In other words, observers would come to completely different conclusions regarding the BEF relationship depending on what region was being analysed and what scale it was being analysed at, highlighting the importance of context dependency and spatial scale.

Pasari *et al.* (2012) investigated the relative effects of alpha, beta and gamma diversity on individual functions and multi-functionality in grassland communities. Alpha diversity had a strongly positive effect on both individual functions and multi-functionality, while beta and gamma diversity only positively correlated with multi-functionality. A global analysis of drylands found plant species richness to be positively related to ecosystem multi-functionality and to carbon, nitrogen and phosphorous cycling when each was tested individually. These initial few studies have shown ecosystem function at the landscape scale is affected by landscape scale diversity levels (Aragon *et al.* 2011, Maestre *et al.* 2012). The relatively small spatial scale on which our current knowledge of biodiversity relationships is based does not correspond to the scale at which society manages biodiversity and its functional outputs. Conservation strategies are more likely to focus at the field or landscape scale rather than the scale at which researchers have been working at however available space is an issue in many experimental designs. Understanding how both alpha and gamma diversity contribute to ecosystem function is central to maintaining functional outputs both locally and globally.

1.7 Biodiversity-stability relationships across trophic levels

Along similar lines, our understanding of how diversity affects function and stability may be biased by the specific life forms measured – predominantly plants. An expanded focus that

considers more of the community could come with several benefits. Many important ecosystem functions, such as carbon storage and nutrient cycling, result from the activities of organisms at multiple trophic levels. Because positive relationships between the diversity of primary producers and the diversity of associated consumers are common, actual differences in diversities between plots may be considerably larger than those apparent just among plants, obscuring relevant aspects of the diversity-function relationship. Plant diversity and abundance have previously been shown to influence both aboveground and soil faunal diversity and abundance (Brown & Southwood 1983, Haddad *et al.* 2001, Wardle & Van Der Putten 2002, Wardle 2005, Scherber *et al.* 2010) (Figure 1.4), with fewer studies showing no significant correlation (Gastine *et al.* 2003, Salamon *et al.* 2004).

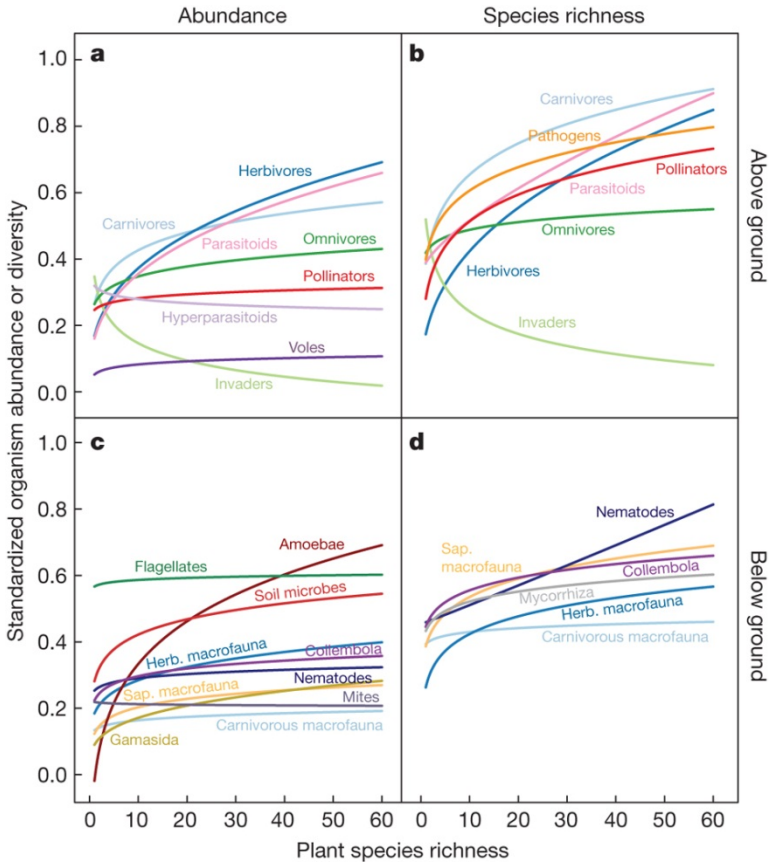


Figure 1.4 Relationships between plant species richness and above- and belowground organisms in temperate grasslands (from Scherber et al. 2010).

Stability likewise is not a property of just a single trophic level, and is likely not determined by interactions and processes restricted to a single trophic level, making it important to consider stability across multiple (Naeem *et al.* 2000). Wardle and colleagues (2004) pointed out that both above- and belowground communities are powerful mutual drivers, with numerous negative and positive feedbacks linking them. Wimp *et al.* (2010) found that primary production determined the community structure of arthropods in intertidal salt marshes, while Stein (2010) showed that herbivore abundance and richness affected plant species richness and composition in montane grasslands. Thus an additional benefit of a more comprehensive focus is that by delineating the relationships between plant and consumer diversities and abundances we may gain better predictive power over the consequences of declines in plant diversity for higher trophic levels and vice versa.

1.8 Thesis structure

This discussion has illustrated the variability of diversity-function and diversity-stability relationships that can be seen between scales, measures of diversity, stability and function, natural versus artificial communities, and potentially between different trophic levels. There is a need for a rigorous examination of constancy, resistance and recovery in biodiversity, ecosystem function, and the biodiversity-ecosystem function relationship in natural communities across different diversity metrics, spatial scales, and trophic levels. In established, naturally-occurring plant communities is there a biodiversity-biomass production relationship? If so does this vary by spatial scale from plot to field? Does this vary with the measure of diversity? Does diversity correlate with stability of both plant numbers and biomass with and without the external disturbance such as an extreme weather event? How does plant diversity vary with diversity of other organisms such as belowground invertebrates? The examination of these questions is the aim of this thesis.

Using an experiment, a series of 200 $1m^2$ plots of grassland nested into eight grassland habitats, at the Silwood Park campus of Imperial College, Chapter 3 presents patterns of plant diversity within and across sites. It will then cover the results of tests of diversity-function and diversity-stability relationships at these two spatial scales. Beginning with measurements of how species richness of plant communities fluctuates annually and when exposed to an extreme weather event. Finally it will present evidence of whether there is a

relationship between species richness and biomass production, and whether the shape of that relationship varies with site or scale. This work examines how the form and magnitude of relationships change as we use different definitions and measures of stability, and therefore how our starting definitions constrain our understanding of how diversity is structured across spatial and temporal scales.

Stability in these tests is split into constancy, resistance and recovery. In this context, constancy is defined as the amount of change in biodiversity and its functional output across years under ambient conditions; resistance is defined as the amount of community compositional change and its functional output immediately following an extreme weather event; and recovery is defined as the extent to which communities return to pre-manipulation levels of diversity and functional output one year following the extreme weather event. All of this work is presented in Chapter 2.

The Third Chapter presents experimental results that examine how the diversity of plants corresponds to the diversity of invertebrate consumers within individual grassland patches. It will illustrate how the form and strength of these relationships change as we define plant community attributes in different ways. Having established patterns of diversity and correlations among these, the focus then expands to function, asking how soil invertebrate biomass corresponds to either plant diversity or biomass, and to the stabilities of these communities when exposed to an experimentally simulated extreme weather event.

Chapter 4 describes research asking how much the view of diversity-function relationships depends upon the specific measures of diversity and function we consider. Chapter 2 focused only on species richness, but this experiment provides an opportunity to compare the performance of this metric in predicting function with the performance of other metrics. Can we generalize from published studies to true, fundamental relationships, or do these results depend on specific definitions and measurements? We cannot test this from the published literature, because only select measures are provided in each instance, but we can test it here by considering diversity-relationships through the lens of multiple measures of diversity. By comparing various taxonomic and phylogenetic diversity measures one can highlight the relative utility of incorporating community structure and relatedness into biodiversity-ecosystem function relationships in natural communities.

All of this is studied within natural plots of grassland and existing variation in diversity, rather than in assembled communities or otherwise manipulated diversity levels. This approach deprives us of the ability to control and replicate specific diversity levels, but this potential downside is outweighed by the additional relevance conferred by looking exclusively at natural processes. Focusing on real ecological communities, assembled through natural processes over extended timescales, we can be confident that comparisons of taxonomic, phylogenetic, and functional diversities are informative with respect to real-world relationships and that experimental results reflect responses to treatment itself rather than to treatment and observer assembly.

Chapter 2

Ecosystem function and community stability vary independently of biodiversity in natural grassland under ambient weather variation and under simulated weather extremes.

2.1 Abstract

Ecologists have debated the nature of the biodiversity-ecosystem function relationship for over 50 years. Previous evidence points towards a generally positive relationship, where an increase in biodiversity leads to increases in ecosystem functions and stability (Tilman *et al.* 1997, Levine 1999, Fridley 2001, Loreau *et al.* 2001). Most experimental evidence for significant relationships between diversity and function or stability has come from communities in which diversity itself is experimentally manipulated. It is important to relate these findings to real ecosystems in which diversity is established by natural processes. Here I report on research in which the functionality and stability of grassland plots are examined across natural gradients of plant diversity. Function is tested in terms of aboveground plant production and stability is examined in terms of community change against natural variation in climate and against a simulated weather extreme. A weak positive correlation was identified between primary production and species richness in one year only. Primary production itself varied considerably across years and in response to a simulated extreme weather event, but this variation was independent of species richness. Species-rich plots exhibited short-term compositional changes similar to species-poor plots, indicating that stability likewise varied independently of diversity.

2.2 Introduction

Diversity has been proposed or demonstrated to affect levels of primary and secondary production (Tilman *et al.* 1996), nutrient cycling and storage (Hooper & Vitousek 1998, Conti & Diaz 2012), and stability against invasion and other perturbations (Levine 2000, Naeem *et al.* 2000, Kennedy *et al.* 2002). Most studies examining these relationships have however used artificially sown communities in which diversity levels are experimentally set and maintained. This is an essential first step in understanding the relationships between diversity and function, and diversity and stability, allowing researchers to limit confounding factors, highlight causal links, and test wide diversity gradients; but with theoretical and experimental foundations now well established, it is important to relate these findings to real ecosystems.

Higher diversity of species could lead to increases in productivity and other functions due to a number of different mechanisms: complementarity, where a more species-rich community occupies greater niche breadth and so utilises more resources (Tilman *et al.* 1997, Fridley 2001, Loreau *et al.* 2001); mutualisms and facilitations, where individual species produce more favourable growth conditions for other species (Levine 1999); and sampling effects, where more species-rich communities have a statistically higher likelihood of containing high-performance species for those conditions (Hector *et al.* 2002). Similarly, higher numbers of species could lead to greater stability of communities through several alternative mechanisms: portfolio effects, where aggregate means statistically dampen variation in their individual components in proportion to the size of the aggregate (Doak *et al.* 1998); competition, individual species negatively co-vary; and functional redundancy, where greater numbers of species are more likely to share traits and so species can be lost without a change in function of the aggregate (Walker 1992). To understand the role of these processes in nature, and the patterns they generate, we need to allow them to play out against the very real, very many confounding factors that exist in actual ecosystems.

Challenging conventional wisdom on diversity-function relationships, in a multi-site experiment focused in natural communities, species richness had a weak to negligible relationship to production, and where relationships were significant they were negative (Grace *et al.* 2007). Relationships uncovered in this study were site dependent, indicating

that other factors such as environment and climatic variables rather than biodiversity were driving production. The move to consider more abiotic and biotic factors to explain productivity and diversity was echoed by Adler *et al.* (2011). In an experiment replicated across 40 sites worldwide positive and negative linear, non-significant and quadratic relationships were found. Despite earlier evidence, more recent work has proven species richness alone is not a good predictor of production.

Challenges to conventional wisdom on diversity-stability relationships came much earlier, beginning with theoretical work by Robert May in the 1970s. May's models indicated that species-poor communities, by having fewer connections altogether, offered reduced opportunity for connections to break down, and therefore exhibited higher stability than more diverse communities with greater numbers of connections (May 1972, May 1973). Many large-scale experiments (e.g. Cedar Creek, Jena, Biodepth at Silwood Park) have tested the diversity-stability relationship in the decades following May's work, and these have generally found it to be positive to negligible, but not negative (Tilman 1996, Naeem & Li 1997, Hector *et al.* 1999, Tilman *et al.* 2001, Proulx *et al.* 2010). The Park Grass Experiment, one of the longest ecological experiments in the world, found greater variability in species-rich plots thus a negative richness-stability relationship (Dodd *et al.* 1994). In a direct comparison between sown and naturally occurring plant communities Bezemer and van der Putten (2007) found that species-rich communities were more stable when sown and less stable when naturally assembled. In non-weeded plots or when weeding ceased in experimental communities at Jena novel species did not impact the number of resident species but negatively impacted their relative cover (Roscher *et al.* 2013). Over time the artificially created communities differed greatly from the original composition. Based on these results, it is worth considering the extent to which our understanding of the biodiversity-ecosystem function relationship and the role of biodiversity in stabilising communities may be biased by the carefully controlled and heavily manipulated structure of our research.

In an extensive study spanning 40 local sites across 15 countries Adler *et al.* (2011) tested the productivity-richness relationship (PRR) at local and regional scales. Depending upon the anthropogenic origin, site locality and a number of other measures the relationship was humped, positive, negative or non-significant. The relationships spanned the whole range of

possible shapes thus demonstrating the complexity of the relationship. Sites were selected to represent the variance found in natural grasslands making it the closest and most comprehensive investigation into PRR in naturally occurring grassland communities to date. These results have elicited great debate, in particular claims the data actually shows strong support for a positive linear PRR (Pan *et al.* 2012) or the humped-back model (Fridley *et al.* 2012). There are many theories and mechanisms (many conflicting) used to predict the biodiversity-ecosystem function relationship and as this study show we have not been able to resolve the underlying ones.

Before undertaking the challenge of identifying the role of diversity for community stability, it is critical to clarify exactly how 'stability' is defined: is it constancy under ambient conditions, resistance to perturbations, recovery following perturbations, or some combination of these or other metric altogether? Since its introduction in ecology, the term has been used in a wide variety of ways in the literature. To focus on stability as 'resistance' or 'recovery', some external perturbation is needed. This can be a chance natural event, as in Tilman's work following a prolonged drought at the Cedar Creek study site (Tilman & Dowling 1994), or a simulated weather extreme. Extreme weather events, such as increased rainfall events or droughts, are predicted to increase in frequency and magnitude (Easterling *et al.* 2000, IPCC 2011), and by several measures these increases are already apparent (Hansen *et al.* 2012). What is currently lacking in ecology research is strong emphasis on the ecological consequences of extreme weather events (EWE) and experiments testing them (Jentsch *et al.* 2007, Jentsch & Beierkuhnlein 2008, Smith 2011). Furthermore, extreme events can also alter ecosystem functioning and structure, and the provisioning of ecosystem services (Reichstein *et al.* 2007, Jentsch & Bierkuhnlein 2008). What factors make ecosystems more or less susceptible to extreme weather events, are not well understood, in part because most evidence has so far come from observational research without a strong experimental counterpart.

Few studies have looked at more than one measure of stability, and due to the lack of standardised definitions or measures it is hard to draw cross study comparisons. In an effort to disentangle the effects of diversity on different definitions of stability, van Ruijen *et al.* (2010) used the response of experimental plants communities to a natural drought – initially it appeared resistance to drought decreased as species richness increased but once

differences in production were accounted for this relationship disappeared. Alternatively (using their definitions) recovery was strongly positively correlated with species richness, and resilience was the same regardless of diversity. Recent theoretical work has shown that resilience and resistance illicit opposite trends and may, in fact, be independent from each other (Vallina & Le Quere 2011). They showed that resistance rather than resilience might govern the overall stability of complex food webs. Depending on your definition of stability you may find different biodiversity-stability relationships. Given the variety of ways an ecosystem is able to respond to a perturbation, to focus on one single form of stability we risk underestimating the extent the perturbation may affect a community, i.e. whilst a community may be able to resist significant changes in the short term there may be longer term (i.e. poor recovery) consequences that are not identified if only looking at resistance.

Here results from the DExtER experiment at Silwood Park will be reported. The experiment uses natural gradients in plant species richness, and tests function and stability in plant communities against both natural variation in weather and a simulated weather extreme, asking whether these vary as a function of plant species richness. Firstly the relationships between species richness and primary production and species richness and community stability (constancy) in ambient conditions are examined. Aboveground production is a reasonable proxy for production, an ecosystem function. The variability between ambient conditions and those subjected to an extreme weather event for both production and community stability (resistance and recovery) is then quantified. Finally whether the fore-mentioned variability is correlated with species richness is tested. The hypothesis is the previously widely accepted positive relationship between function, stability and diversity would be inconsistent with relationships found in complex natural systems, i.e. due to the idiosyncratic nature of natural systems there would not be a straightforward relationships between function, stability and richness.

2.3 Materials and methods

The DExtER (Disturbance Extremes and Ecological Responses) experiment was established at Silwood Park, Imperial College London in South-East England (51°24’23.16”N, 0°38’55.33”W) in 2011. The DExtER experiment was used to measure baseline relationships between plant species richness and aboveground plant biomass, as a simple proxy the

diversity-function relationship. I examine how the relationship between plant richness and biomass varies with ambient climate across years, and how it responds to an external shock in the form of a simulated weather extreme. Finally, I compare the degree of variation in both biomass and species composition as a function of initial plant species richness to explore questions of stability in these systems. The focus in this chapter is therefore on variables of plant species richness, plant community composition and aboveground plant biomass, which I use to test questions of diversity-function and diversity-stability in the Silwood Park grasslands.

2.3.1 Natural history of the study system

Grassland provides a suitable habitat type for these tests because plant diversity varies and is readily measurable over small (meter to meter) scales to intermediate (grassland to grassland) scales. Grasslands are important habitats globally as they cover approximately 40% of the earth's land surface ((GLCCD 1998) and provide important ecosystem services beyond human nutrition such as carbon and water storage, wildlife habitat, and soil protection and regeneration. Grasslands at Silwood Park support populations of roe deer, muntjac, moles and rabbits. Soil characteristics vary across Silwood's grasslands from sandy loam to silty loam, and pH varies between 4 and 6 (low base). Average annual rainfall from 2000 to 2010 was 698.38ml $\pm$121.006 (mean $\pm$ s.d.). Annual rainfall in Year One (2011) was relatively low at 595.90ml, anomalously high at 862.90ml in Year Two (2012), and close to the annual average in Year Three (2013) at 699.90ml.

Richness of vascular plant species in Silwood Park grasslands ranges from approximately five species in low-diversity habitats and years, to twenty in high-diversity habitats or years. Composition varies considerably from grassland to grassland, but the perennial grasses *Holcus lanatus* and/or *Agrostic capillaris* are present in most systems. Approximately 30 vascular plant species of the 114 found in grasslands at Silwood Park (Crawley 2007) were present across experimental sites in the first year of this research (2011).

2.3.2 Experimental sites

The experiment comprised of eight sites, selected in a manner that attempted to balance the needs for a wide range in intra-site and inter-site species richness, access to a water line for irrigation, the presence of one or two common grasses (*Holcus lanatus* and *Agrostis capillaris*), and maximum distances from tree-lines so that plots would receive similar levels of sunlight, and from other on-going experiments at Silwood Park. Eight sites at Silwood Park suitably balanced these criteria in my judgment, so all eight were selected for research (Figure 2.1; details of each site given in Table 2.1). Unfortunately one site was dropped in Year Two due to a malfunction in the adjacent water line, therefore enough water could not be transported to the site to carry out the watering treatment.

Table 2.1 Characteristics for each study site in the meta-experiment.

Site	Lattitude, Longitude	Altitude (m a.s.l.)	Soil Type	Species Range per plot (m^2)	Total Species Richness (site $100m^2$)
A	51.4079, -0.6483	98.9	Sandy loam	5 - 12	16
B	51.4085, -0.6438	136.6	Medium loam	3 - 5	5
C	51.4116, -0.6409	133.1	Sandy/silty loam	3 - 5	6
D	51.4127, -0.6422	84.6	Sandy loam	3 - 9	12
E	51.4129, -0.6432	128.6	Silty loam	4 - 8	10
F	51.4140, -0.6507	107.4	Medium loam	4 - 13	18
G	54.4146, -0.6522	121.0	Sandy/medium loam	4 - 9	13
H	51.4156, -0.6529	114.5	Sandy/medium loam	6 - 12	15



Figure 2.1 The meta-experiment. Twenty-five plots are arrayed at each of seven sites within Silwood Park, with treatments imposed in a randomized block design within each site.

Twenty-five plots measuring $1m^2$ were laid down in a regular three-row grid of 8, 9, and 8 plots at each site. Plots in each row and from one row to the next were separated by 2m edge to edge (Figure 2.2). This regular 8-9-8 grid ensured equal total areas sampled and covered at each site. Plot size was set by total available space at the smaller sites, with $1m^2$ maximizing the number of plots within a site, while allowing sufficient separation among plots to allow sampling and maintain treatment fidelity, and assuring adequate space for mixtures of species to coexist in appreciable numbers (from 3 to 13). Each $1m^2$ plot was surrounded on all sides by a 1m buffer zone to allow space for observer movement and sampling, and to avoid lateral movement of water from treatment to control plots. Digging a 15cm deep trench along the far edge of each buffer strip further reduced non-target effects of water addition. Identical trenches were dug around control plots as a physical-disturbance control, such that all plots were surrounded on all sides by 15cm deep trench.

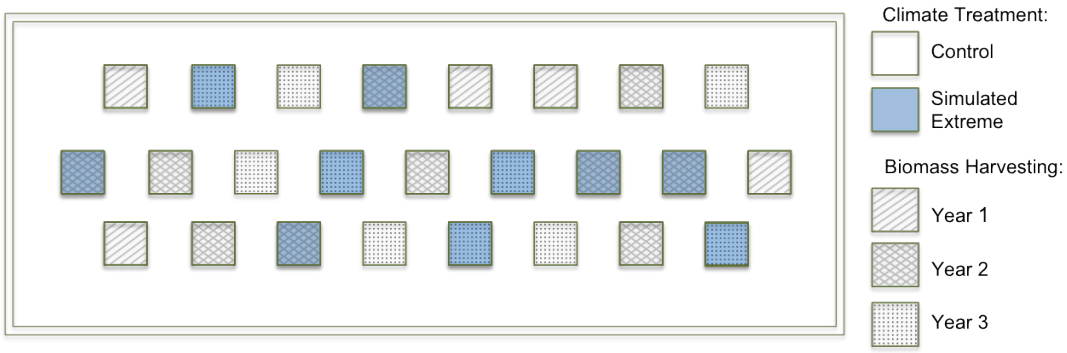


Figure 2.2 Representative schematic of the plot layout in each study site. Colors indicate climate treatment and hashmarks denote the years each plot is harvested for biomass and eliminated from the design.

The 25 plots at each site were divided evenly into five groups for manipulation and sampling. The five plots in one of these groups were sampled in Year One to establish baselines for all measures and relationships against which subsequent changes would be assessed. The remaining four groups were randomly assigned into one of two treatment categories: ten days of continuous water addition simulating an extreme rainfall event, and an un-watered control experiencing only ambient conditions. Because sampling is destructive, the two groups in each watering treatment (simulated extreme and control) were further divided between those for sampling in Year Two and those for sampling in Year Three. Note that field research was designed to run for three years in total, with baseline data collected in Year One, the extreme weather event

(EWE) treatment imposed and its immediate effects measured in Year Two, and follow-up data on ecological recovery collected in Year Three (Figure 2.3).

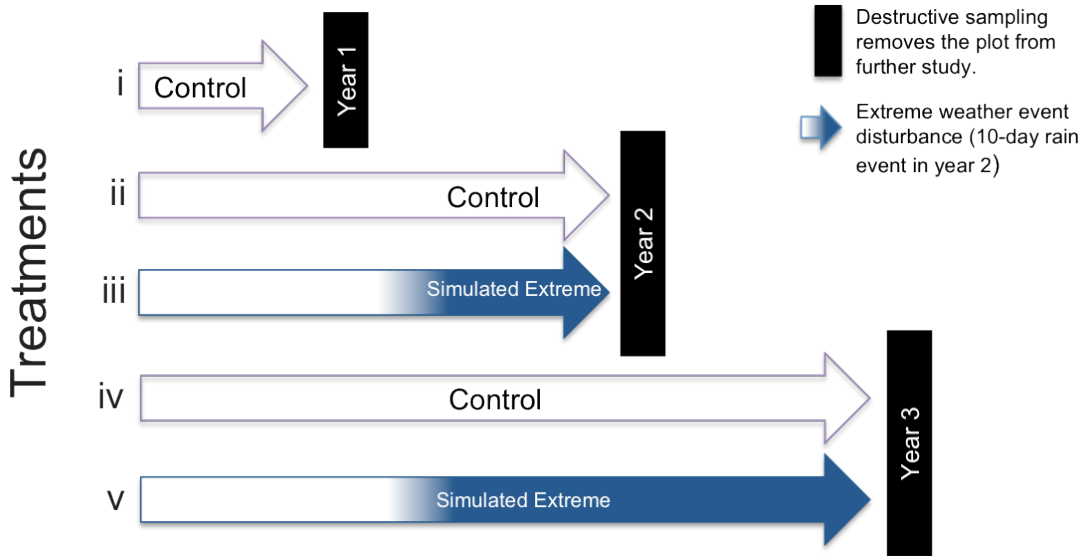


Figure 2.3 Climate conditions and destructive harvest schedule for each treatment. Each treatment was applied to five plots in each site. Treatments iii and v are subjected to a simulated extreme weather event in Year Two (2012). Black boxes denote destructive collection of aboveground plant biomass.

In total, five plots were sampled for baseline data in Year One; five control plots and five EWE plots were sampled in Year Two; and five control plots and five EWE plots were sampled in Year Three (Figure 2.3).

2.3.3 The extreme weather treatment

The weather extreme was imposed via a watering manipulation that consisted of 10 days of continuous water addition in a manner designed to simulate rainfall (Figure 2.4). Supplemental rainfall was delivered by hose nozzle suspended approximately 1m above each plot and calibrated to emit a diffuse spray of water as uniformly as possible across the surface area of the plot. Water addition began on July 5th 2012 and continued for 10 days in total. Approximately 2017.13 liters of water ($\pm$ 346.41) were deposited on each of the 70 designated plots per day over the 10 days. Following a pilot study the previous summer, a 10-day water manipulated was chosen as it was sufficient enough to perturb the system. Shorter precipitation events had little to no impact on the plants or soil

invertebrates. Soil moisture remained above ambient conditions for the following four weeks therefore simulating flooded conditions.

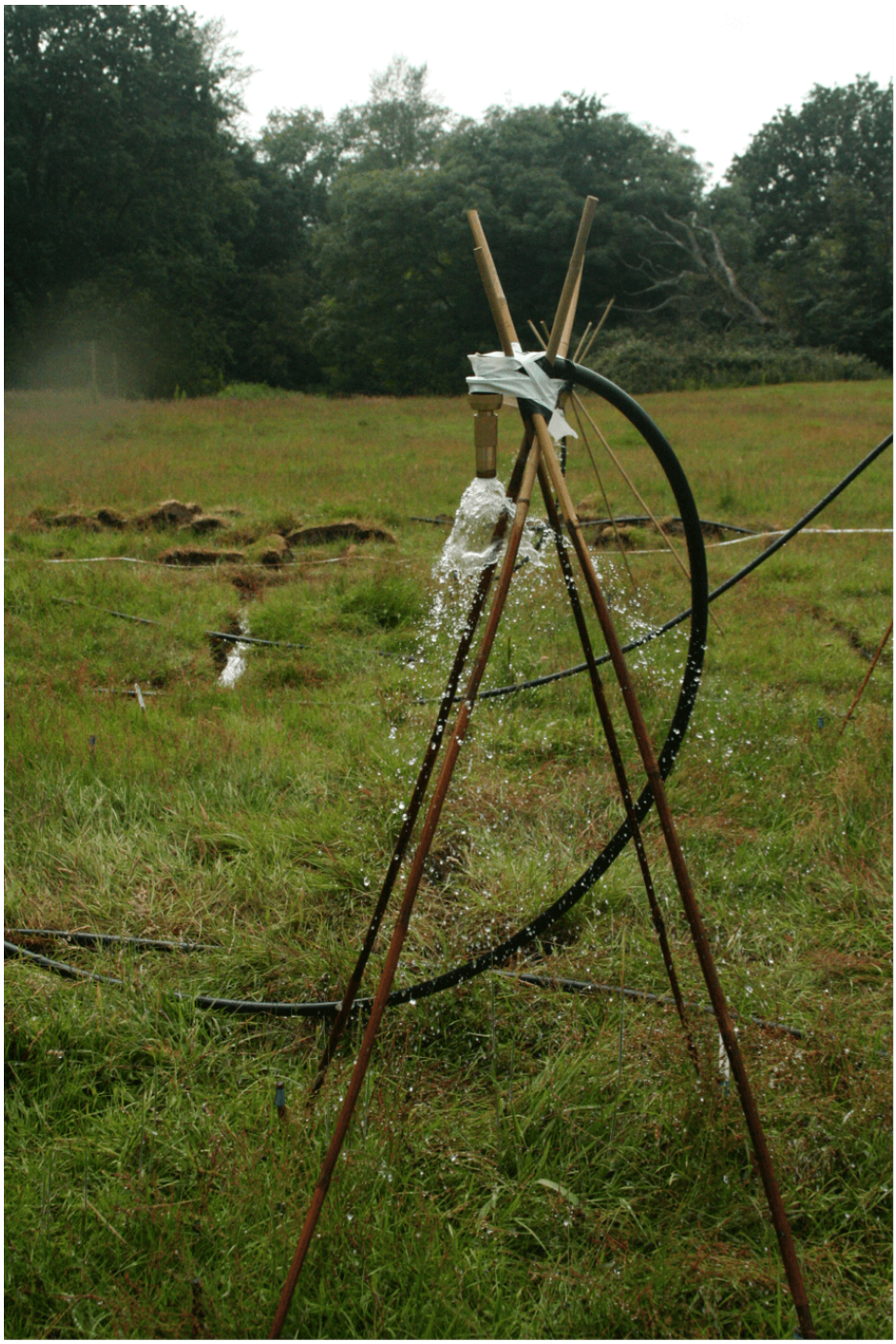


Figure 2.4 The basic watering manipulation. A hose nozzle suspended one meter over the plot distributes water in a diffuse spray

2.3.4 Response variables

Plant Production

In 2011 (Year One), 35 control plots were harvested for aboveground biomass to provide baseline values. The remaining 140 plots were split into two groups: control group of 70 plots experiencing ambient conditions and the manipulated group of 70 plots subjected to an extreme weather event. Due to the destructive nature of sampling biomass the 70 plots in each watering treatment were further divided between those sampled in Year 2 and those in Year 3 (35 control plots and 35 manipulated plots in 2012 (Year 2), and finally 35 control plots and 35 manipulated plots in 2013 (Year 3)). By splitting the groups we are able to capture both initial effects of the water manipulation treatment and the longer-term effects. Similarly to the species richness counts all biomass was removed from the central $0.25m^2$ square to ensure against edge effects. The collected biomass was dried at 80^0C for 72hrs and then weighed. The link between species richness and aboveground biomass production is tenuous when only a part of the plot is sampled. Furthermore, the extent of patchiness present in natural communities renders multiple biomass sub-sampling inefficient therefore whole plots were harvested. Once biomass was collected the plot was no longer used in the experiment.

The nature of this test requires that whole plots be sampled and then eliminated from future sample collection and hypothesis testing: the experiment is designed to examine how diversity related to biomass, and by proxy ecosystem function. Diversity itself can be repeat-sampled in a single plot multiple times, as it is in many of the plots in this experiment. Biomass, however, *with an aim toward relating it to patterns of diversity*, cannot be repeat sampled: if repeat sampling was undertaken at the plot scale, the first sample would represent a different type of plant production, and would be expected to hold a fundamentally different relationship to plant diversity, than subsequent samples that measured re-growth in cleared patches; if repeat sampling was undertaken at a subplot scale, where spatially distinct subsamples of each plot were harvested sequentially, it would undermine the essential test against diversity. Grasslands are inherently patchy in their species composition, and any subsample of a plot might be expected to hold a lower diversity of plant species than the whole plot due to species-area relationships along. It is therefore essential to include each species in the

production measurement, as subsampling negates the basic intent of the test against diversity.

Compositional Stability

Plant community compositional change is defined as the natural log of proportion of the total number of species shared across the two time points (Figure 2.5). It is naturally logged to account for differences in proportions. I calculated plant community compositional change between 2011-2012, 2012-2013, and 2011-2013 in 35 plots in ambient conditions, and 35 plots subjected to a simulated weather extreme.

$$\text{Compositional Change} = \ln\left(\frac{\text{Shared Species}_{T_1 \& T_2}}{\text{Total Species}_{T_1 \& T_2}}\right)$$

Figure 2.5 Calculation for compositional change between one time point (T_1) and another (T_2)

Compositional stability is divided into the following five measures: (a) constancy, or the annual change in plant community composition under ambient conditions; (b) long-term constancy, or the net compositional change across the whole experiment under ambient conditions; (c) resistance, or the change in plant community composition immediately following a simulated weather extreme; (d) recovery, or the change in plant composition from immediately following a simulated weather extreme to one year later; and (e) long-term trend, or the change in plant community composition from *BEFORE* a simulated weather extreme to one year after the weather extreme.

These stability measures were calculated as follows:

- **Constancy** = Number of species shared in 2011 and 2012 in control plots/total number of species overall in both time points. (N.B. this is calculated for both 2011-2012 and 2012-13).
- **Long-term Constancy** = Number of species shared in 2011 and 2013 in control plots/total number of species overall in both time points.
- **Resistance** = Number of species commonly shared in 2011 and 2012 in flooded plots/total number of species overall in both time points.
- **Recovery** = Number of species shared in 2012 and 2013 in flooded plots/total number of species overall in both time points.

- **Long-term Trend** = Number of species shared in 2011 and 2013 in flooded plots/total number of species overall in both time points.

To test if constancy in biomass varied with species richness the richness-biomass relationship slope in 2011 was compared with the slope in 2012, then the slope in 2012 with the slope 2013. A comparison of the richness-biomass relationship slopes in control plots and flooded plots in 2012 was carried out to see if resistance in biomass production varied with species richness. Furthermore to assess if recovery in biomass production varied with species richness the richness-biomass relationship slopes were compared between control plots and flooded plots in 2013. A guide for how to interpret these results can be found in Appendix 1.1.

To test whether the flooding caused greater compositional change than ambient weather variation, compositional changes in control plots from 2011 to 2012 were compared with compositional changes in flooded plots from 2011 to 2012. To assess whether the flooding caused greater community compositional change compositional change in control plots from 2011 to 2012 was compared with compositional change in flooded plots from 2011 to 2012. Lastly, control plots were compared with flooded plots between 2011 to 2013 to identify long-term compositional change.

2.3.5 Statistical analyses

To control for site effects mixed-effects models were employed with site as a random factor. Linear mixed models were used to test for correlations between species richness and function, and stability in ambient conditions. Nested analysis of variance (ANOVA) models were used to test for the effects of the extreme weather manipulation on both aboveground production and community composition both immediately after the manipulation and one year hence. Nested analysis of covariance (ANCOVA) models were utilized to test for the effect of the extreme weather manipulation on the relationships between species richness and production, and species richness and compositional change. All mixed effects models were conducted in R (R core Team, 2012) with the package 'lme4' (Bates & Sarkar 2007). I examined the residuals versus fitted plots and normal qq-plots of the linear models to ensure model assumptions were not violated. I used likelihood-ratio tests of the full models with both random and fixed effects with those with just random effects to calculate p-values.

As compositional change values were calculated with species richness data, any significant correlations between compositional change and original species richness were verified by permutation tests using the coin package in R (Hothorn *et al.* 2008).

2.4 Results

2.4.1. Annual variation in plant richness and production

Species richness did not significantly change under either ambient conditions or subjected to a flood (nested ANOVA: $F_{3,4}$ = 0.9716, T = 0.7730, P=0.434) (Figure 2.6). Site accounted for 60% of the variance attributed to random factors in the nested ANOVA. Plant biomass varied significantly between 2011 and 2012 (nested ANOVA: $F_{3,4}$ = 71.353, T = 8.447, P<0.001), and 2012 and 2013 (nested ANOVA: $F_{3,4}$ = 40.734, T = -6.382, P<0.001). The flood did not significantly affect plant biomass immediately following the event in 2012 when compared with control plots in 2012 (nested ANOVA: $F_{3,4}$ = 2.5868, T =1.608, P = 0.109). In 2013, one year after the flood, plant biomass significantly increased compared with control plots in 2013 (nested ANOVA: $F_{3,4}$ = 12.017, T=3.467, P<0.001). Site accounted for 54% of the variance attributed to random factors.

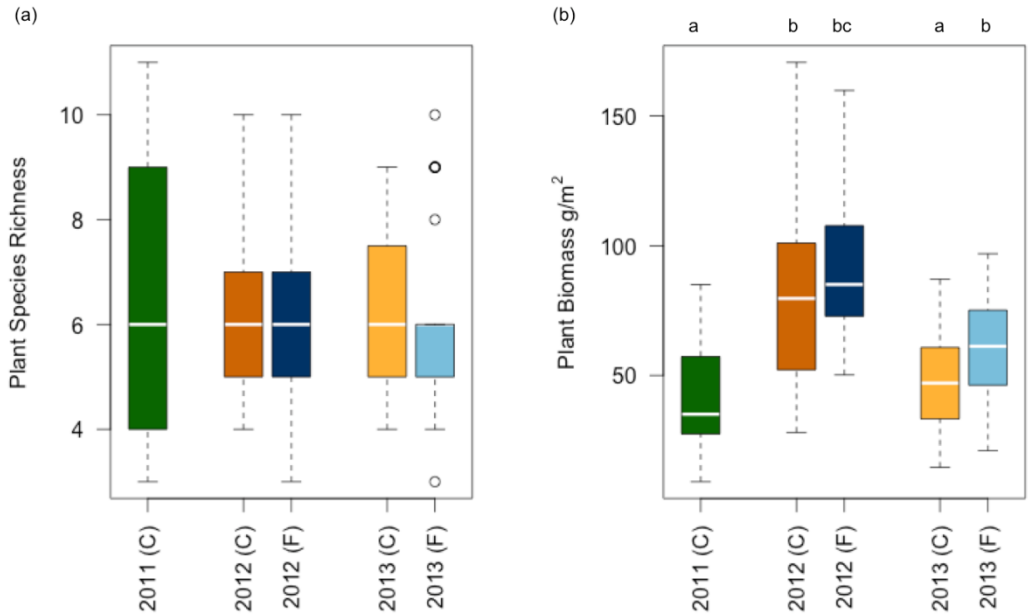


Figure 2.6 Changes in (a) plant species richness and (b) primary production under ambient conditions across years and in response to a ten-day experimental rain event. (C) = control plots; (F) = flooded plots. Letters denote significant groupings. Species richness did not vary significantly across the three years or after the flooding treatment apart from a narrowed range in flooded plots in 2013. Primary production increased significantly a year after the flooding treatment (p<0.001) and varied significantly from year to year in ambient conditions (p<0.001).

2.4.2 Richness-biomass relationship

There was no overall relationship between plant species richness and plant biomass when pooled across years (GLMM: $F_{4,5}$ = 0.436, T = -0.660, P = 0.521). See Appendix 1.2 for percentage of the total variance attributed to random factors. The relationship between species richness and plant biomass was also non-significant in 2011 (GLMM: $F_{3,4}$ = 0.3042, T = -0.551, P = 0.649) and 2012 (GLMM: $F_{3,4}$ = 1.4805, T = -1.217, P = 0.246). Plant species richness was positively correlated with plant biomass in 2013 (GLMM: $F_{3,4}$ = 4.2439, T = 2.060, P<0.05). Within and across years there was no general relationship between species richness and aboveground production in the natural grassland communities tested (Figure 2.7).

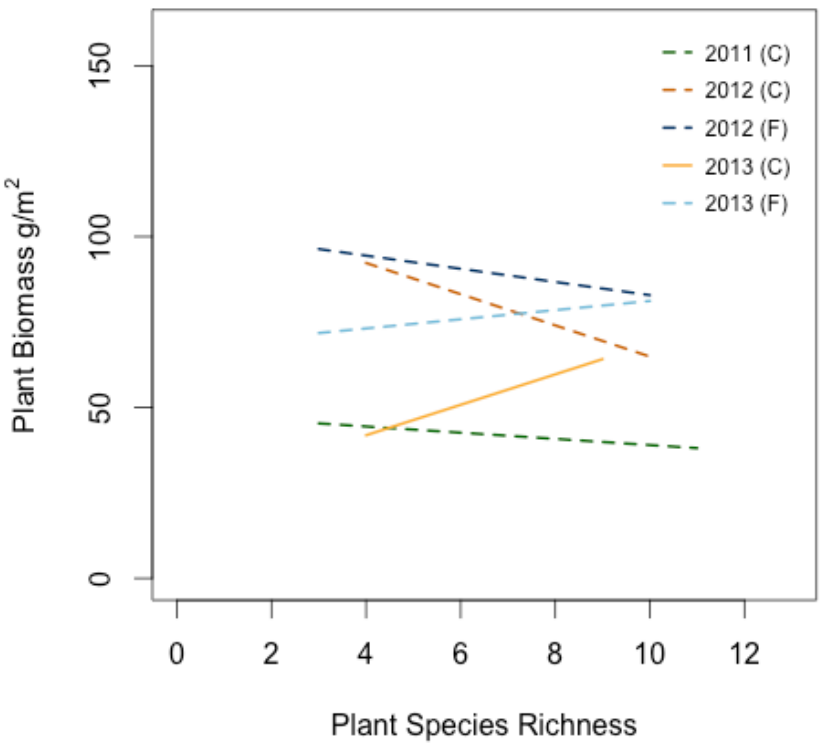


Figure 2.7 Relationship between species richness and primary production in the natural grassland communities at Silwood Park. (C) = control plots, (F) = flooded plots. Dashed lines indicate non-significant regression lines, and solid lines denote significant regression lines. Flooded plots were subjected to a 10-day flood in 2012. The only significant richness-biomass relationship was identified in control plots in 2013 (p<0.05).

2.4.3 Stability in the species richness–biomass relationship

Comparison of the slopes of the relationship between plant biomass and species richness illustrates the stability of the relationship under ambient conditions and in response to a weather extreme treatment (Figure 2.7).

The slope of the relationship between richness and biomass was not significantly different when comparing control plots in 2011 with control plots in 2012 nor comparing control plots in 2012 with control plots in 2013. Constancy in biomass varied independently of plant species richness. The slope of the richness-biomass relationship in control plots in 2012 was not significantly different to the slope in flooded plots in 2012 (Table 2.2). Resistance in biomass production varied independently of species richness. There was no significant difference between the richness-biomass relationships in control plots compared with flooded plots in 2013. Recovery in biomass production following a perturbation was independent of plant species richness. Site accounted for ~40% of the variance attributed to random factors in each nested ANCOVAs.

Table 2.2 Nested ANCOVA analysis of the plant species richness and aboveground plant biomass relationships

Relationship slope comparison	F value	T value	P value
2011 Control vs. 2012 Control	0.7543	0.868	0.380
2012 Control vs. 2013 Control	2.1873	1.479	0.133
2012 Control vs. 2012 Flooded	0.9796	0.990	0.318
2013 Control vs. 2013 Flooded	1.3354	-1.156	0.230

2.4.4 Plant Community Compositional Change

The largest amount of community compositional change was seen in control plots from 2011 to 2012 (mean -1.019 ± 0.654 s.d.) (Figure 2.8). Amount of change was lower in control plots from 2012 to 2013 (mean -0.660 ± 0.349 s.d.) and lowest across two years in control plots (2011 to 2013) (mean -0.543 ± 0.377 s.d.). Compositional change was not significantly different between 2011-2012 and 2012-2013 (nested ANOVA: $F_{3,4}$ = 2.633, T = 1.623, P = 0.105). Amount of compositional change in 2011-2013 control plots varied significantly with that of the 2011-2013 control plots (nested ANOVA: $F_{3,4}$ =

14.094, T = 3.754, P<0.001); and 2012-2013 control plots (nested ANOVA: $F_{3,4}$ = 9.318, T = 3.053, P<0.01). Degree of compositional change over two years was significantly lower than in-between individual years.

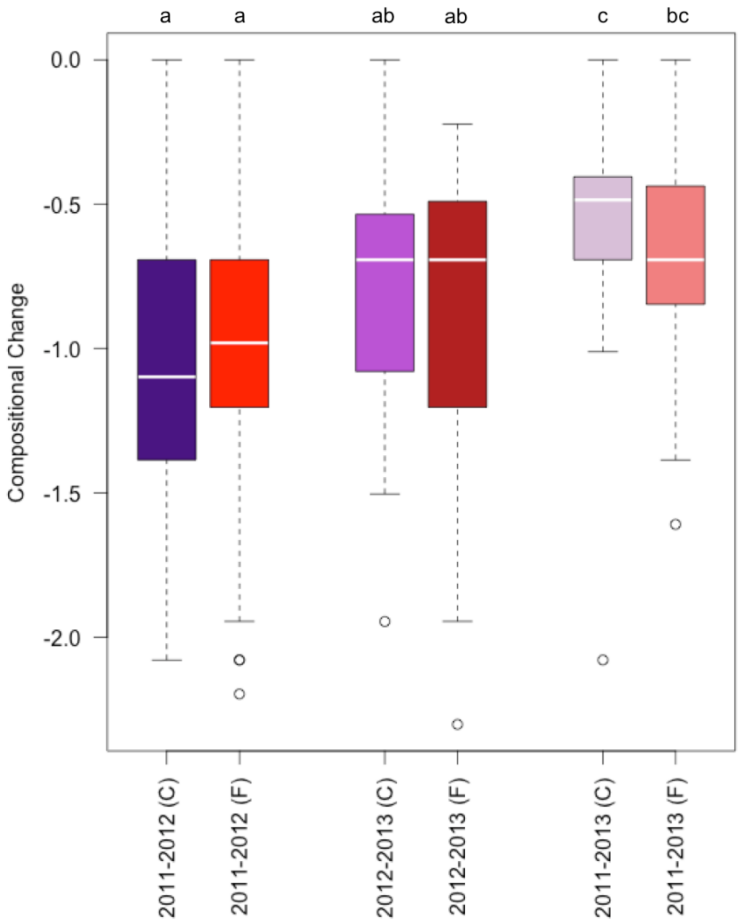


Figure 2.8 Changes in plant species composition across years and in response to a ten-day experimental rain event. Letters denote significant groupings. 2011-2012 (C) = Constancy in control plots between 2011 & 2012; 2011-2012 (F) = Recovery; 2012-2013 (F) = Resistance; 2011-2013 (C) = Long-term Constancy; 2011-2013 (F) = Long-term Trend. Composition in control plots varied significantly less between 2012-2013 compared with 2011-12. Community composition in flooded plots did not vary more or less than composition within control plots. Compositional change across two years (2011-2013) was significantly lower than between only one year; despite annual changes in plant assemblages communities return to similar compositions in the longer term.

The amount of compositional change did not vary significantly between 2011-2012 control plots and 2011-2012 flooded plots (nested ANOVA: $F_{3,4}$ = 0.781, T = -0.8850, P = 0.374). Compositional change did not vary significantly between control and flooded plots from 2012 to 2013 (nested ANOVA: $F_{3,4}$ = 0.784, T = -0.885, P = 0.374).

Compositional change did not significantly vary between control plots from 2011 to 2013 and flooded plots from 2011 to 2013 (nested ANOVA: $F_{3,4} = 2.066$, T = -1.437, P = 0.151). In all tests site accounted for ~41% of the total variance attributed to random factors.

2.4.5 Stability in the species richness–composition relationship

Despite a negative trend there was no relationship between compositional change and species richness in control plots between 2011-2012 or 2012-2013 (Figure 2.9). Equally there was no significant correlation between compositional change and species richness in flooded plots between 2011-2012 or between 2012-2013 (Table 2.3). Compositional change varied independently of initial plant species richness in control and flooded plots across individual years (2011-2012 or 2012-2013).

Table 2.3 Generalised linear mixed model analysis comparing species richness with plant community compositional change

Compositional Change measure	Plots used	F value	T value	P value
Constancy	2011 and 2012 control plots	1.673	-1.293	0.189
Constancy	2012 and 2013 control plots	1.554	-1.247	0.204
Recovery	2011 control and 2012 flooded plots	1.821	-1.349	0.163
Resistance	2012 and 2013 flooded plots	1.085	1.041	0.332
Long-term constancy	2011 and 2013 control plots	6.054	-2.461	<0.05*
Long-term trend	2011 control and 2013 flooded plots	5.1296	-2.064	0.06

There was a significant relationship between compositional change across two years (2011-2013) and initial plant species richness in control plots (T = -2.461, P<0.05). This test result was verified through a permutation test (p=0.0129). When measured over two years, community compositional change was greater in species-plots (Figure 2.9). Compositional change across two years in flooded plots was not correlated with species richness.

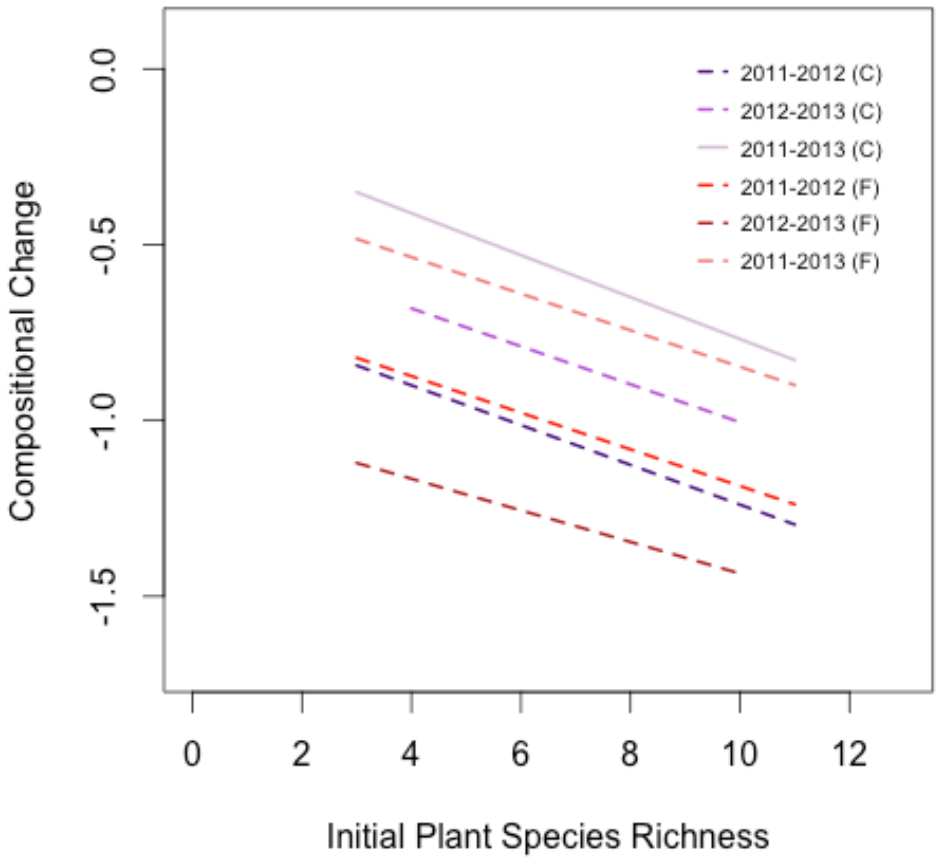


Figure 2.9 Relationships between initial plant species richness and compositional change under ambient climate variation across years and in response to a ten-day experimental rain event. 2011-2012 (C) = Constancy in control plots between 2011 & 2012; 2011-2012 (F) = Recovery from the effects of a flood in 2012; 2012-2013 (F) = Resistance; 2011-2013 (C) = Long-term Constancy; 2011-2013 (F) = Long-term Trend. Dashed lines indicate non-significant relationships and solid lines indicate significant correlations (P<0.05). Long-term constancy varies with initial species richness: community composition is less stable in species-rich plots than depauperate ones (P<0.05).

Comparison of the slopes of the relationship between plant species richness and compositional change illustrates the stability of the relationship under ambient conditions and in response to weather extreme. The relationship between species richness and compositional change in control plots from 2011-2012 is not significantly different to the relationship found in control plots from 2012-2013 (Table 2.4). The relationship slope of the species richness-compositional change relationship in control plots from 2012 to 2013 is not significantly different than the flooded plots from 2012 to 2013. The slope of the species richness-compositional change relationship in control

plots 2011 to 2012 is not significant to the slope in flooded plots from 2011 to 2012. Following a simulated weather extreme compositional change varied independently of initial plant species richness. Across two years the slope of the species richness-compositional change relationship in control plots was not significantly different to the slope in the flooded plots. Over two years the amount of community compositional change was independent of plant species richness.

Table 2.4 Nested ANCOVA analysis of the plant species richness and plant community compositional change relationships

Relationships comparisons	F value	T value	P value
2011-2012 Control vs. 2012-2013 Control	0.007	-0.082	0.933
2011-2012 Control vs. 2011-2012 Flooded	0.013	0.117	0.904
2012-2013 Control vs. 2012-2013 Flooded	1.598	1.1264	0.198
2011-2013 Control vs. 2011-2013 Flooded	0.056	0.237	0.799

2.4.6 Results summary

Plant species richness remained constant throughout the experiment under both ambient and extreme weather conditions. Aboveground plant biomass varied from year to year in control conditions and increased one year following the simulated weather extreme. There was no significant difference between biomass-species richness slopes, indicating stability in biomass varied independently of plant species richness.

The amount of compositional change within communities varied annually in ambient conditions. The flooding treatment did not impact the degree of compositional change in plant communities. Depauperate communities undergo similar compositional change (i.e. are as constant, resist and recover) to species rich communities in a natural grassland system under both ambient and extreme conditions.

2.5 Discussion

2.5.1 Annual variation in plant richness, community composition and production

Richness did not vary from year to year. Community composition was fairly constant from year to year at Silwood Park and communities underwent less compositional change in the long-term compared with annual changes. This would indicate that whilst there is a degree of plant substitutions each year, overall plants are still present in the system. Even in hardy perennial systems such as the grasslands at Silwood Park, natural communities undergo a degree of annual change. Communities in experimentally manipulated biodiversity experiments must be maintained through weeding to ensure constancy, in fact when weeding was ceased in some Jena plots they quickly transformed into completely different communities, although the original species were still present (Roscher *et al.* 2012). If the community composition is naturally unstable in these experiments to what extent is the imposed community maintenance affecting our understanding of the actual role of richness in plant communities?

Plant biomass significantly increased under ambient conditions in 2012 compared with 2011, this may be due to the increased precipitation in 2012. 2011 was a dry year and biomass harvests were very low as grasses suffered from severe water limitation. The following wet growing season in 2012 positively impacted biomass production, increased annual precipitation has been demonstrated to impact plant density positively and I would posit this is the case here also (e.g. Knapp & Smith, 2001 St. Clair *et al.* 2009). The fact that richness did not vary and production did vary significantly between years was the first indication there may be no causal link between them in the natural grassland communities at Silwood Park.

2.5.2. Richness-biomass relationship

The natural grassland communities at Silwood exhibited no general relationship between primary production and plant species richness over the course of three years. In 2011 and 2012 we saw negative trends but they were not significant, however in 2013 as species richness increased so did production. The positive linear relationship espoused by previous work may only be apparent in particular circumstances in natural communities at Silwood Park.

Relationships identified in previous experiments using natural communities were weakly negative, where present at all (Grace *et al.* 2007, Bezemer and van der Putten 2007). Very few positive linear correlations between production and species richness were identified in the NutNet study by Adler et al (2011), in fact the same number of positive linear correlations was found as negative linear ones (approximate five sites each) (Adler *et al.* 2011). Two NutNet sites are situated at Silwood Park, one site exhibits a positive biodiversity-ecosystem function relationship and the other site shows evidence of a negative linear correlation (M.Crawley, *pers. comm.*). By measuring across multiple years the results seem to mirror the variety of relationships found in studies in natural communities. Not only is there temporal variation in production in natural communities at Silwood Park, it is apparent there is temporal variation in the strength of the biodiversity-ecosystem function relationship.

If there is no such causal relationship between species richness and ecosystem functioning in natural systems then the two mechanisms (niche complementarity and sampling effect) suggested to explain this relationship are redundant (Huston 1979, Loreau & Hector 2001). It is not apparent in this study that species rich communities utilise community resources more efficiently and therefore produce more than species poor communities as predicted under niche complementarity. Nor is it shown here that the addition of species increases the chances of containing more productive species (e.g. sampling effect). Neither the portfolio effect (Doak *et al.* 1998) nor the idea of functional redundancy (Walker 1992) seem to explain the lack of relationship unless the critical number of species needed in a community for stability and functionality is greater than that used in this experiment. Our results show species-poor plots are just as likely to contain highly functional and stable plant species as species-rich communities.

Unfortunately this study cannot identity the causes of production and compositional stability but has shown that the previously accepted clear positive correlations between species richness and production and stability are not universally present in the complex natural systems at Silwood Park. The relationship between production and species richness is temporally dependent, potentially indicating more abiotic variables are involved. Another limitation is the restricted species richness range with fewer replicates at the very top and bottom. Despite this the formerly described strong positive linear correlation (e.g. at Cedar Creek, Biodepth, Jena) was only present at

lower species richness counts and petered off as species richness increased so even with a limited range if there was such a relationship we should nonetheless capture it.

2.5.3. Stability in the species richness – biomass and richness – composition relationships

An extreme flooding event had little immediate impact on production but caused as increased yield one year later. April 2012 was one of the wettest Aprils on record (Met Office Records 2012), in fact just prior to the treatment commencing there were two weeks of heavy rainfall. Unfortunately, this may have diminished the immediate impact of the flood. The increased yield observed in flooded plots in 2013 was not dependent on the number of species within a community. Despite the severity of the flood, it had very little impact on changes in species composition. Similarly to production, compositional stability in all its forms is not universally governed by species richness.

Should we really expect such straightforward biodiversity-ecosystem function or -stability relationships in natural grasslands when we define diversity as the number of species in a community? Whilst species richness is a simple, easy to calculate measure (making it attractive for ecologists to use as a predictor), in its simplicity it is omitting critical community characteristics. It is therefore unsurprising that our results show species richness does not correlate with either production or stability, it quite simply contains no real ecological information about the communities. Species identity and representation (i.e. dominance or evenness) are completely omitted from the measure, aspects that have previously been shown to be important at governing production and stability (Wilsey & Potvin 2000, Wittebolle *et al.* 2009). In particular it tells us nothing about traits of the species present, an important aspect when assessing stability. If more water tolerant species are present then the impacts of a flood would be diminished, but in this case higher species numbers did not increase the chances of more water tolerant species. Whilst the measures used for compositional change are informative they do not afford us information on the identity of the evicted or newly installed species. If replacement species are functionally similar the composition may change but the functional output will not.

Overall naturally assembled communities were not compositional constant and this constancy was independent of species richness in the short-term. Whilst the flooding treatment did not significantly affect compositional stability it does appear to cause an

overall increase in stability both in the short and longer terms (Figure 2.8). All flooded plots exhibited some degree of compositional change in 2013 (in control plots there were many instances of no change) indicating extreme events could impact long-term stability. Depauperate communities undergo as much compositional change (i.e. are as stable) as species rich communities in a natural grassland system under both ambient and extreme conditions.

2.6 Conclusion

This is one of many first steps to compare the evidence of the biodiversity-ecosystem function relationship obtained in manipulated biodiversity experiments with those found in a natural system. Natural systems are complex and we need to take note that the simplistic mechanisms highlighted in heavily controlled experiments may not be present to the same degree (if at all) in naturally assembled communities. Species richness may not be a good predictor for function or stability in natural grassland communities. For this reason more complex controlled studies are needed in order to tease apart the alternative underlying mechanisms that direct production and stability in natural communities.

Chapter 3

Aboveground-belowground linkages in diversity-function relationships: the importance of plant community attributes for production and stability in soil invertebrate communities

3.1 Abstract

The aboveground-belowground relationship in natural communities is a complex subject. In particular soil mesofauna are an historically understudied group. Soil mesofauna consume, pulverize, decompose and distribute much of the floral and faunal litter enabling the release of the nutrients into the soil environment (Seastedt 1984, Ingham *et al.* 1985, Moore *et al.* 1988, Bal 1992, Wardle *et al.* 1998). Current evidence points toward a positive relationship between primary production or plant species richness, and soil biota abundance or biomass (Wimp *et al.* 2010, Scherber *et al.* 2010). Soil mesofauna exhibit few dispersal behaviours or adaptations and mites are only able to move through pre-existing pores in the soil (Norton 1985, Lindo 2004), which may increase their susceptibility to perturbations and severe disturbances (Renker *et al.* 2005). The impact of an extreme weather event on multiple aspects of the soil mesofauna community was looked at, and additionally whether it was dependent upon plant species richness or primary production in natural communities across Silwood Park.

Secondary production (total soil mesofaunal biomass) and mite biomass are negatively correlated with plant species richness in ambient conditions. The simulated flooding event immediately negative impacted total soil mesofaunal biomass and mite biomass but positively impacted collembola biomass one year after. Constancy in secondary production and mite biomass was dependent upon primary production (aboveground plant biomass). Resistance in secondary production was dependent upon plant species richness. Constancy and recovery in collembola biomass was dependent upon plant species richness. Further studies are needed to see how widespread these relationships are or if they are context dependent (e.g. temporally or spatially specific).

3.2 Introduction

Even with actual documentation of species losses rare, the weight of evidence indicates that biodiversity is declining in many regions of the world (Butchart *et al.* 2010), and that these declines are likely to accelerate into the future (Butchart *et al.* 2004). If we are to prevent these losses and mitigate their consequences for human societies, it is imperative that we understand how biodiversity affects ecosystem functions and services. Grasslands can play a valuable role in this research, allowing scientists to test patterns and mechanisms over experimentally tractable temporal and spatial scales. Researchers have used grassland experiments to investigate the role of floral diversity in both stability and functioning of grassland communities, and have found that higher diversity can lead to greater levels of biomass production (Tilman *et al.* 1996) and soil carbon storage (Diaz *et al.* 2009), more efficient cycling of nutrients (Hooper & Vitousek 1998), and greater compositional and functional stability (Tilman post-fire or drought: Tilman *et al.* 2001). In other cases, research has uncovered no effect of grassland plant diversity on aspects of function or stability, and indeed, this current study (Chapter 2) found no significant relationship between plant diversity and primary production or stability in natural grasslands. There are obviously dependencies of timing, location, and context in diversity-function and diversity-stability relationships, but even in well-studied systems such as Silwood Park, declaring diversity-function or diversity-stability relationships absent because they are not evident among plants (or declaring them important because they do) may be premature.

There are many components of the diversity, functionality and stability of grassland communities that are not restricted to the plants themselves, and limiting the scope of our investigations to plants may therefore limit the view into diversity-function and diversity-stability relationships that operate in these systems. The emphasis in grassland experiments into diversity-function and diversity-stability relationships generally, and in the present study, has been on plant-based variables. An expanded focus that considers more of the community could offer improved and potentially more generalizable understanding. Primary production has been commonly used as an ecosystem function measure (e.g. Tilman *et al.* 1996, Hector *et al.* 1999, etc). Production measures are rate dependent therefore are difficult to accurately quantify thus the need for suitable proxies. Secondary production is the rate of biomass generation in heterotrophs (Allaby 2006). In the same way, peak aboveground plant biomass is used

as a proxy for primary production potentially invertebrate biomass may be a surrogate measure for secondary production. An expanded focus that considers more of the community such as secondary production could offer improved and potentially more generalizable understanding.

Heterotrophs often make up a substantial portion of grassland diversity (e.g. Suttle *et al.* 2007), and contribute to essential ecosystem functions such as decomposition and nutrient cycling (Elliot *et al.* 1988, De Deyn *et al.* 2003, Wardle *et al.* 2004, Bardgett *et al.* 2005, Gobat *et al.* 2010). Even measurements of ecosystem function that are entirely plant based, such as primary production, depend fundamentally on the decomposition and nutrient cycling activities of animals. Consumers are seldom included in experimental research into diversity-function and diversity-stability relationships in part because the spatial scales required for unbiased investigation would not be experimentally tractable. The mobility of animals, as opposed to plants, means either that their life histories are constrained (if experimental infrastructure is used to contain experimental populations for study) or that responses include aggregation and avoidance that cannot be distinguished accurately from the demographic responses under focus (if experimental plots are open). In either case, substantial bias is introduced for which it is difficult to control. The result is an understanding of diversity-function and diversity-stability relationships that is limited to a single trophic level in what are actually mutli-trophic level communities.

We can broaden the view and at the same time minimize sources of artificiality and bias by including in grassland research guilds of animals that are characterized by very low mobility. For litter and shallow soil invertebrates, such as collembola and mites, which make up functionally important components of most grassland food webs themselves, life histories may allow for realistic responses to environmental manipulations at a scale that is experimentally tractable. Subterranean biota consume and decompose much of the flora and fauna from previous and current seasons therefore releasing nutrients into the soil environment (Ingham *et al.* 1985, Wardle *et al.* 1998). Due to their location and relatively small size (particularly meso-fauna) soil organisms remain relatively arcane.

Grassland soils contain rich animal communities (Bardgett and Cook, 1998). The two most abundant mesofauna (invertebrates between 0.2 and 3mm in size) in shallow soils of most grassland communities are collembola and mites (Moore *et al.* 1988, Lavelle 1997). Belowground mites are a diverse and cosmopolitan group found in the majority

of soil types worldwide (Maraun *et al.* 2007). Contentious classification and identification of soil mites makes them a particularly difficult group to study (Evans 1992). The sheer complexity of behaviours can be seen in the wide range of feeding habits; they can be mycophagous, phytophagous, saprophagous, predatory and/or parasitic. For example, in a long-term study oribatid mites were found occupying up to four trophic levels (Schneider *et al.* 2004). They play a pivotal role in pulverising and distributing organic matter (Seastedt 1984, Moore *et al.* 1988, Bal 1992). In contrast to their diverse range of feeding habits, they exhibit few dispersal behaviours or adaptations (Lindo 2004) and are only able to move through pre-existing pores in the soil (Norton 1985). Limited mobility may make them more susceptible to perturbations and severe disturbances (Renker *et al.* 2005).

Collembola, or springtails as they are more commonly known, are the other major mesofaunal component of shallow soils (Hopkins 1997). In sheer abundances they are considered one of the most plentiful mesofaunal groups with estimates of over 100,000 per cubic meter of soil (Hopkins 1997), and probably rival mites in global abundance. Similarly to mites, soil collembola have relatively low mobility and are sensitive to specific physical and chemical features of the soil environment (Xu *et al.* 2012). Most families exhibit some degree of omnivory, but feeding habits are predominantly mycophagous, and population abundances have been found to scale with microbial and fungal activity (Siepel 1996, Siddiky *et al.* 2012). Contrary to mites, springtails can interact with the soil matrix in their movements in ways that affect soil porosity and aeration (Kampchler & Bruckler 2009, Menta *et al.* 2011). Additionally, collembola have been useful as bioindicators for soil properties such as nutrient distribution and soil health (Barbercheck *et al.* 2009, Blasi *et al.* 2012). For these reasons collembola play a pivotal role in maintaining soil fertility and dissemination of soil organisms and nutrients.

Above- and belowground communities are powerful mutual drivers, and the functions performed by any one community can have important feedbacks for the other (Wardle *et al.* 2004). Collembola contribute to the mechanical breakdown of plant litter and therefore play an important role in decomposition and nutrient cycling. Experimental work has shown a decrease in leaf composition rates in microcosms when collembola are excluded (Tueben 1991, Tueben and Verhoef 1992) and in field mesocosms when collembola numbers are reduced by heavy predation pressure (Lensing and Wise 2007). Aboveground effects on belowground communities are very well documented, with

extensive research investigating how plant diversity and abundance can influence the diversity and abundance of soil fauna (Brown & Southwood 1983, Haddad *et al.* 2001, Wardle & Van Der Putten 2002, Gastine *et al.* 2003, Salamon *et al.* 2004, Wardle 2005, Scherber *et al.* 2010, Eisenhauer *et al.* 2013), with some studies showing strong effects and some showing weak to negligible effects (Figure 1.4 in Chapter 1, & Figure 3.1). Wimp *et al.* (2010) found that primary production determined the community structure of arthropods in intertidal salt marshes, while Stein (2010) showed that herbivore abundance and richness affected plant species richness and composition in montane grasslands. Whilst there is extensive evidence soil fauna contribute to ecosystem functioning when theoretical losses were simulated communities persisted without significant loss of plant production, indicating compensatory mechanisms (Hunt & Wall 2008). The link between stability of individual invertebrate species or functional groups and maintenance of function may not be straightforward.

Stability, likewise, is not a property of just a single trophic level, and is likely not determined by interactions and processes restricted to a single trophic level, making it important to consider stability across multiple levels (Naeem *et al.* 2000). Proulx and colleagues (2010) demonstrated temporal stability of aboveground invertebrates increased with plant species richness. Given the plethora of definitions of stability, it is imperative we clarify exactly what that stability is in reference to (Grimm & Wissel 1997). Constancy and persistence relate to stability in ambient or slow changing conditions but to focus on stability as 'resistance' or 'recovery', some external perturbation is needed.

Climate change is increasingly the focus of ecological studies, mainly in terms of long-term trends such as increasing temperature or slight changes in rainfall and how these will affect biodiversity and function (Chapin *et al.* 2000, Thomas *et al.* 2004, Butchart *et al.* 2010, Harley 2011). Extreme climatic events, pulse perturbations such as increased rainfall events or droughts, are, however, also predicted to increase in frequency and magnitude (Easterling *et al.* 2000, IPCC 2013), and by several measures these increases are already apparent (Hansen *et al.* 2012). What is currently lacking is strong emphasis on the ecological consequences of these disturbances and experiments testing them (Jentsch *et al.* 2007, Jentsch & Beierkuhnlein 2008).

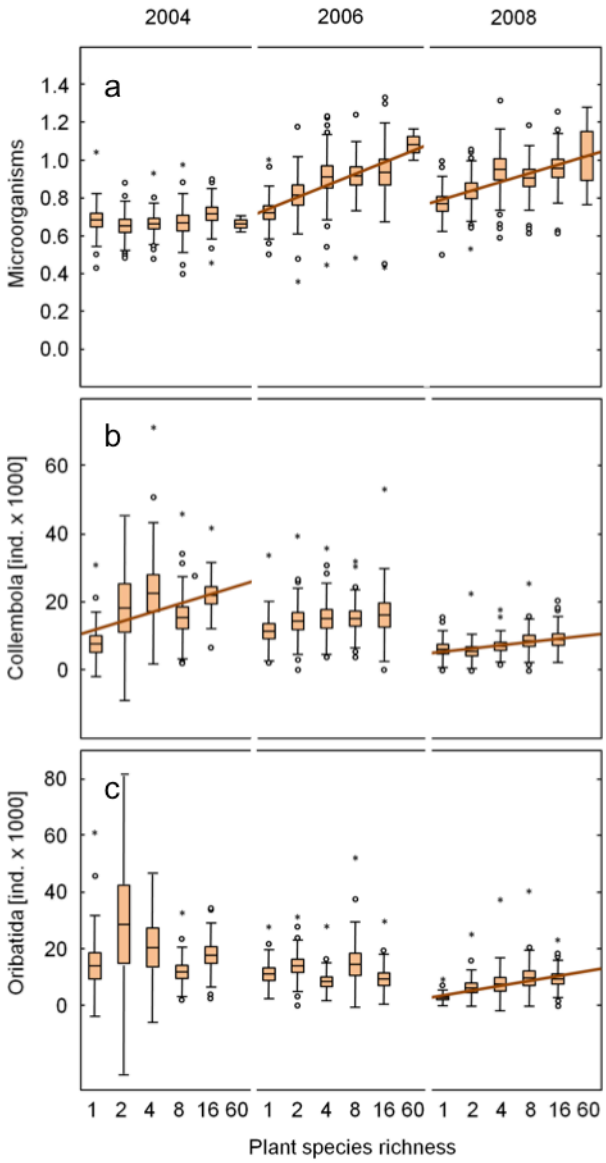


Figure 3.1 The effect of plant species richness on (a) microorganisms, (b) collembola and (c) oribatid density in the grassland communities at Jena in 2004, 2006 and 2008 (from Eisenhauer et al. 2011). Regression lines indicate significant effects ($p<0.05$).

Effects of long-term climate change on soil biota are not well understood, yet even less is known about the impacts of short-term weather extremes (Bokhurst *et al.* 2012, Eisenhauer *et al.* 2012), which are expected to be a major feature of global climate change. Temperature and moisture are important influences on soil fauna (Bedano *et al.* 2005, Minor & Cianciolo 2006, Lindo & Visser 2004), so we can expect potentially strong effects of weather extremes. Warming events in sub-Arctic dwarf shrub heathland and peatland caused a decrease in Acari and Collembola populations (Bokhurst *et al.* 2012, Krab *et al.* 2013). In tropical climates, Badejo (1990) found that mites abundances were positively correlated with soil moisture, but theorized that the moisture effect was

indirect, brokered by changes in temperature, as wetter soils were colder and colder temperatures favor higher levels of mite activity and abundance. Moisture can have direct effects as well: both collembola and mite assemblages were affected by experimentally induced summer droughts, the recovery rates taxon specific with collembola taking longer to recover (Siepal 1996, Lindberg & Bengtsson 2005, Lindberg & Bengtsson 2006). Furthermore plants may influence mesofauna resistance to perturbations (Taylor & Walters 2005). In an extended drought the extent the oribatid community structure was significantly altered was dependent on plant litter type. If an increase in plant species richness results in more diverse litter and resources, we can posit plant diversity may influence soil faunal stability as well as abundances and richness.

Much of what we currently know is based on empirical studies using artificially created and maintained communities (Tilman *et al.* 1996, Hector *et al.* 1999, Eisenhauer *et al.* 2011). The majority of recent papers on the importance of plant diversity for soil biota are solely from a single experiment that utilises designed and weeded plant communities (e.g. Eisenhauer *et al.* 2013). Whilst this is an essential first step in understanding the relationship between diversity, function, and stability across trophic levels (e.g. there are fewer confounding factors) it is important to relate these findings to real communities and evaluate how the relevant mechanisms play out against the very real, very many confounding factors that exist in any real ecosystem. How much of our understanding of the role of plant species diversity in influencing soil invertebrate communities may be biased by the carefully controlled and heavily manipulated structure of research? Interestingly Roscher *et al.* (2013) noted once weeding of the artificial communities was halted colonization destabilized the resident species composition, and populations of resident species were less temporally stable. The artificially created communities did not persist without the controlled weeding.

Despite multiple studies on the relationship between plants and soil biota diversity and functioning, the correlation and potential impacts upon ecosystem functioning are still uncertain (Hooper 2000, Wardle 2006, Milcu *et al.* 2008, Eisenhauer *et al.* 2010). The benefit of a more comprehensive focus is that by delineating the relationships between plant and consumer biomass (e.g. plant diversity or primary production and secondary production) we may gain better predictive power over the consequences of declines in plant diversity for higher trophic levels and vice versa. I aim to provide an overview of the effect of plant community diversity and primary productivity on soil biota and a

measure of secondary production in grassland communities. In particular I looked at the impact of an extreme weather event on multiple aspects of the soil mesofauna community, and whether it is dependent upon plant species richness or primary production. Soil fauna such as collembola and mites are dependent on the amount and variety of dead vegetation entering the soil environment (Sanzer *et al.* 2011). It is therefore reasonable to assume that plant diversity and production would impact the abundance, biomass, diversity and stability of soil mesofauna therefore I would expect to see greater biomass and stability of soil mesofauna in plants species rich plots.

3.3 Materials and methods

3.3.1 Experiment site

The DExtER (Disturbance Extremes and Ecological Responses) experiment was established at Silwood Park, Imperial College London in South-East England (51°24'23.16"N, 0°38'55.33"W) in 2011. It consisted of 200 plots spread across eight sites. Richness of vascular plant species in these grassland plots ranges from approximately five species in low-diversity habitats and years, to twenty in high-diversity habitats or years. Belowground, twelve collembolan families were identified across the sites. These were Tomoceridae, Sminthurididae, Sminthuridae, Poduridae, Onychiuridae, Neelidae, Neanuridae, Katiannidae, Isotomidae, Hypogastruridae, Entomobryidae and Dicyrtomidae. Most plots contained Isotomidae and Emtomobryidae and one to two further species therefore collembolan family diversity varied from three to five families per plot. Due to the difficulty of mite identification, mites were identified to six distinct morphotypes. Most plots contained four or five of the mite morphotypes. Additionally ant adults and larvae, dipteran larvae and arachnid larvae are found belowground in each site.

3.3.2 Sampling

Plant Production

Aboveground plant biomass was collected from the central 0.25m^2 square in 35 plots in Year One (2011) to provide baseline production values. The remaining 140 plots were split into two groups: control group of 70 plots experiencing ambient conditions and the manipulated group of 70 plots subjected to an extreme weather event in Year Two

(2012). Due to the destructive nature of sampling biomass the 70 plots in each watering treatment were further divided between those where biomass was collected in Year 2 and those in Year Three. By splitting the groups we are able to capture both initial resistance to the effects of the water manipulation treatment and the long-term recovery. Data acquisition was carried out in the central 0.25m^2 to circumvent any edge effects. The collected biomass was dried at 80^{0}C for 72hrs and then weighed.

Belowground invertebrate sampling

Abundances of mites and collembola were sampled from 6cm-diameter soil cores to a depth of 10cm (283cm^3) in all plots in July 2011, 2012 and 2013. A single soil core was collected with a steel corer for each plot. Mesofauna were extracted from soil cores over 72 hours immediately after collection using a Tullgren funnel apparatus modified to extract all samples simultaneously (Figure 3.3). After extraction, all collected invertebrates were transferred to 95% alcohol solution for storage and later processing. The samples predominantly consisted of collembola and mites. Collembola were identified to family and counted. Mites were identified to 6 morpho-types and counted. Additional seasonal sampling of the ten remaining plots in each site from years two to three was carried out at one month post EWE (15th August), three months (15th October), six months (15th January) nine months (15th April) and the remaining annual collection on 15th July. N.B. As the samples were so extensive identification is still ongoing in collaboration with Professor Simon Leather at Harper Adams University.



Figure 3.2 Representative schematic of plot-wise sampling. Plots measure 1m². Plant richness and biomass are sampled in the central 0.25m² subplot. Soil invertebrates are sampled with 6cm-diameter soil cores to a depth of 10cm. Numbers in parentheses indicate sampling dates.

Soil Mesofaunal Biomass

Invertebrate biomass was used as a proxy for secondary production (mg/283cm³). Invertebrate biomass was measured as the estimated total biomass of invertebrates in a sample. 30 representatives of each collembola family were briefly air-dried and then weighed to attain a mean mass for each family (Appendix 2.1). This process was repeated for 30 representatives of each mite morphotype (Appendix 2.2). Total sample biomass was calculated by multiplying the mean weight for each family or morphotype by the number of individuals in that family or morphotype, and summing across each.



Figure 3.3 Extraction of soil-dwelling invertebrates from soil cores collected from experimental plots. A modified Soil Tullgren-Berlese Funnel was constructed in the lab to enable simultaneous processing of all soil cores. Soil invertebrates travel down through the soil core to escape the heat and light and drop into alcohol below. Care was taken in the design phase to ensure temperature and light differences were nominal between the inner and outer rows.

3.3.3 The extreme weather treatment

The simulated weather extreme was designed to add a 10-day continuous rain event on top of ambient variation, delivered by hose nozzle suspended approximately 1m above each plot and calibrated to emit a diffuse spray of water as uniformly as possible across the surface area of each plot. Water addition commenced on July 5th 2012 and continued for 10 days in total. Approximately 2017.13 liters of water (± 346.41) were deposited on each of the 70 designated plots per day over the 10 days. Soil moisture remained above ambient conditions for the following four weeks therefore simulating flooded conditions.

3.3.4 Statistical analyses

To control for site effects (therefore avoiding spatial pseudo-replication) generalized linear mixed-effects models were employed with site as a random factor. Mixed models were used to test for correlations between plant species richness or primary function and secondary function and belowground faunal constancy in ambient conditions. Nested ANOVA models were used to test for the effects of inter-annual changes and of the extreme weather manipulation on secondary production, biomass of collembola and mites both immediately after the manipulation and one year hence. Nested ANCOVA models were utilized to test for the effect of the extreme weather manipulation on the relationships between species richness or primary production and secondary production and biomass of collembola and mites. All mixed effects models were conducted in R (R Develoment Team 2012) with the package 'lme4' (Bates & Sarkar 2007). As species richness is count data a Poisson error structure was used. The residuals versus fitted plots and normal qq-plots of the linear models to ensure model assumptions were not violated. Where necessary generalized linear mixed models were used with a Poisson error structure. Likelihood-ratio comparison tests of the full models with both random and fixed effects with those with just random effects to calculate p-values for my response variables.

3.4 Results

3.4.1 Background relationships between soil invertebrates and overlying plant community

Plant species richness

Soil mesofaunal biomass was negatively correlated with plant species richness when the data were combined across all three years (overall) and in 2013 (Table 3.1). There was no relationship between plant species richness and total mesofaunal biomass in either 2011 or in 2012. Similarly soil mite biomass was negatively correlated with plant species richness both overall and in 2013, but no correlation in 2011 or 2012. There was a negative correlation between collembola biomass and plant species richness in 2011 but not in the other years or overall. See Appendix 2.3 for the percentages of the total variances attributed to random factors in the GLMMs.

Table 3.1 Generalised linear mixed model analysis of the relationship between plant species richness and soil invertebrate biomass. Overall refers to combining across all years (2011-2013).

Invertebrate Biomass	Year	T value	P value	Slope
Total Soil Mesofaunal Biomass (mg/283cm^3)	2011	0.699	0.458	n.s.
	2012	0.417	0.709	n.s.
	2013	2.215	<0.05 *	negative
	Overall	4.400	<0.001 ***	negative
Mite Biomass (µg/283cm^3)	2011	0.378	0.675	n.s.
	2012	0.477	0.667	n.s.
	2013	2.564	<0.05*	negative
	Overall	4.345	<0.001 ***	negative
Collembola Biomass (µg/283cm^3)	2011	3.012	<0.01**	negative
	2012	0.527	0.530	n.s.
	2013	1.845	0.071	n.s.
	Overall	1.613	0.106	n.s.

Plant Production

There was no relationship between total soil mesofaunal biomass and plant species richness either over all three years or during individual years (Table 3.2). Neither soil mite biomass nor collembola biomass correlated with plant biomass at all.

Table 3.2 Linear mixed model analysis of the relationship between plant biomass and soil invertebrate biomass. Overall refers to combining data across all years (2011-2013).

Invertebrate Biomass	Year	T value	P value	Slope
Secondary Production (mg/283cm³)	2011	1.726	0.081	n.s.
	2012	1.383	0.166	n.s.
	2013	0.161	0.846	n.s.
	Overall	1.811	0.077	n.s.
Mite Biomass (µg/283cm³)	2011	1.486	0.130	n.s.
	2012	1.325	0.189	n.s.
	2013	0.254	0.774	n.s.
	Overall	1.848	0.071	n.s.
Collembola Biomass (µg/283cm³)	2011	1.072	0.361	n.s.
	2012	1.682	0.099	n.s.
	2013	0.476	0.638	n.s.
	Overall	1.387	0.152	n.s.

3.4.2 Variation in soil mesofaunal biomass across years and in response to flooding

N.B. The experiment was conducted against a backdrop of marked inter-annual differences in weather. 2011 was the second driest year on record leading into 2012 where we saw one of the wettest April and June on record compared with one of the driest April in 2011

Total soil mesofaunal biomass varied significantly between control plots in 2011 and 2012 (nested ANOVA: $F_{4,5} = 24.499$, T = -5.654, P<0.001) (Figure 3.4a) but did not vary significantly between control plots in 2012 and in 2013 (nested ANOVA: $F_{4,5} = 1.086$, T = 1.042, P = 0.296). The flood negatively impacted total mesofaunal biomass, a significant decrease in biomass was found in the 2012 flooded plots compared with the 2012 control plots (nested ANOVA $F_{4,5} = 7.512$, T = -2.741, P<0.01). The flood did not impact

total mesofaunal biomass as it was not significantly different in the 2013 flooded plots than in the 2013 control plots (nested ANOVA: $F_{4,5}$ = 0.057, T = 0.238, P = 0.810). Site accounted for 34-59% of the total variance attributed to random factors.

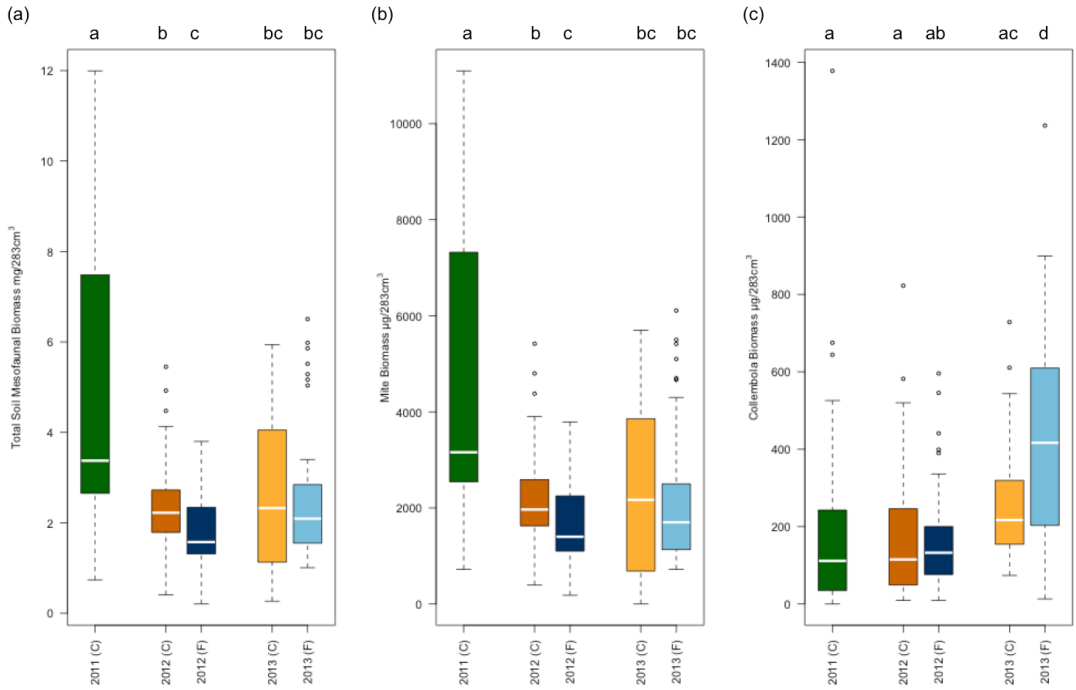


Figure 3.4 Soil invertebrate biomass across years and in response to a ten-day experimental rain event. Data represent interquartile ranges and medians for (a) total soil mesofaunal biomass; (b) mite biomass; and (c) collembola biomass. Letters denote significant groupings. (C) = control plots; (F) = flooded plots. Secondary production (total soil mesofaunal biomass) and mite biomass significantly decreased following the flood (p<0.05). Collembola biomass increased significantly one year after the flooding event (p<0.01).

Mite biomass varied significantly between control plots in 2011 and 2012 (nested ANOVA: $F_{4,5}$ = 27.116, T = -6.645, P<0.001) (Figure 3.4b) but did not vary significantly between control plots in 2012 and in 2013 (nested ANOVA: $F_{4,5}$ = 0.5887, T = 0.767, P = 0.440). The flood negatively impacted mite biomass, a significant decrease was found in the 2012 flooded plots compared with the 2012 control plots (nested ANOVA $F_{4,5}$ = 7.512, T = -2.741, P<0.01). Similarly to total mesofaunal biomass, there was no long-term effect of the flood on mite biomass as the biomass found 2013 flooded plots were not significantly different than in the 2013 control plots (nested ANOVA: $F_{4,5}$ = 0.171, T = -0.413, P = 0.677). Site accounted for 34-58% of the total variance attributed to random factors.

There was no inter-annual difference in soil collembola biomass in ambient conditions: 2011-2012 control plots - nested ANOVA: $F_{4,5}$ = 1.133, T = -0.295, P = 0.766; or 2012-2013 control plots -nested ANOVA: $F_{4,5}$ = 3.4163, T = 1.848, P = 0.066 (Figure 3.4c). Contrary to the mites, collembola biomass was not immediately impacted by the flood in 2012 (nested ANOVA: $F_{4,5}$ = 0.102, T = -0.319, P = 0.748). A significant increase in collembola biomass was found in 2013 flooded plots compared with the 2013 control plots (nested ANOVA: $F_{4,5}$ = 10.191, T = 3.192, P<0.01). Site accounted for between 4% and 23% of the total variance attributed to random factors.

3.4.3 Stability in soil invertebrate communities as a function of overlying plant richness.

Flooding immediately negatively affected both total soil mesofaunal biomass and mite biomass and caused an increase in collembola biomass one year later (Figure 3.4). Also total soil mesofaunal biomass varied significant from year to year. To identify whether these impacts on biomass varied with either plant species richness or plant biomass, cthe plant-invertebrate relationship in control plots was compared across years and then with the relationship in the flooded plots. If soil mesofaunal stability was dependent on a plant community attribute such as diversity the slopes of the relationships would be significantly different.

The soil mesofaunal biomass – plant species richness relationships in ambient conditions did not vary between the years (i.e. the slope of the relationship in 2011 was not significantly different to the slope in 2012) (Table 3.3 and Figure 3.5a). The slope of the total mesofaunal biomass relationship – plant species richness was significantly different in the 2012 flooded plots than in the 2012 control plots (T = 2.473, P<0.01) (Figure 3.5b). One year after the flood (2013) there was no significant differences between the relationships when comparing the control with the flooded plots (Figure 3.5c).

Table 3.3 Nested ANCOVA comparisons of the total mesofaunal invertebrate biomass and plant species richness relationships. N.B. Constancy was tested by comparing the invertebrate biomass-plant species richness relationships slope in the 2011 control plots with the relationship slope in the 2012 control plots.

Stability Measure	Slope Comparisons (Year/s)	F value	T value	P value
Constancy	Control Plots *(2011-2012)*	1.1343	1.323	0.173
	Control plots *(2012-2013)*	0.039	0.197	0.834
Long Term Constancy	Control plots *(2011-2013)*	1.1343	1.139	0.241
Resistance	Control vs. Flooded plots *(2012)*	6.118	2.476	<0.01 **
Recovery	Control vs. Flooded plots *(2013)*	1.045	1.022	0.302

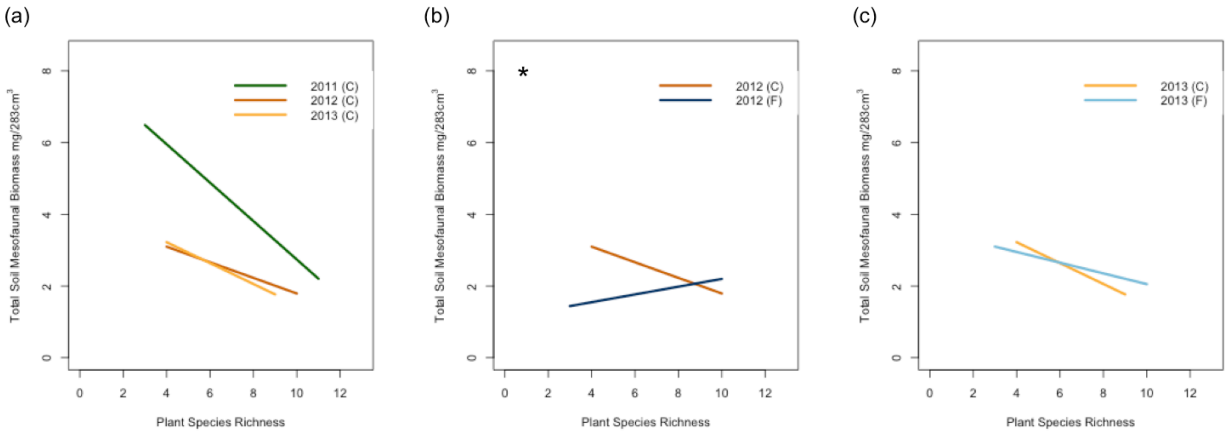


*Figure 3.5 Relationships between stability of secondary production and plant species richness. (a) Constancy = relationships between total mesofaunal biomass and plant species richness in control plots each year; (b) Recovery = effect of the flooding treatment on the relationship between total mesofaunal biomass and plant species richness; (c) Recovery = effect of the flooding on the relationship between total mesofaunal biomass and plant species richness. * denotes a significant difference between the slopes at p<0.05; resistance in total soil mesofaunal biomass varies with upon plant species richness.*

The mite biomass – plant species richness relationship slopes were not significantly different between 2011 control plots and 2012 control plots, and between 2011 control

plots and 2013 control plots (Table 3.4). The relationship slopes differed significantly between the 2012 control and 2012 flooded plots indicating resistance was correlated with species richness ($T=2.543$, $p<0.05$) (Figure 3.6b). The slopes of the mite biomass – plant species richness relationships in the 2013 control and 2013 flooded plots were not significantly different (Figure 3.6c). Constancy, long-term constancy and recovery of the mite biomass were independent of plant species richness. Resistance to change in mite biomass varied with plant species richness (Table 3.4 and Figure 3.6).

Table 3.4 Nested ANCOVA comparisons of the soil mite biomass and plant species richness relationships.

Stability Measure	Slope Comparisons (Year/s)	F value	T value	P value
Constancy	Control Plots *(2011-2012)*	0.508	0.911	0.346
	Control plots *(2012-2013)*	0.039	0.198	0.834
Long Term Constancy	Control plots *(2011-2013)*	0.508	0.724	0.453
Resistance	Control vs. Flooded plots *(2012)*	4.466	2.543	<0.05 *
Recovery	Control vs. Flooded plots *(2013)*	2.612	1.616	0.104

The relationship between collembola biomass and plant species richness is significantly different in 2011 control plots to the relationship found in 2012 ($p<0.01$) or 2013 ($p<0.01$) control plots (Table 3.5 and Figure 3.6d). The relationship does not differ however between 2012 and 2013 control plots. In 2012 the collembola biomass – plant species richness relationship did not vary between the control plots and the flooded plots (Figure 3.6e). The slope of the plant species richness – collembola biomass relationship in 2013 flooded plots was significantly different to the slope in 2013 control plots ($p<0.05$) (Figure 3.6f). Constancy, long-term constancy and recovery of the collembola biomass – plant species richness relationship varied with initial plant species richness.

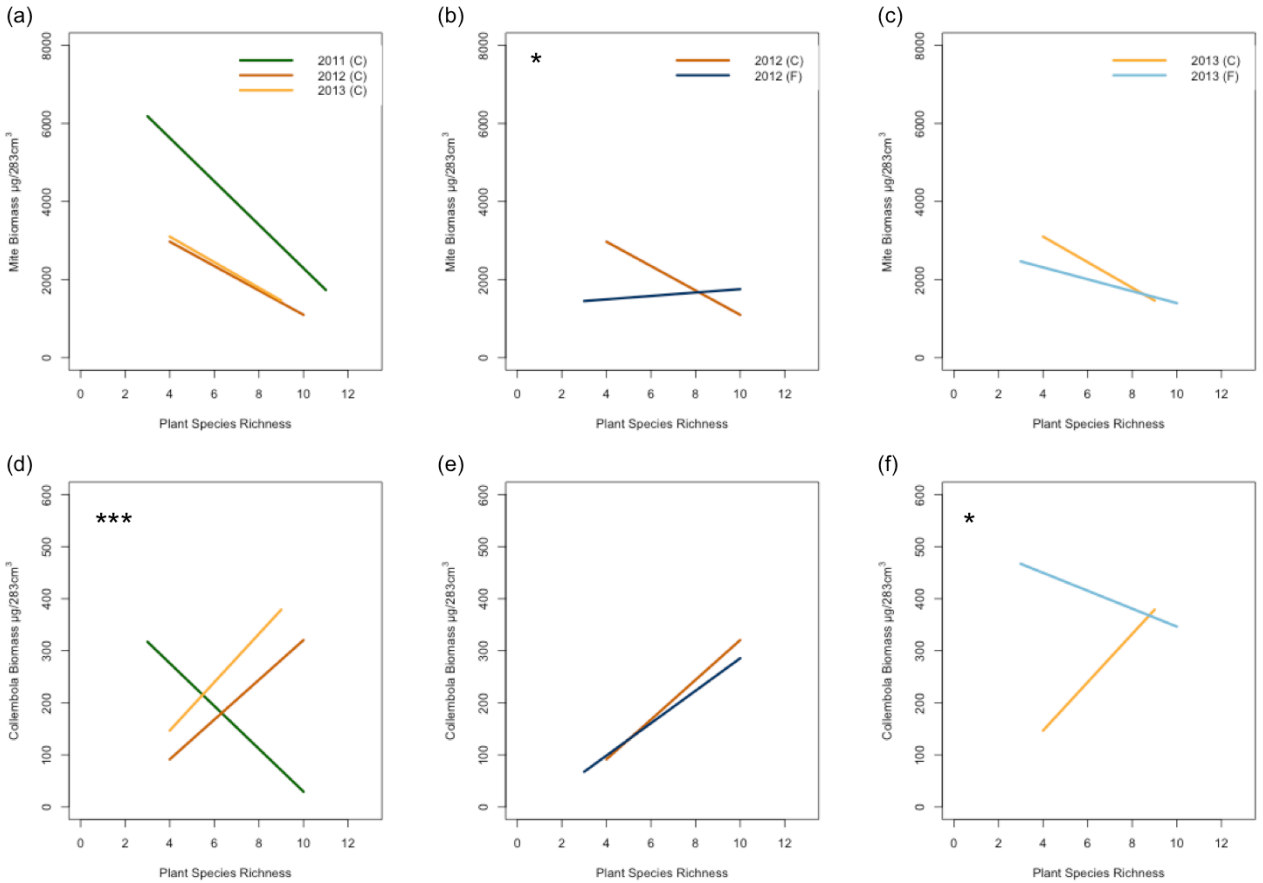


*Figure 3.6 Relationships between stability of (a-c) mite and (d-f) collembola biomass and plant species richness. (a) & (d) Constancy = relationships between invertebrate biomass and plant species richness in control plots each year; (b) & (e) Recovery = effect of the flooding treatment on the relationship between invertebrate biomass and plant species richness; (c) & (f) Recovery = effect of the flooding on the relationship between invertebrate biomass and plant species richness. * denotes a significant difference between the slopes at p<0.05, ** at p<0.01, *** at p<0.001 indicating stability (in its various forms) varies with the number of plants in the community. Constancy and recovery in collembola biomass and resistance in mite biomass vary with plant species richness.*

Table 3.5. Nested ANCOVA comparisons of the soil collembola biomass and plant species richness relationships.

Stability Measure	Comparisons (Year/s)	F value	T value	P value
Constancy	Control plots *(2011-2012)*	7.081	2.006	<0.01 **
	Control plots *(2012-2013)*	0.011	0.1067	0.895
Long Term Constancy	Control plots *(2011-2013)*	7.082	3.114	<0.01 **
Resistance	Control vs. Flooded plots *(2012)*	0.121	0.348	0.7324
Recovery	Control vs. Flooded plots *(2013)*	5.612	2.369	<0.05 *

3.4.4 Stability in soil invertebrate communities as a function of overlying plant biomass

The slopes of the total soil mesofaunal biomass - plant biomass relationships were significantly different in 2011 control plots compared with 2012 control plots ($p<0.001$), between the 2011 control plots and 2013 control plots ($p<0.01$), and between the 2012 and 2013 control plots ($p<0.01$) (Figure 3.7a and Table 3.6). The relationship in the flooded plots in 2012 was not significantly different to the relationship in the control plots (Figure 3.7b). Similarly the no difference was found in the 2013 flooded plots slope compared with the 2013 control plots (Figure 3.7c). Stability (constancy and long-term constancy) of soil mesofaunal biomass varied with plant biomass in control conditions only. Plots with greater plant biomass exhibited greater annual differences in total soil mesofaunal biomass.

Table 3.6 Nested ANCOVA comparisons of the total mesofaunal invertebrate biomass and plant biomass relationships.

Stability Measure	Slope Comparisons (Year/s)	F value	T value	P value
Constancy	Control Plots *(2011-2012)*	4.383	3.985	<0.001 ***
	Control plots *(2012-2013)*	8.257	2.873	<0.01 **
Long Term Constancy	Control plots *(2011-2013)*	4.383	2.876	<0.01 **
Resistance	Control vs. Flooded plots *(2012)*	0.4558	0.675	0.502
Recovery	Control vs. Flooded plots *(2013)*	2.361	1.537	0.122

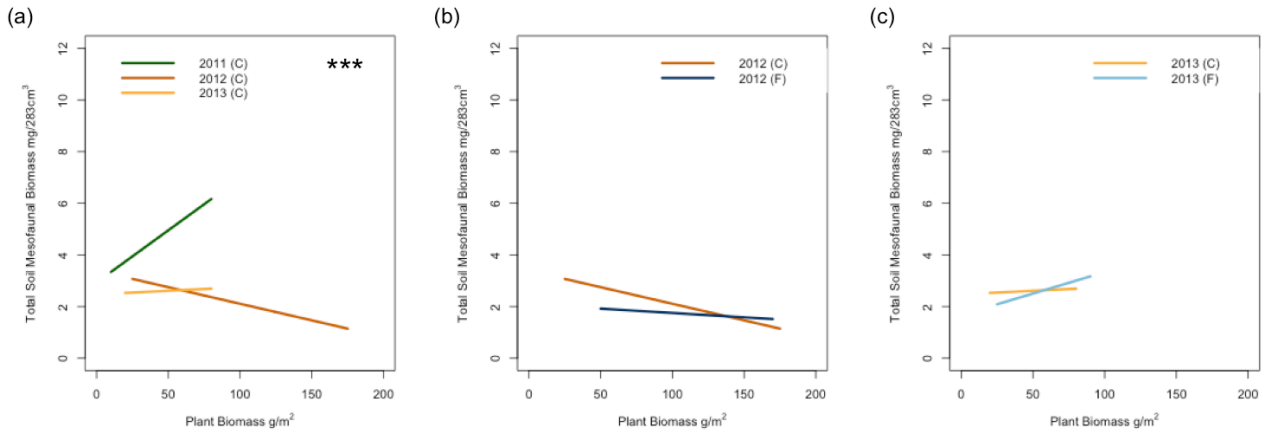


*Figure 3.7 Relationships between stability of secondary production and primary production. (a) Constancy = relationships between total mesofaunal biomass and primary production in control plots each year; (b) Recovery = effect of the flooding treatment on the relationship between total mesofaunal biomass and primary production; (c) Recovery = effect of the flooding on the relationship between total mesofaunal biomass and primary production. . *** denotes a significant difference between the slopes at p<0.001 indicating stability (in its various forms) varies with on the biomass provided by the plants in the community. Constancy in secondary production varies with primary production (aboveground plant biomass).*

The slopes of the mite biomass – plant biomass relationship were significantly different between the 2011 and 2012 control plots (p<0.001); the 2011 and 2013 control plots

(p<0.01); and the 2012 and 2013 control plots (p<0.01) (Table 3.7 and Figure 3.8a). No significant difference was found between the mite biomass – plant biomass relationships in 2012 flooded plots compared with 2012 control plots (Figure 3.8b), nor in 2013 flooded plots compared with 2012 control plots (Figure 3.8c). Constancy (both short and long-term) of mite biomass varied with plant biomass, greater annual variation in mite biomass was found in communities with greater plant biomass.

Table 3.7 Nested ANCOVA comparisons of the soil mite biomass and plant biomass relationships.

Stability Measure	**Slope Comparisons (Year/s)**	**F value**	**T value**	**P value**
Constancy	Control Plots *(2011-2012)*	4.255	3.824	<0.001 ***
	Control plots *(2012-2013)*	7.254	2.693	<0.01 **
Long Term Constancy	Control plots *(2011-2013)*	7.254	2.693	<0.01 **
Resistance	Control vs. Flooded plots *(2012)*	0.479	0.692	0.490
Recovery	Control vs. Flooded plots *(2013)*	3.688	1.920	0.054

There was no significant difference between the slope of the collembola biomass – plant biomass relationship when comparing control plots in 2011, 2012 or 2013 (Table 3.8 and Figure 3.3d). No significant difference was found between the collembola biomass – plant biomass relationships in 2012 flooded plots compared with 2012 control plots (Figure 3.8e), nor in 2013 flooded plots compared with 2012 control plots (Figure 3.8f). Stability of collembola biomass does not vary with plant biomass.

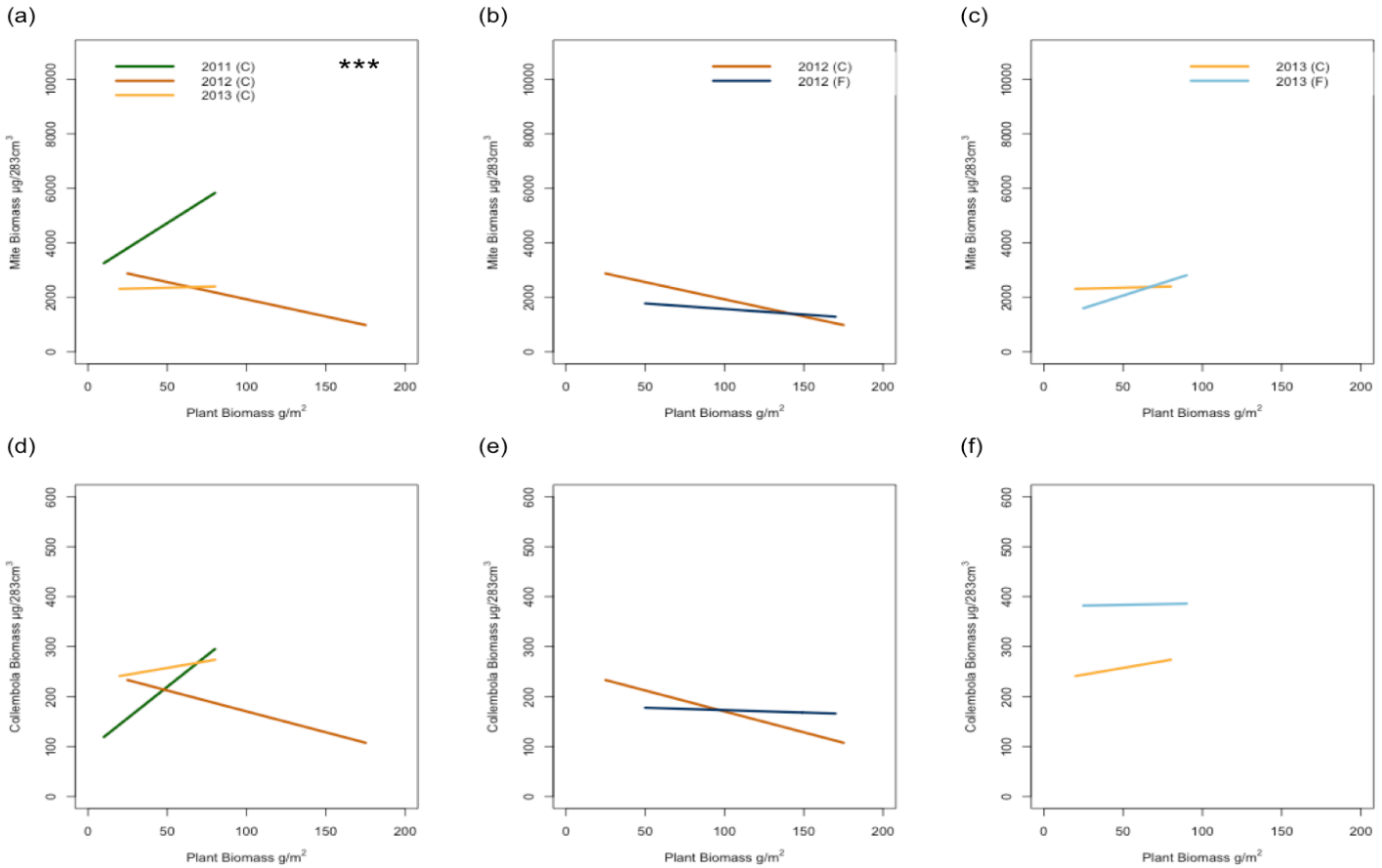


*Figure 3.8 Relationships between stability of (a-c) mite and (d-f) collembola biomass and primary production. (a) & (d) Constancy = relationships between invertebrate biomass and primary production in control plots each year; (b) & (e) Recovery = effect of the flooding treatment on the relationship between invertebrate biomass and primary production richness; (c) & (f) Recovery = effect of the flooding on the relationship between invertebrate biomass and primary production. *** denotes a significant difference between the slopes at p<0.001 indicating stability (in its various forms) varies with on the biomass provided by the plants in the community. Constancy in mite biomass varies with primary production (aboveground plant biomass).*

Table 3.8 Nested ANCOVA comparisons of the collembola biomass and plant biomass relationships.

Stability Measure	Slope Comparisons (Year/s)	F value	T value	P value
Constancy	Control Plots *(2011-2012)*	1.230	1.665	0.100
	Control plots *(2012-2013)*	1.378	1.336	0.389
Long Term Constancy	Control plots *(2011-2013)*	1.230	1.136	0.250
Resistance	Control vs. Flooded plots *(2012)*	0.001	0.16	0.997
Recovery	Control vs. Flooded plots *(2013)*	1.611	1.530	0.193

Overall (across the three years the experiment was running) grassland communities at Silwood with very diverse plant assemblages contained low mite biomass. There was no relationship between collembola biomass and plant diversity. Constancy in mite biomass was determined by primary production. Mite biomass decreased immediately post the 10-day flood and recovered to normal amounts a year later. Resistance to the flooding correlated with plant species richness and independent of primary production. Mite biomass in communities rich in plant species was more resistant to flood induced change. Whilst collembola biomass remained fairly stable annually, any degree of constancy from year to year varied with plant species richness. Collembola were not affected immediately after the flood but biomass increased one year later. Longer-term recovery from the flood correlated with plant species richness but was independent of plant biomass.

3.5 Discussion

3.5.1 The background relationship between secondary production and plant diversity and biomass

Secondary production, as estimated from standing total soil mesofaunal biomass, was highest in communities with few plant species, a result in complete contradiction to that found previously in studies with experimentally manipulated diversity (Haddad *et al.* 2001, Otway *et al.* 2005, Eisenhauer *et al.* 2012). Even with this contradiction a negative relationship is not surprising, it could be due to both bottom-up and top-down effects. The "resource concentration hypothesis"; a theory that predicts the density of herbivore specialists decreases with increasing plant species richness as the ideal resources become scarce and non-target plants are introduced (Rosenheim 1998). Another theory to explain this type of relationship is the 'enemy hypothesis'; this theory makes the assumption that as plant diversity increases herbivore enemies are provided with increased prey diversity and refuge. Under this theory herbivores are suppressed by their natural enemies in plant species rich communities (Rosenheim 1998).

Samples were not taken of any natural enemies therefore I cannot provide evidence for or against the 'enemy hypothesis', but as species richness increased in the plots dominance decreased and the communities became more even so there may be some evidence of the 'resource concentration hypothesis'. Whilst soil mites themselves are mycophagous, phytophagous, saprophagous, predatory and/or parasitic, the organisms upon which they feed are likely to be herbivore specialists. Further fungal and bacterial analyses may contribute more to our understanding of how the plant diversity affects the soil mites (samples are being analysed spring 2013).

Despite identifying an overall relationship, when delving further into individual years the negative correlation was only apparent in 2013. This could signal a longer-term relationship between plant diversity and soil biota, and highlight the importance of multi-year experiments. Interestingly plant species richness correlated (again negatively) with collembola biomass solely in 2011. Neither secondary production nor collembola biomass were correlated with primary production, indicating that the quality and type of litter materials entering the system may be more important that quantity.

3.5.2 Variation in soil mesofaunal biomass across years and in response to flooding

Secondary production and mite biomass was negatively affected immediately after the flood. As mites constituted ~69% of the secondary production and there was no immediate impact seen in collembola we can assume this event negatively affected the mites only. Mites are limited to air-filled pores and in their reduced ability to disperse, often relying upon other organisms to create soil pores or channels. The sheer amount of water deposited on the plots may also have compacted the soils therefore decreasing porosity and causing the mites to 'drown'. Collembola, however, are able to adjust to anoxic conditions (Hodkinson & Bird 2004) through vertical movement towards the surface and population aggregations (e.g. Hopkin 1997, Lensing *et al.* 2005). This survival mechanism may be why collembola did not suffer the same negative impact as mites.

Whilst mite biomass returned to 'normal' levels one year after the flood, there was a large increase in collembola biomass. Precipitation experiments have in fact shown a positive effect on some soil biota that intensified through time, sometimes with an initial lag (e.g. Blankinship *et al.* 2011, Kardol *et al.* 2011). Increased water availability in the soil enhances plant biomass production, which results in increased release of carbon and in turn increases growth of soil microfauna. This growth of soil microfauna can result in microorganism 'blooms' (large aggregations) post the extreme event creating a large food source for the collembola and recovering/recolonizing mites. An increase microfauna availability following the flood could explain the lagged positive response.

3.5.3 Stability in soil invertebrate communities as a function of overlying plant richness or biomass

Stability of secondary production and collembola biomass varied relative to different attributes of the plant community. This was dependent upon the type of stability being tested, the meso-organism and the plant community attribute being tested (Table 3.9). In ambient conditions secondary production varied annually independently of species richness but related to plant biomass therefore constancy of secondary production was determined by primary production. When primary production was low there was greater variability in secondary production and mite biomass across the years. As primary production (aboveground plant biomass) increases the litter layer is more

likely to increase in volume, resulting in increased likelihood of quality food sources and associated microbes (potential soil mesofaunal food sources). Furthermore diversity of litter materials can encourage larger soil engineer herbivores such as termites, ants and earthworms, which increase the soil porosity. This in turn may create extra mobility for the soil mesofauna; increasing their chances of persistence.

Table 3.9 Stability of soil invertebrate biomass varies with plant richness or biomass.

	Constancy	Resistance	Recovery
Secondary Production	Varies with **primary production**	Varies with **plant species richness**	
Mite Biomass	Varies with **primary production**	Varies with **plant species richness**	
Collembola Biomass	Varies with **plant species richness**		Varies the **plant species richness**

Contrastingly resistance in secondary production to the flooding correlated with plant species richness, not plant biomass. Greater species richness may provide greater habitat heterogeneity with the soil (through root variety) and therefore greater refuge; this may diminish the impact of the flood. Recovery in secondary production to the flooding event was independent of both richness and primary production. Microhabitat diversity resulting from species richness does impact mite community structure therefore it is reasonable to assume it is the reason species rich communities contain more stable soil invertebrate biomass (Hansen 2000, St John *et al.* 2006). The same results were found for mite biomass.

Whilst biomass of collembola did not significantly vary annually in ambient conditions, any variation correlated with plant species richness therefore constancy of collembola biomass varied with the number of species in a plot. Resistance in collembola biomass is independent of the number of plants in the community. Recovery following the flooding event for collembola biomass correlated with the number of plant species in the community. Collembola biomass was more stable in mid-range plant richness

communities (around 6 species per plot) hinting at a trade-off between habitat specialism/heterogeneity. Increases in plant species richness result in higher root diversity, production of cementing materials and creation of soil pores thus enhancing the potential habitat structure of the soil but equally may result in favourable plants losing space. Equally plant diversity may not only directly impact collembola stability but also indirectly. There is evidence of a strong correlation between plant species richness and fungi (van der Heijden *et al.* 1998, Burrows and Pfleger 2002, Smith *et al.* 1999, Vogelsang *et al.* 2006) and the importance of fungi for collembola stability (A'Bear *et al.* 2013). Finally constancy, resistance and recovery of collembola biomass were independent of primary production.

3.6 Conclusion

The aboveground-belowground relationship in natural communities is a complex and arcane subject. Some of the results of this study are in complete contradiction with those seen in other experiments so it is difficult to draw broad conclusions. Soil biota, particularly meso-fauna, are an historically understudied group, particularly in naturally occurring communities so it is important to encourage research on both experimentally and naturally occurring soil communities. A significant (negative) correlation was only found between collembola biomass and plant species richness during one year of the experiment and no correlation with plant biomass at all. Secondary production and mite biomass however were negatively correlated with plant species richness across multiple years. The 10-day flood both negatively and positively affected soil biota and the timing of the effect was taxon specific. In species rich communities secondary production was more resistant to change. Collembola biomass was more constant in plots containing the mean number of plant species (approximately 6 plant species per plot) providing potential evidence for a hump-shaped diversity-stability relationship. The relationships found in this study illustrated the idiosyncratic nature of diversity-stability-function interactions when looking at more than one guild, incorporating temporal variation, and in natural communities.

Chapter 4

Accounting for phylogeny and abundance in measures of diversity and in diversity-function relationships

4.1 Abstract

Plant species richness has been shown to correlate with production both positively (Naeem *et al.* 1994, Tilman *et al.* 1996) and negatively (Grace *et al.* 2007). In most cases diversity is defined as species richness, despite the clarity associated with this measure there are also many disadvantages. Focus has recently expanded to include those diversity measures that incorporate abundances and relatedness (Helmus *et al.* 2007). Using data from a three year experiment (DExtER at Silwood Park) I tested the extent to which primary and secondary productivity can be explained by abundance weighted taxonomic diversity measures and/or their phylogenetic. I compared each diversity measure with species richness pooled across all three years and in individual years then the comparative taxonomic and phylogenetic measures. I examined how incorporating abundance and relatedness information influenced the diversity-ecosystem function relationship, firstly with primary productivity (aboveground plant biomass) then secondary productivity (soil mesofaunal biomass).

Species richness does not vary annually however in 2013 there was less even representation thus increased dominance, and more phylogenetically clustered communities than in 2011 or 2012. Species Richness was a good proxy for Simpson's D, Berger-Parker Index, Faith's PD, and Quadratic Diversity both overall and during each individual year. Phylogenetic clustering and increased dominance correlated with an increase in primary production. Depending on the year in phylogenetically divergent communities where species are more evenly represented we saw both higher and lower secondary production (soil mesofaunal biomass).

4.2 Introduction

Experiments during the past few decades have extensively tested the theory that plant diversity is positively related to productivity (Naeem *et al.* 1994, Tilman *et al.* 1996, Hector *et al.* 1999, Tilman *et al.* 2001, Cardinale *et al.* 2007, Weigelt *et al.* 2010). Species richness is the most straightforward measure of diversity and the most widely used diversity metric in this research. From a logistical standpoint, the advantage of species richness as a measure of diversity is clear – its meaning is universal and unambiguous, and it is straightforward to measure. From a biological standpoint, however, there are drawbacks – with no accounting for relative abundances or abundances, richness equally weights all species as interchangeable presences or absences, which abstracts a great deal of potentially meaningful information. This is particularly the case with respect to examinations of functional relationships, where first principles would suggest the functional contribution of rare species to be different to that of abundant or dominant species. It is also the case with respect to examinations of stability relationships, where all elements of turnover in community composition not reflected as changes in the total number of different species are missed.

4.2.1 Diversity measures

Aside from species richness, there are multitudes of different metrics of taxonomic diversity that emphasize different features of community structure. Most common among these are Simpson's Diversity index (which is weighted towards the most abundant species and thereby accounts for dominance within a community); and the Shannon-Weiner diversity index (which emphasizes evenness, or the likelihood that one species has an equal probably of being represented in a random sample as all other species), but there are many others. Evenness alone can be expressed by at least 14 different measures (Smith and Wilson 1996), ranging from the Berger-Parker index (a metric that measures dominance exclusive of total species richness) at the simplest end of the spectrum to more complex measures derived from other diversity indices, such as Shannon's Evenness.

Taxonomic variety is not the only way to express the diversity among species, and may not be the most informative in many cases. Functional traits of species most directly link species to ecosystem functions, making measures of functional trait diversity in a

community potentially most relevant to research relating diversity to ecosystem functions such as production and carbon storage. . For example, root depth and density, nitrogen fixing capacity, specific leaf area (SLA), leaf size, leaf dry matter content (LDMC) and leaf nitrogen are correlated with nutrient cycling and biomass production (e.g. Klumpp & Soussana 2009, de Bello *et al.* 2010). During the past decade, there has been a increasing shift to functional trait variation metrics when testing biodiversity effects on ecosystem functioning (Lanta and Leps 2006, Diaz *et al.* 2007, Flynn *et al.* 2011, Cadotte *et al.* 2011,)

Functional trait data can be obtained directly from field and greenhouse measurements, or indirectly from databases and literature sources (Hill *et al.* 1999, Kleye *et al.* 2008, Royal Botanic Gardens, Kew 2008, Kattge *et al.* 2010). Indirect sources can be highly variable in quality, and the source data may come from an environment considerably different to the study system under focus. Additionally, traits can vary in meaningful ways not just inter-specifically but also intra-specifically. Whilst the extent and consequences of such disparity within populations is not widely understood, intra-specific differences may impact ecosystem processes in important ways (Fridley and Grime 2010, Bolnick *et al.* 2011). The lack of comprehensive, widely available data on functional and physiological traits is a major stumbling block to their full inclusion in biodiversity-ecosystem function research, but there are efforts underway to create worldwide trait databases (e.g. TRY database Kattge *et al.* 2010). A potential drawback to how functional diversity has been used so far is that studies tend to include solely those traits that are thought to be associated with the function under consideration, which makes substantial *a priori* assumptions about the comprehensiveness of our understanding of the fundamental traits for each function.

Owing to a lack of knowledge on apposite traits for different functions and the deficit in high-quality data on traits, researchers have adopted phylogenetic diversity measures as a useful middle ground between taxonomic and functional measures (Swenson & Enquist 2009, Pavoine *et al.* 2010). Phylogenetic measures may in fact provide a happy medium by integrating evolutionary history and patterns of relatedness into our understanding of taxonomic diversity, and by extension patterns of shared traits, and therefore provides a decent proxy for functional diversity (Cadotte *et al.* 2009, Cadotte *et al.* 2010, Salles *et al.* 2012, Mouquet *et al.* 2012). If we assume that phenotypic variation is correlated with evolutionary deviation, then the more divergent two species are to one another the greater the chance they differ ecologically.

Before the influence of different diversity measures on ecosystem functions is considered, relationships between the measures should be considered. If they are closely related, could one less complex one be used reliably as a proxy for another? Phylogenetic diversity has been shown to correlate with species richness but the strength and robustness of this relationship is not clear (Cadotte *et al.* 2008, Cadotte *et al.* 2011). Usefully, some phylogenetic measures are calculated in a similar fashion to simpler taxonomic measures but with the addition of phylogenetic information, allowing for direct comparability between taxonomic and phylogenetic metrics (Allen *et al.* 2009) (Table 4.1). Faith's PD measure is the counterpart to species richness; Rao's quadratic diversity (Q_{RAO}) the counterpart to Simpsons index (D); and Phylogenetic-species-evenness (PSE) the counterpart to Macintosh Evenness (E). By testing each phylogenetic measure against its similar taxonomic counterpart we can identify the importance of evolutionary distinction for ecosystem function.

Table 4.1 Comparable taxonomic and phylogenetic diversity metrics

	Presence/Absence	Diversity Indices (Presence & Abundance)	Evenness Indices (Abundance)	
Taxonomic	Species Richness (S)	Simpsons Index (D) (Simpson 1949)	McIntosh Evenness (E) (Smith & Wilson 1996)	Berger-Parker Dominance Index (BPD) (Berger & Parker 1970)
Phylogenetic (Adding relatedness)	Phylogenetic Diversity (Faith's PD) (Faith 1992)	Quadratic Diversity (Q) (Rao 1982)	Phylogenetic-Species-Evenness (Helmus *et al.* 2007)	

4.2.2 Defining diversity in the biodiversity-function relationship

The sheer plethora of ways to describe "diversity" may introduce more confusion into our understanding of how diversity influences function. [A comprehensive review of taxonomic diversity measures is provided by Magurran (2010); functional diversity measures by Petchey *et al.* (2009); and phylogenetic diversity measures by Pearse *et al.* (in press)]. With the inclusion of further diversity metrics we need to ask if one measure

is more appropriate or relevant than another. Furthermore, to what extent does this depend on the particular functions being studied. For example, the extent of dominance apparent in the species composition of a community may be a better predictor of ecosystem function and stability than the raw number of species (Smith & Knapp 2003, Orwin *et al.* 2013). There are many measures available that account for variation in abundances of species and relatedness, all of which can be rightly used to describe the community "diversity". Our understanding of how diversity impacts function and stability is driven by the particular ways the terms are defined, and thus may not convey an inherent "true" relationship between these variables more broadly considered.

Contrary to species richness, both negative and positive relationships between evenness and biomass have been observed in experimental grassland communities (Mulder *et al.* 2004, Kirwan *et al.* 2007). In natural communities, however production can be independent of species richness (Bezemer and van der Putten 2007, Grace *et al.* 2007). Due to its use as proxy for functional diversity it is not surprising phylogenetic diversity has also proven to be a useful predictor of ecosystem function as well (Connolly et at 2011, Flynn *et al.* 2011, Pavoine & Bonsall 2011, Cadotte *et al.* 2012), with one direct comparison showing comparable predictive power between the two (Flynn *et al.* 2011).

Many ecologists working on diversity-ecosystem function relationships have shifted towards using functional and phylogenetic diversity rather than species number alone, but much our view into these is still based on from experimental communities (Diaz & Cabido 2001, Lavorel & Garnier 2002, Petchey & Gaston 2006, Cadotte *et al.* 2011, Grigulis *et al.* 2013). In these experiments species pools and richness are heavily controlled and decided *a priori* rather than functional trait or phylogenetic diversity. Are comparable functional and phylogenetic diversity measures found in natural systems or are they skewed by the artificially created community composition? It is worth considering the extent to which the understanding of the diversity-ecosystem function relationship (diversity in all its forms) may be biased by the carefully controlled and heavily manipulated structure of our research. Notwithstanding, relationships of species, functional, and phylogenetic richness to ecosystem function are poorly understood for natural systems (Naeem 2002).

Data from a three year experiment (DExtER at Silwood Park Campus of Imperial College, London) was used to elucidate the extent to which primary and secondary productivity can be explained by abundance weighted taxonomic diversity measures and/or their

phylogenetic counterparts in natural systems. Firstly diversity metrics were compared with species richness pooled across all three years and in individual years. Secondly a comparison between comparative taxonomic and phylogenetic measures (e.g. Phylogenetic-species-evenness to McIntosh's Evenness) was carried out. Finally the extent to which each diversity measure correlates with primary (aboveground plant biomass) and secondary productivity (soil mesofaunal biomass) was tested. All analyses will look at pooled data across the three years and individual years.

4.3 Materials and methods

4.3.1 Study site

Data was collected from the DExtER (Disturbance Extremes and Ecological Responses) experiment at Silwood park, Imperial College London in South-East England (51°24'23.16"N, 0°38'55.33"W). As described in previous chapters the experiment utilises a natural richness gradient of vascular plant species at Silwood Park. Plant species richness was measured annually in late July in 2011, 2012 and 2013 when most vascular plants occurring in the grasslands are present as aboveground tissues.

4.3.2 Calculating diversity measures

Species richness data were collected by surveying each plot annually in July. All further diversity metrics were generated using the original species richness and abundance data in R (R Development Team 2012) (Table 4.2). To generate data on Simpson's D , McIntosh's Evenness (E), Berger Parker index, Faith's PD, Phylogenetic-species-evenness, Rao quadratic diversity the packages picante, vegan and BiodiversityR were used (Kembel *et al.* 2010, Oksanen *et al.* 2013, Kindt 2013).

Phylogenetic diversity metrics are calculated using a phylogeny, for this analysis the freely available DaPhnE tree was used – a dated phylogeny of European Flora (Durka and Michalski 2012). To calculate the phylogenetic diversity measure the DaPhnE tree was trimmed to only include vascular plants present in the experiment (Figure 4.1).

Table 4.2 Indices of diversity and evenness for use in the biodiversity-ecosystem function analysis

Index	Equation	Description	Reference
Species Richness	S	Total number of species found in the community.	
Simpsons Index (D)	$D = \sum \frac{(n_i(n_i - 1))}{(N(N-1))}$	Probability that two randomly selected individuals belong to the same species – increases denote greater dominance and lower evenness.	Simpson 1949
McIntosh Evenness	$E = \frac{N - \sqrt{(\sum n_i^2)}}{N - N/\sqrt{S}}$	[Derived from McIntosh Diversity Index] – values closer to 1 indicates individuals are distributed equally (more even).	McIntosh 1967
Berger-Parker Index	$BPI = \frac{N_{\max}}{N}$	Proportion of dominant species – increases denote increased dominance.	Berger & Parker 1970
Faiths PD	$PD = \sum_{branches} l(b)$	Sum of the lengths of all branches of species represented in the community – increases denote more divergent communities .	Faith 1992
Quadratic diversity	$Q = \sum_{i>j} d_{ij} p_i p_j$	Mean phylogenetic distance between two randomly chosen individuals - increases denote further spread throughout the phylogeny (more divergent species) and are evenly represented.	Rao 1982
Phylogenetic-Species-Evenness	$PSE = \frac{Ndiag(C)'M - M'CM}{N^2 - \bar{n}_i N}$	[Derived from PSV] Degree to which species are phylogenetically related and represented equally - decreases when community members are closely related AND when members are unevenly present.	Helmus *et al.* 2007

S = number of species; n_i = the number of individuals in the *i*th species; N = total number of individuals; l(b) = length of branch *b*; d_{ij} = the branch length of the shortest path between corresponding leaves of a phylogeny; p_i = proportion of individuals in species *i*; C = community phylogeny; M = column vector containing values of n_i; apostrophe = denotes transpose; diag = column vectors of the main diagonal of the community phylogeny.

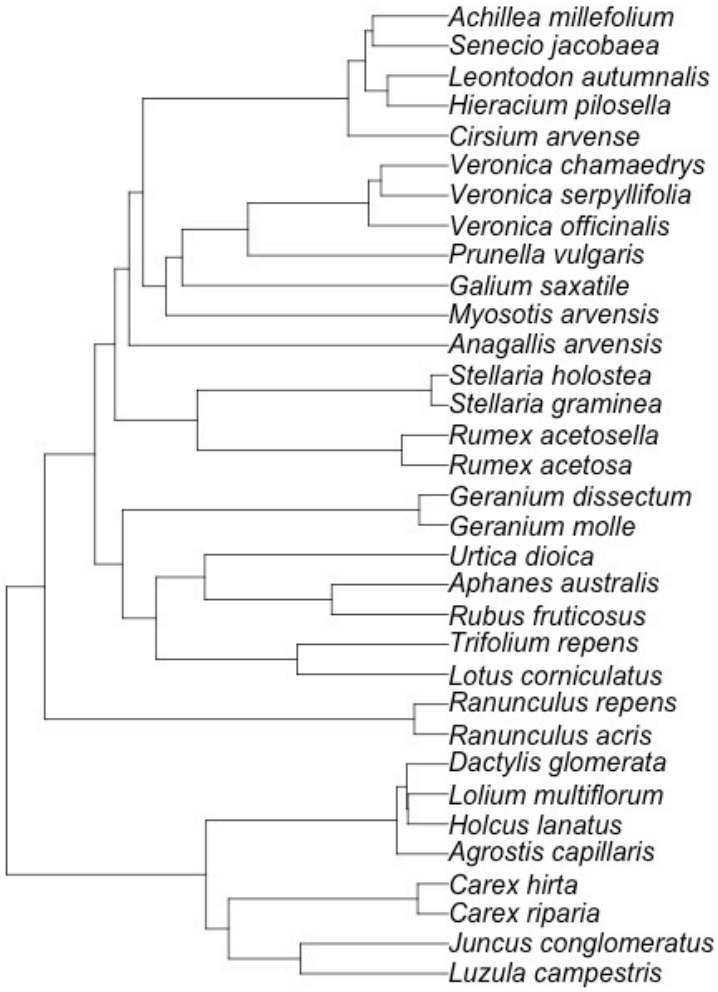


Figure 4.1 Phylogenetic tree of plant species found in the experiment. Tree is a trimmed version of the DaPhnE tree (Durka and Michalski 2012).

4.3.3 Sampling

Plant production

Species richness and abundance data were collected in all plots each year. Species richness was blocked in each site from low to high values and 35 plots (five in each site, one from each block) were harvested each August (2011, 2012 and 2013). Once a plot was harvested it was no longer used in the experiment. Data acquisition was carried out in the central 0.25m^2 to circumvent any edge effects. The collected biomass was dried at 80^{0}C for 72hrs and then weighed. Peak aboveground plant biomass (g/m^2) was used as a proxy for primary production.

Soil mesofaunal biomass

10cm deep soil cores were taken from all plots in July 2011, 2012 and 2013 using a steel corer (6cm diameter). One soil core (283cm^3) was taken for each plot. Soil mesofauna were extracted using a Tullgren funnel apparatus (over 72 hrs) and transferred to alcohol for storage. The samples predominantly consisted of collembola and mites. Collembola were identified to family level and counted. Overall, 30 representatives of each collembola family identified were collected, dried and weighed (Appendix 2.1). We then took the mean weight for each family. We multiplied the number of individuals in each family by the mean family dry weight and summed this to generate biomass data. This was repeated for the six mite morphotypes (Appendix 2.2). Total soil mesofaunal biomass (mg/283cm^3) was used as a proxy for secondary production.

4.3.4 Statistical analyses

Controlling for site effects, linear mixed-effects models were employed with site as a random factor for each year. When pooling across all three years, year was nested within site as a random factor. Generalised linear mixed models were used to test for correlations between plant species richness and Simpson's D, McIntosh E, Berger-Parker, Faith's PD, Phylogenetic-Species-Evenness and Rao Q. Generalised linear mixed models were used to test for correlations between taxonomic diversity measures and the corresponding phylogenetic diversitymeasure (Table 4.1). Lastly generalized linear mixed models were used to test the correlation between each diversity measure and primary and secondary function. All mixed effects models were conducted in R (R Development Team 2012) with the package 'lme4' (Bates & Sarkar 2007). Residuals versus fitted plots and normal qq-plots of the linear models were examined to ensure model assumptions were not violated. Likelihood-ratio tests of the full models with both random and fixed effects with those with just random effects to calculate p-values.

4.4 Results

4.4.1 Background variation in plant diversity across years

Taxonomic diversity measures

Species richness did not significantly vary between 2011 and 2012, between 2012 and 2013 or overall between 2011 and 2013 (Figure 4.2a and Table 4.3). Site accounted for 54-57% of the total variation attributed to random factors. Six plant species per plot was the median value across all years. Simpson's D did not significantly vary between 2011 and 2012, between 2012 and 2013 or overall between 2011 and 2013 (Figure 4.2b and Table 4.3). Site accounted for 20%-24% of the total variation attributed to random factors. McIntosh E did not significantly vary between 2011 and 2012 or between 2012 and 2013 (Table 4.3). McIntosh E was significantly lower in 2013 compared with 2011 ($T = -2.760$, $P<0.01$) (Figure 4.2c). Site accounted for 4%-19% of the total variation attributed to random factors. Berger-Parker Index did not significantly vary between 2011 and 2012 or between 2012 and 2013. Berger-Parker Index was significantly higher in 2013 compared with 2011 ($T = 2.175$, $P<0.05$) (Figure 4.2d). Site accounted for 2%-25% of the total variation attributed to random factors.

Table 4.3 Nested ANOVA results comparing yearly variation in taxonomic diversity indices.

Index	Years compared	F value	T value	P value
Species richness	2011-2012	0.359	0.599	0.547
	2012-2013	0.228	-0.477	0.631
	2011-2013	0.929	-0.964	0.333
Simpson's D	2011-2012	0.105	-0.324	0.744
	2012-2013	3.112	-1.764	0.079
	2011-2013	3.2075	-1.051	0.072
McIntosh E	2011-2012	1.738	-1.318	0.187
	2012-2013	1.936	-1.391	0.164
	2011-2013	7.620	-2.760	<0.01
Berger-Parker	2011-2012	0.018	0.125	0.892
	2012-2013	2.641	1.625	0.105
	2011-2013	3.762	2.175	<0.05

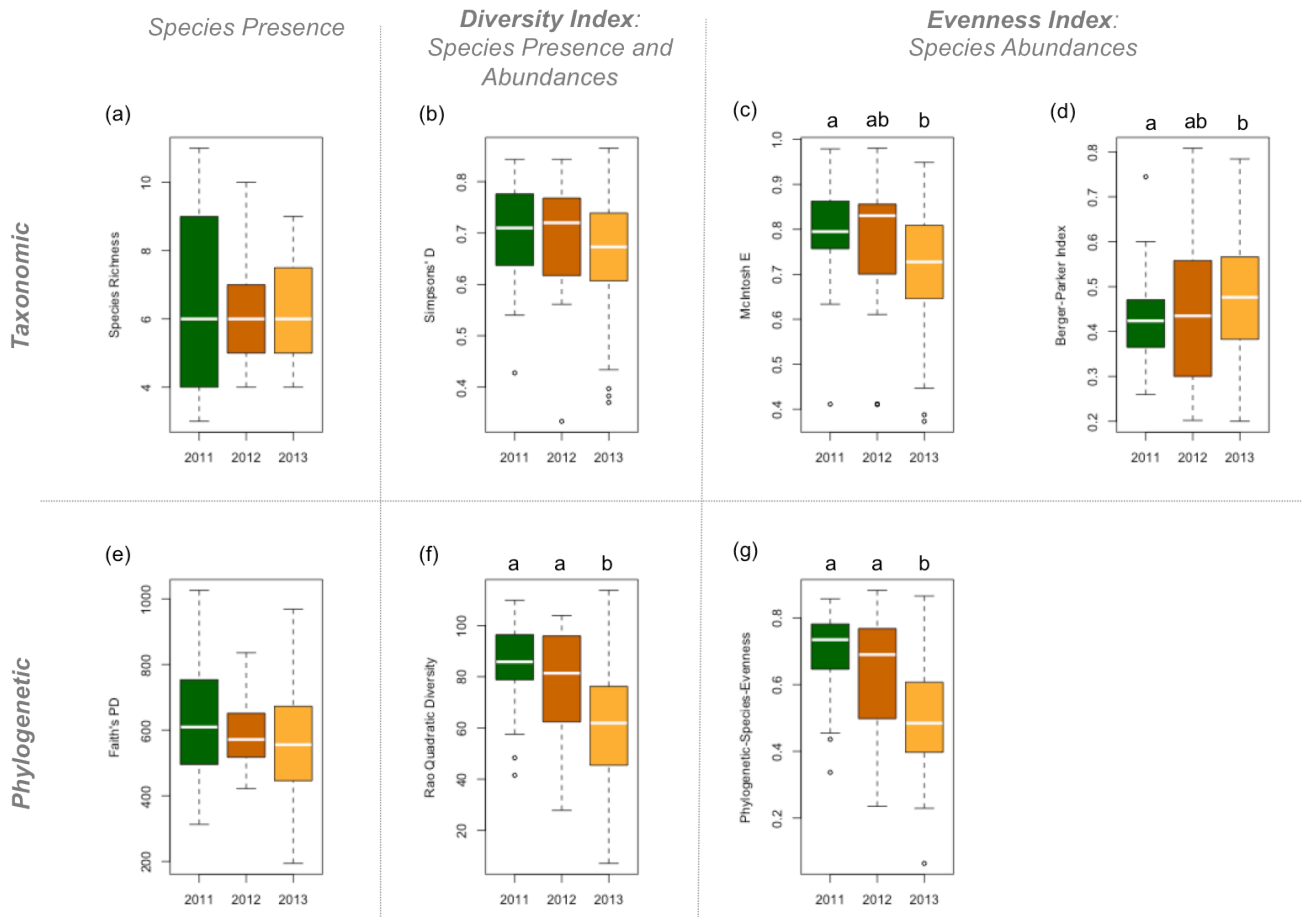


Figure 4.2 Temporal constancy of grassland plant diversity subject to definition of diversity. Taxonomic measures: (a) Species Richness; (b) Simpson's D; (c) McIntosh E; (d) Berger-Parker Index; and Phylogenetic measures: (e) Faith's PD; (f) Rao Quadratic Diversity; and (g) Phylogenetic Species Evenness. Letters denote significant groupings. Dominance decreased in communities in 2013 compared with 2011 according to both McIntosh E ($p<0.01$) and Berger-Parker ($p<0.05$) values. Phylogenetic clustering increased in 2013 communities compared with 2011 and 2012 according to both Qrao ($p<0.01$) and PSE ($p<0.001$).

Phylogenetic Diversity Measures

Faith's PD did not significantly vary between 2011 and 2012, between 2012 and 2013 or overall between 2011 and 2013 (Figure 4.2e and Table 4.4). Site accounted for 51-59% of the total variation attributed to random factors. Rao Quadratic Diversity was not significantly different in 2011 compared with 2012. Rao Q was significantly lower in 2013 compared with 2012 ($T = -3.164$, $P<0.01$), and compared with 2011 ($T = -5.655$, $P<0.001$) (Figure 4.2f). Site accounted for 11-33% of the total variance attributed to random effects. Phylogenetic-Species-Evenness was not significantly different in 2011 compared with 2012 (Table 4.4) however it was significantly lower in 2013 compared with 2012 ($T = -3.200$, $P<0.01$), and compared with 2011 ($T = -5.952$, $P<0.001$) (Figure 4.2g). Site accounted for 1-15% of the total variance attributed to random effects.

Table 4.4 Nested ANOVA results comparing yearly variation in phylogenetic diversity indices.

Index	Years compared	F value	T value	P value
Faith's PD	2011-2012	1.508	-1.228	0.219
	2012-2013	0.561	-0.748	0.451
	2011-2013	3.045	-1.208	0.700
Rao Q	2011-2012	2.656	0.104	0.104
	2012-2013	10.008	-3.164	<0.01
	2011-2013	31.727	-5.655	<0.001
Phylogenetic-Species-Evenness	2011-2012	3.780	-1.904	0.063
	2012-2013	10.241	-3.200	<0.01
	2011-2013	35.430	-5.952	<0.001

4.4.2 Comparing richness with diversity metrics

Plant species richness was positively correlated with Simpson's D when data were pooled across the entire experiment ($T = 7.282$, $P<0.001$) (Figure 4.3b and Table 4.5). Plant species richness positively correlated with Simpson's D in 2011 ($T = 5.602$, $P<0.001$), in 2012 ($T = 4.054$, $P<0.001$), and in 2013 ($T = 4.468$, $P<0.001$).

Table 4.5 Generalised linear mixed model analysis of the correlation between plant species richness and diversity metrics during each year (overall includes data pooled from all three years).

Index	Year	F value	T value	P value	Slope
Simpson's D	2011	31.379	5.602	<0.001***	positive
	2012	16.43	4.054	<0.001***	positive
	2013	19.964	4.468	<0.001***	positive
	Overall	53.034	7.282	<0.001***	positive
McIntosh E	2011	0.5336	-0.739	0.454	n.s.
	2012	0.483	0.695	0.470	n.s.
	2013	3.615	1.901	0.057	n.s.
	Overall	3.370	1.836	0.081	n.s.
Berger-Parker	2011	6.029	-2.455	<0.001***	negative
	2012	12.052	-3.473	<0.001***	negative
	2013	8.469	-2.910	<0.01**	negative
	Overall	24.253	-4.925	<0.001***	negative
Faith's PD	2011	260.33	16.138	<0.001***	positive
	2012	106.47	10.319	<0.001***	positive
	2013	70.282	8.385	<0.001***	positive
	Overall	247.87	15.744	<0.001***	positive
Rao Q	2011	9.045	3.007	<0.01**	positive
	2012	5.575	2.361	<0.05*	positive
	2013	10.624	3.260	<0.01**	positive
	Overall	18.116	4.256	<0.001***	positive
Phylogenetic Species Evenness	2011	0.007	-0.082	0.898	n.s.
	2012	1.194	1.093	0.303	n.s.
	2013	5.952	2.434	<0.05*	positive
	Overall	1.593	1.262	0.199	n.s.

Plant species richness was not correlated with McIntosh E when data were pooled across the entire experiment, in 2011, 2012 or in 2013 (Table 4.5). Plant species richness was negatively correlated with Berger-Parker Index when data were pooled across the entire experiment (over the three years) ($T = -4.925$, $P<0.001$) (Figure 4.3d). Plant species richness negatively correlated with Berger-Parker Index in 2011 ($T = -2.455$, $P<0.001$), in 2012 ($T = -3.473$, $P<0.001$), and in 2013 ($T = -2.910$, $P<0.01$).

Plant species richness was positively correlated with Faith's PD when data were pooled across the entire experiment ($T = 15.744$, $P<0.001$) (Figure 4.3e). Plant species richness positively correlated with Faith's PD in 2011 ($T = 16.138$, $P<0.001$), in 2012 ($T = 10.319$, $P<0.001$), and in 2013 ($T = 8.385$, $P<0.001$). Plant species richness was positively correlated with Rao Quadratic Diversity when data were pooled across the entire experiment ($T = 4.256$, $P<0.001$) (Figure 4.3f). Plant species richness positively correlated with Rao Quadratic Diversity in 2011 ($T = 3.007$, $P<0.01$), in 2012 ($T = 2.361$, $P<0.05$), and in 2013 ($T = 3.260$, $P<0.01$). Plant species richness was not correlated with Phylogenetic-Species-Evenness across the entire experiment (all years), in 2011 or in 2012 (Figure 4.3g). Plant species richness was positively correlated with Phylogenetic-Species-Evenness in 2013 only ($T = 2.434$, $P<0.05$). See Appendix 3.1 for percentages of the total variances attributed to random factor in the GLMM analysis.

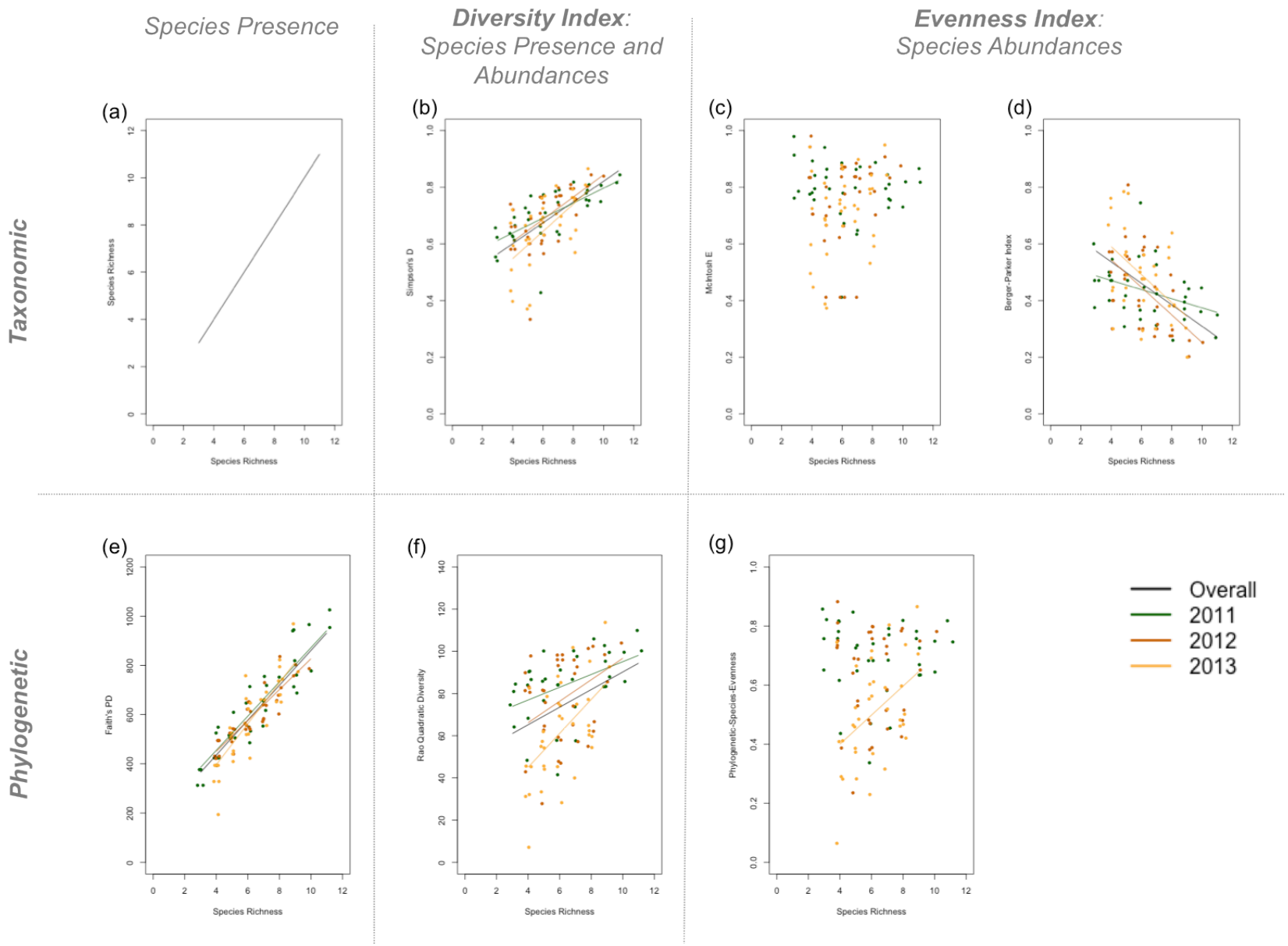


Figure 4.3 Relationships between species richness and the diversity measures overall and for each year. Taxonomic diversity measures: (a) Species Richness; (b) Simpson's D; (c) McIntosh E; (d) Berger-Parker Index; and Phylogenetic diversity measures: (e) Faith's PD; (f) Rao Quadratic Diversity; and (g) Phylogenetic Species Evenness. Regression lines denote significant relationships. Species richness is a good overall predictor for Simpson's D, Berger-Parker Index, Faith's PD, and Qrao.

Comparing taxonomic measures with their phylogenetic counterpart.

The comparison between species richness and the phylogenetic counterpart, Faith's PD, is described in detail above (Figure 4.3e). Simpson's D was positively correlated with Rao Quadratic Diversity over the entire experiment (Table 4.6) and during individual years. McIntosh E was positively correlated with Phylogenetic-Species-Evenness over the entire experiment and during individual years.

Table 4.6 Linear mixed model analyses between taxonomic diversity measures and the phylogenetic counterparts.

Taxonomic index	Phylogenetic index	Year	F value	T value	P value	Slope
Species Richness	**Faith's PD**	2011	260.33	16.138	<0.001***	positive
		2012	106.47	10.319	<0.001***	positive
		2013	70.282	8.385	<0.001***	positive
		Overall	247.87	15.744	<0.001***	positive
Simpsons D	**Rao Q**	2011	58.228	7.631	<0.001***	positive
		2012	33.347	5.775	<0.001***	positive
		2013	19.342	4.398	<0.001***	positive
		Overall	98.215	9.911	<0.001***	positive
McIntosh E	**Phylogenetic -Species-Evenness**	2011	61.862	7.865	<0.001***	negative
		2012	16.265	4.033	<0.001***	negative
		2013	14.291	3780	<0.001***	negative
		Overall	70.796	8.414	<0.001***	negative

4.4.3 Diversity measures in the biodiversity-ecosystem function relationship

Plant diversity-plant production relationships

In 2011, 2012 and when plots from all years was pooled (2011-2013) species richness was not correlated with plant biomass (Figure 4.4a). In 2013 there was a positive relationship between plant richness and biomass in 2013 ($T = 2.060$, $P<0.05$) (Table 4.6). Across the length of the experiment plant biomass was not significantly correlated with Simpson's D (Figure 4.4b). Similarly there was no correlation during individual years. McIntosh E was negatively correlated with plant biomass across the length of the

experiment (T = -2.062, P<0.05) (Figure 4.4c). The negative relationship was also identified in 2012 (T = -2.178, P<0.05) but not in 2011 or 2013 (Table 4.7). Overall, pooled across the length of the experiment, and in 2011 and 2013 the Berger-Parker Index was not correlated with plant biomass (Figure 4.4d). Berger-Parker Index positively correlated with plant biomass in 2012 (T = 2.382, P<0.05).

Faith's PD was not correlated with plant biomass, either when data was pooled across the experiment or when looking at individual years (Figure 4.4e). Over the length of the experiment Rao Quadratic Diversity negatively correlated with plant biomass (T = -2.499, P<0.05) (Figure 4.4f). A similar negative relationship was also found in 2012 (T = -2.874, P<0.01) but not in 2011 or 2013 (Table 4.7). Pooled across the length of the experiment Phylogenetic-Species-Evenness was negatively correlated with plant biomass (T = -2.488, P<0.05) (Fig. 4.4g). Additionally Phylogenetic-Species-Evenness was negatively correlated with plant biomass in 2012 (T = -2.809, P<0.01) but no correlation was found 2011 or 2013. Percentage of the total variance attributed to random effects for each test can be seen in Appendix 3.2.

Table 4.7 Generalised linear mixed model analysis of the relationship between different plant diversity indices and aboveground plant biomass. Overall refers to combining data across all years (2011-2013).

Index	Year	F value	T value	P value	Slope
Species Richness	2011	0.098	-0.313	0.823	n.s.
	2012	1.481	-1.217	0.246	n.s.
	2013	4.243	2.060	<0.05*	positive
	Overall	0.345	-0.587	0.570	n.s.
Simpson's D	2011	0.348	0.590	0.529	n.s.
	2012	3.232	-1.307	0.061	n.s.
	2013	1.113	1.055	0.279	n.s.
	Overall	2.628	-1.621	0.108	n.s.
McIntosh E	2011	0.365	0.604	0.551	n.s.
	2012	4.742	-2.178	<0.05*	negative
	2013	0.449	0.670	0.500	n.s.
	Overall	5.252	-2.062	<0.05*	negative
Berger-Parker	2011	0.010	-0.102	0.912	n.s.
	2012	5.673	2.382	<0.05*	positive
	2013	0.650	-0.806	0.415	n.s.
	Overall	3.044	1.744	0.082	n.s.
Faith's PD	2011	0.111	-0.331	0.853	n.s.
	2012	1.663	-1.129	0.204	n.s.
	2013	0.011	0.104	0.820	n.s.
	Overall	1.423	-1.197	0.245	n.s.
Rao Q	2011	0.274	0.524	0.576	n.s.
	2012	8.256	-2.874	<0.01**	negative
	2013	0.234	-0.483	0.690	n.s.
	Overall	6.2472	-2.499	<0.05*	negative
Phylogenetic Species Evenness	2011	0.258	0.508	0.606	n.s.
	2012	7.890	-2.809	<0.01**	negative
	2013	0.549	-0.741	0.505	n.s.
	Overall	6.189	-2.488	<0.05*	negative

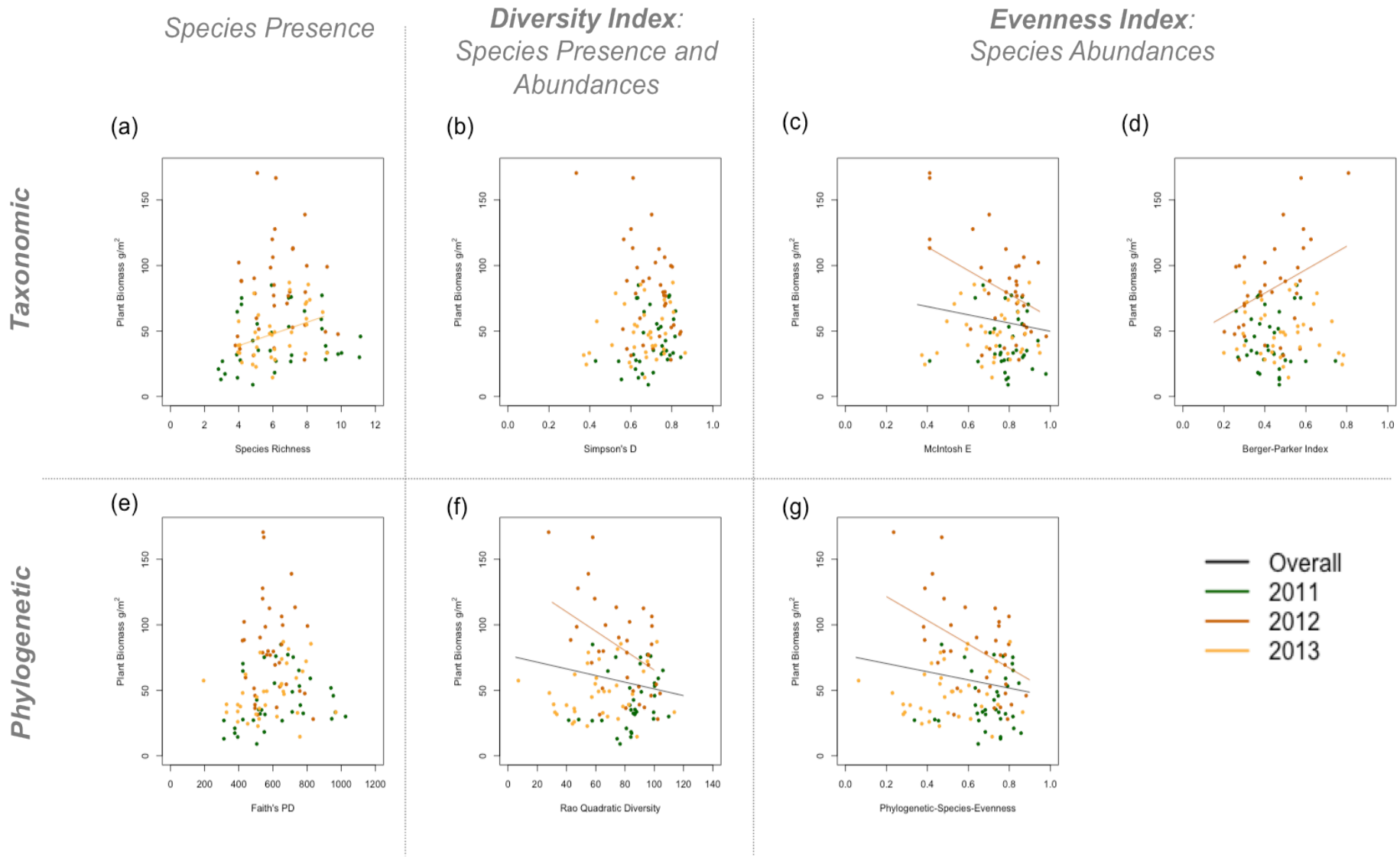


Figure 4.4 Relationships between different forms of plant diversity and primary production (g/m² of aboveground plant biomass) across all three years and in individual years. Regression lines denote significant correlations. Taxonomic diversity measures: (a) Species Richness; (b) Simpson's D; (c) McIntosh E; (d) Berger-Parker Index; and Phylogenetic diversity measures: (e) Faith's PD; (f) Rao Quadratic Diversity; and (g) Phylogenetic Species Evenness. In 2013 primary production increased with species richness. In 2012 primary production increased with species dominance. Overall and in 2012 primary production decreased with evenness (and even phylogenetic spread).

Plant diversity – secondary production relationships

Plant species richness was negatively correlated with soil mesofaunal biomass when data was pooled across the three years ($T = -4.,313$, $P<0.001$) and in 2013 ($T = -2.215$, $P<0.05$) (Figure 4.5a). In 2011, 2012 and across the length of the experiment soil mesofaunal biomass was not significantly correlated with Simpson's D (Figure 4.5b). In 2013 Simpson's D was negatively correlated with soil mesofaunal biomass ($T = -2.246$, $P<0.05$) (Table 4.8). There was no relationship between McIntosh E and soil mesofaunal biomass plant across the length of the experiment, in during individual years (Figure 4.5c). Berger-Parker Index was positively correlated with soil mesofaunal biomass in 2012 ($T = 2.186$, $P<0.05$) however this relationship was not found when including all years in the analysis or in 2011 or 2013 (Fig. 4.5d). Percentage of the total variance attributed to random effects for each test can be seen in Appendix 3.3.

Faith's PD was negatively correlated with soil mesofaunal biomass when data was pooled across the experiment ($T = -2.029$, $P<0.05$) (Figure 4.5e). In 2011 and 2012 no relationship was found however, in 2013 Faith's PD was negatively correlated with soil mesofaunal biomass ($T = -2.226$, $P<0.05$). There was no relationship between Rao Quadratic Diversity and soil mesofaunal biomass when data was pooled across all three years ($T = 1.803$, $P = 0.071$) (Figure 4.5f). A significant negative relationship was only found in 2013 (not 2011 or 2012) ($T = -3.530$, $P<0.01$). Phylogenetic-Species-Evenness was positively correlated with soil mesofaunal biomass when data was pooled across the three years ($T = 2.629$, $P<0.01$) (Figure 4.5g). A significant relationship was identified in each individual year however the direction of the relationship varied. There was a positive relationship between PSE and soil mesofaunal biomass in 2011 ($T = 2.485$, $P<0.05$), and in 2012 ($T = 2.400$, $P <0.05$). Phylogenetic-Species-Evenness was negatively correlated with plant biomass in 2012 ($T = -3.476$, $P<0.01$).

Table 4.8 Generalised linear mixed model analysis of the relationship between different plant diversity indices and soil mesofaunal biomass. Overall refers to combining data across all years (2011-2013).

Index	Year	F value	T value	P value	Slope
Species Richness	2011	0.595	0.772	0.414	n.s.
	2012	0.174	0.417	0.709	n.s.
	2013	4.908	-2.215	<0.05*	negative
	Overall	18.606	-4.313	<0.001***	negative
Simpson's D	2011	1.201	1.096	0.279	n.s.
	2012	0.729	0.854	0.374	n.s.
	2013	5.045	-2.246	<0.05	negative
	Overall	0.287	-0.536	0.595	n.s.
McIntosh E	2011	3.759	0.193	0.055	n.s.
	2012	0.054	0.233	0.752	n.s.
	2013	3.818	-1.973	0.061	n.s.
	Overall	1.395	1.182	0.231	n.s
Berger-Parker	2011	1.768	-1.330	0.188	n.s.
	2012	0.570	-0.755	0.431	n.s.
	2013	4.780	2.186	<0.05*	positive
	Overall	0.134	0.366	0.716	n.s.
Faith's PD	2011	0.098	-0.314	0.729	n.s.
	2012	0.083	0.288	0.787	n.s.
	2013	4.953	-2.226	<0.05*	negative
	Overall	4.119	-2.029	<0.05*	negative
Rao Q	2011	4.204	2.050	<0.05*	positive
	2012	5.610	2.369	<0.05*	positive
	2013	12.464	-3.530	<0.01**	negative
	Overall	3.249	1.803	0.071	n.s.
Phylogenetic Species Evenness	2011	6.174	2.485	<0.05*	positive
	2012	5.766	2.400	<0.05*	positive
	2013	12.073	-3.476	<0.01**	positive
	Overall	6.907	2.629	<0.01**	positive

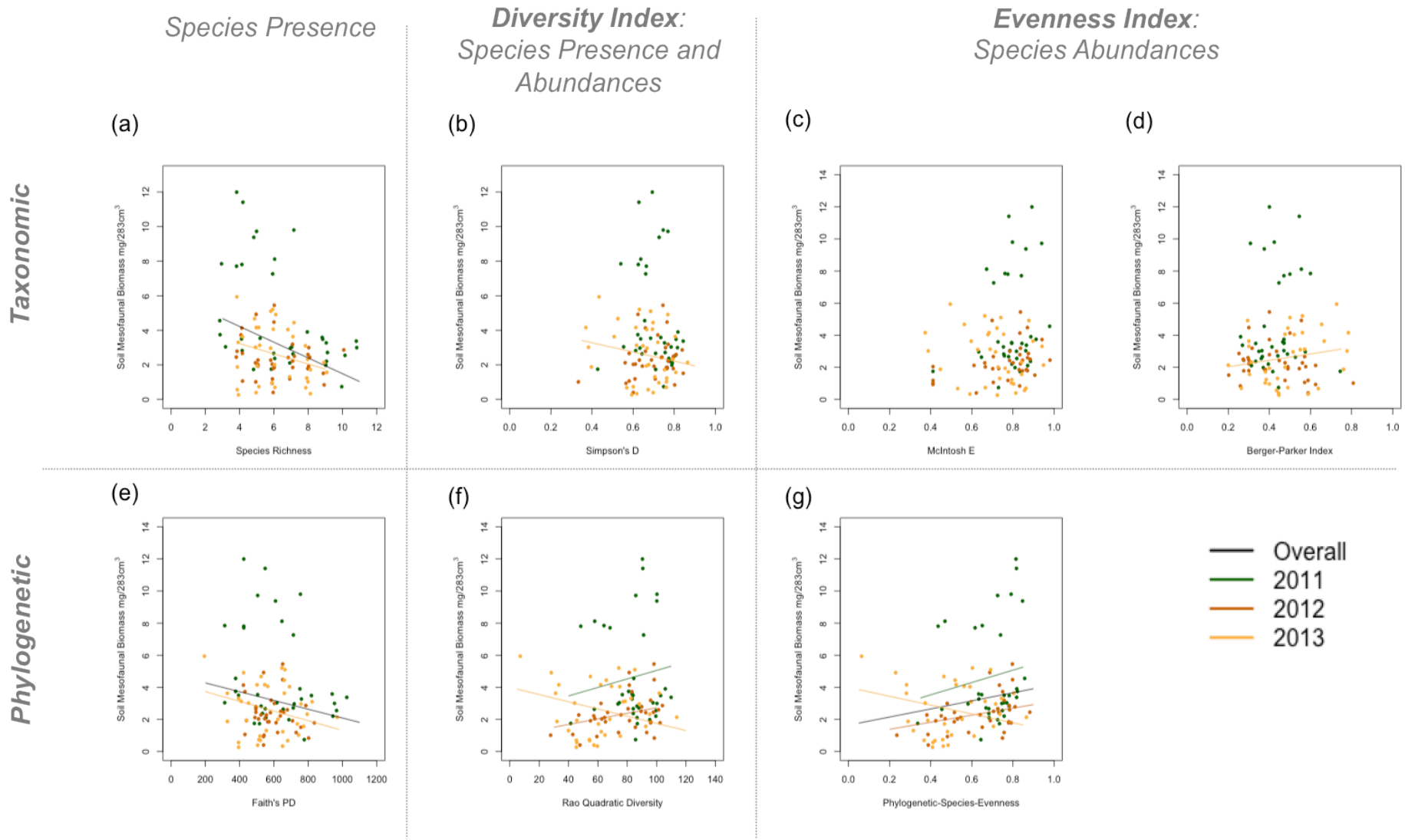


Figure 4.5 Relationships between different forms of plant diversity and secondary production (mg/283cm³ of soil mesofaunal biomass) across all three years and in individual years. Regression lines denote significant correlations. Taxonomic diversity measures: (a) Species Richness; (b) Simpson's D; (c) McIntosh E; (d) Berger-Parker Index; and Phylogenetic diversity measures: (e) Faith's PD; (f) Rao Quadratic Diversity; and (g) Phylogenetic Species Evenness. PSE is the only diversity measure that correlated with secondary production in each year and overall however the direction of the relationship varied temporally.

4.5 Discussion

Species richness did not vary annually. In 2013 there was less even representation thus increased dominance, and more phylogenetically clustered communities than in 2011 or 2012. Whilst species numbers did not vary significantly from year to year these results indicate communities are compositionally different as phylogenetic clustering increases and the communities become less even through time. Species richness was an appropriate proxy for Simpson's D, Berger-Parker, Faith's PD and Rao Q in the natural communities at Silwood. There was no correlation between species richness and McIntosh E, and only in 2013 with Phylogenetic-Species-Evenness. Phylogenetic clustering and dominance increase primary production. In 2013 depauperate communities with increased dominance and more phylogenetically divergent appeared to have lower secondary production. In contrast to this, in 2011 and 2012 communities containing more evenly spread species across the phylogeny and more evenly represented corresponded with increased secondary production.

4.5.1 Background variation in plant diversity across years

Species richness does not vary annually; in fact the median in all three years was 6 species per plot. The evenness indices and phylogenetic diversity index Rao Q indicate annual differences. Whilst the total number of species in a communities stays relatively stable how much space those individual species occupy within the community varies. More interestingly is how the communities are more phylogenetically clustered (lower Rao Q and Phylogenetic-Species-Evenness values) in 2013 compared with 2011 and 2012 illustrating how within a year or two years species were replaced with more phylogenetically similar species. If we assume phylogenetic distance is a surrogate for ecological differences then phylogenetic clustering indicates more ecologically similar species. This in turn means similar species occupying similar niches.

2011 was one of the driest years on record (Met Office Records 2012). Water limitation has a detrimental effect on some grass species (Knapp *et al.* 2001) and in 2011 it was apparent that the grasses in Silwood Park grasslands had suffered from the lack of moisture (*pers obs*). Without grasses to dominate the communities were filled with annual forbs and

smaller annual grasses. 2012 and 2013 were relatively average weather-wise if not more on the wet side (Met Office Records 2012) therefore larger perennial grasses became dominant. From 2011 to 2013 the floral composition shifted from an even spread of annual and perennial forbs and grasses to dominated by tall-growing perennial grass species. Whilst annual conditions did not impact the number of species within a community, they had a large impact on the compositional evenness and species identities. If we were to just use species richness as a measure, or in fact simply a taxonomical diversity measure, we would miss out this information on community dynamics.

4.5.2 Comparing richness with diversity metrics

As species richness is a limited measure it was surprising it correlated so strongly with Simpson's D, Berger-Parker, Faith's PD and Rao Q across all three years. McIntosh's E is the only diversity index where species richness plays a role in the calculation however there was no correlation found. The positive correlation between species richness and Faith's PD indicated with each additional species the phylogenetic distances increased incrementally indicating the addition of phylogenetically dissimilar species. Furthermore this means more ecologically dissimilar species thus higher species richness may lead to higher niche fulfillment. The strong linear relationship between species richness and Simpson's D illustrates how as more species are added to the community space is taken from the dominant species rather than the rarer species. As species richness increases in the natural communities at Silwood Park dominance decreases, species within the communities become more evenly represented, and they are more phylogenetically divergent.

Rather unsurprisingly when you remove species richness from the diversity measures (i.e. evenness indices) the relationship between number of species and evenness isn't as apparent. Species richness and PSE were positively correlated solely in 2013 and there was no relationship with McIntosh E at all. Notwithstanding, Berger-Parker index for dominance was negatively correlated with species richness in all three years. The simplest and most intuitive dominance/evenness measure which doesn't incorporate species richness at all mirrors that of the diversity index Simpson's D: as dominance increases species richness decreases. In the natural grassland communities at Silwood Park there is a strong correlation between number of species and evenness.

4.5.3 Diversity measures in the biodiversity-ecosystem function relationship

Diversity measures that incorporated presence/absence data alone did not correlate with primary production. Once we included abundance data or disregarded species number we saw a strong correlation, in particular with the phylogenetic diversity measures Rao Q and Phylogenetic-Species-Evenness in 2012 ($p<0.01$). Interestingly, the ranges for each of these measures were not significantly different from 2011 and 2013. In 2012, and over the three years, aboveground plant biomass corresponded with phylogenetic clustering and dominance. Communities dominated by more phylogenetically similar species, thus occupying similar niches were producing more. This indicates those species occupying these similar niches are highly productive species. This relationship is not universally found across all three years therefore I cannot state whether this relationship would be found again or remain overall temporally significant with the addition of further years. I can state, however, that this relationship is in complete contradiction to earlier findings (e.g Cadotte *et al.* 2011) where communities with a more even spread and more distantly related species were more productive.

In contrast to this, it appears plant diversity (in any measure) has more closely correlated with secondary production than with primary production. Both overall and in 2013, species richness and Faith's PD negatively correlated with secondary production (soil invertebrate biomass). In fact, except for McIntosh E, in 2012 additional species or increased evenness resulted in lower secondary production. Additionally, in 2012 the phylogenetic measures results all indicated that ecological dissimilarity lead to increases in secondary production, but for 2012 and 2013 the relationship flipped.

Perhaps the most interesting result is the importance of phylogenetic dissimilarity. Despite both Simpson's D and McIntosh E being closely correlated with their phylogenetic counterparts, the addition of phylogenetic information resulted in correlations where before there were none. In Chapter 2 I posited that as secondary production was negatively correlated with species richness it would be positively correlated with dominance in 2012 and this is the case for Simpson's D and Berger-Parker. Increased dominance does cause an increase in secondary production in 2012 but not in other years. There is no relationship

between secondary production and McIntosh E. When information on phylogenetic spread is added rather than evenness alone (Phylogenetic-Species-Evenness) strong correlations during each year and overall were found. The direction and strength of the relationship varied temporally but it was apparent nonetheless. Accounting for secondary production is dependent on the identity of the species present as well as their ecological similarities. In 2011 and 2012 communities with species more even represented and divergent across the phylogeny produced higher quantities of soil invertebrate biomass.

Earlier it was demonstrated that communities became less even and more phylogenetically clustered by 2013 (Rao Q and Phylogenetic-Species-Evenness decreased compared with 2011 and 2012). This would indicate that once dominance and phylogenetic clustering increase to a point the shape of the relationship changes. For presence/absence measures this goes from no relationship to a negative one. For the phylogenetic diversity and evenness measures it shifts from a positive to a negative relationship. In less dominated communities ecological variety (both abundances and phylogenetic) are important for soil invertebrates. Once communities become dominated by phylogenetically similar species, ecological variety is less important.

It is difficult to compare these results to other studies as most grassland studies experimentally manipulated species richness (e.g. Cedar Creek or Jena) and few have compared diversity measures in natural communities. Phylogenetic indices are heavily dependent on the identities of the species present therefore measures from these experiments may be more of an artifact of the experiment design rather than a true representation of the phylogenetic dissimilarity in the community. Despite this we have shown there are annual community dynamics beyond the number of species present but also species richness can be used as reasonable proxy for some of the other diversity measures. There are no general relationships between the diversity measures and primary production. Any apparent relationships illustrate point toward a negative relationship between phylogenetic divergence, dominance and primary production. Again, there is no general relationship between secondary production and the various diversity measures but ones that incorporate phylogenetic relatedness are more closely associated with soil invertebrate biomass. Depending on the year phylogenetic clustering and increased dominance correlates with both increases and decreases in secondary production.

4.6 Conclusion

As there are few studies where diversity of natural communities is measured and tested using a variety of metrics it is difficult to make wide-reaching statements that apply to diversity relationships in grasslands outside of Silwood Park. I have provided evidence that species richness may be a reasonable proxy for more complicated diversity measures. Despite this, diversity measures that incorporated information regarding phylogenetic relationship within the community were more closely correlated with both primary and secondary production. This study demonstrates how the direction and extent of the relationships is dependent upon how you define diversity, the function ordination (primary or secondary) and annual conditions.

Chapter 5
Discussion

5.1 Key results

This research aimed to test the link between plant diversity and ecosystem function in natural grassland communities. Using a natural diversity gradient present at Silwood Park I designed and implemented a 3-year experiment to measure function and stability in plant and invertebrate communities in both ambient and extreme weather conditions, to test whether variation is dependent upon plant diversity.

The extreme weather event (10-day flood) negatively impacted total soil mesofaunal biomass immediately after the event ceased and positively impacted soil collembola biomass and aboveground plant biomass (primary production) one year after. I found no general relationship between plant species richness and primary production; the relationship was only significant (positive) in 2013. Species richness in natural plant communities is a good proxy for many other diversity measures, including ones solely based on evenness. Phylogenetic clustering and increased dominance correlate with greater plant biomass and soil mesofaunal biomass in 2013 and lower soil mesofaunal biomass in 2011 and 2012.

5.2 Extreme weather event

In light of the predicted increases in frequency and severity of extreme weather events (IPCC 2012, Hansen *et al.* 2013) this research provides some evidence as to how a potential perturbation may impact a grassland community. I have demonstrated here how an extreme rainfall event has long-lasting impacts in a grassland system. Despite the severity of the experimentally manipulated flood (10 days continuous rainfall and ~ 4 weeks soil saturation) it had no overall impact on species richness and surprisingly had a positive effect on aboveground plant biomass one year after. Unfortunately due to the limited length of the experiment I do not know just how long-lasting the impacts are. The flooding caused very little compositional change compared with ambient conditions and unfortunately this

measure only accounts for numbers of species lost and gained and not the species identity. More water-tolerant plants but equal producers may replace those lost due to the undesirable wet conditions. Overall, it appears grassland plant communities may not be negatively impacted by an extreme precipitation event in the short-term. This is important to know as extreme weather events such as floods or storms are predicted to increase.

The flooding had the largest impact on soil invertebrates. Mite biomass significantly decreased immediately following the flood and collembola biomass increased one year after. Both of these results are easily explainable through their natural history therefore are unsurprising and again the majority of studies look at soil desiccation rather than water inundation. There is reasonable evidence that droughts negatively impact both mites and collembola and that collembola recovery more quickly (Lindberg & Bengsston 2004, Kardol *et al.* 2011). The results discussed in Chapter 3 mirror those of Tsiafouli *et al.* (2005); they identified how increased irrigation in forest soils negatively impacts mites and positively affects collembola, therefore adding further evidence of the taxon–specific responses in soil mesofauna to changes in climate.

It is difficult to compare my results with other studies as the majority of precipitation experiments tested the impacts of droughts rather than floods. One study that simulated extreme rainfall events (EVENT at the University Bayreuth) has yet to publish any results, despite multiple publications regarding the drought portion of the experiment. The TIGER experiment, carried out at Wytham, Oxfordshire, where rainfall was added during summer found the additional precipitation resulted in a higher sward (Staley *et al.* 2007). Precipitation extremes, in both directions, can impact the functioning and composition of communities; the response would be direction specific and dependent upon the extent of 'extremeness' of the extreme weather event. Nonetheless community ecologists should expand the currently narrow field of studying impacts of extreme events to include those such as heavy rainfall events.

5.3 Natural vs. artificial communities

A key component of my research was testing evidence-based theories in natural communities. I was interested in whether the well-established theories connecting diversity,

productivity and stability would clearly translate from the experimentally manipulated communities to self-assembled communities at Silwood Park. Important to compare my results not only with other studies that utilised natural communities, but also with those that manipulated diversity.

The results presented in Chapter 2 demonstrated both positive (2013) and non-significant relationships (2011 and 2012) between species richness and primary productivity. These results do not completely conform with either the strong positive linear correlation found in the sown communities at Jena, Biodepth or Cedar Creek, nor completely with the weakly negative to negligible relationships identified in natural communities (e.g. Grace *et al.* 2007). Stability of production in plants was found to be independent of species richness, which is contradictory to evidence from both sown (Tilman *et al.* 2001) and natural communities (Bezemer & van der Putten 2007). Previous evidence has indicated a relationship between species richness and stability regardless of whether it is positive or negative, but my results indicate this is not the case in naturally occurring communities at Silwood Park. My sampling technique (unable take repeated biomass samples) may be partly responsible for the contradictory results as I am looking at overall stability rather than individual community stability.

Extending my focus beyond plants to soil invertebrates elicited some interesting results. Species richness was negatively correlated with soil mesofaunal biomass in 2013, contradicting recent evidence from sown communities at Jena (Eisenhauer *et al.* 2013) and that of temperate grassland (Scherber *et al.* 2010). Whilst many studies found positive relationships between plants and invertebrates (e.g. Brown & Southwood 1983, Haddad *et al.* 2001, Wardle & Van Der Putten 2002) others found no correlation (e.g. Gastine *et al.* 2003, Salamon *et al.* 2004). The results of this study show the relationship is not straightforward as it ranged from negative to negligible. Many soil invertebrate communities are dependent upon species identity rather than variety making my results explainable when considering mesofaunal natural history.

Also integrating relatedness into the diversity-productivity relationship again resulted in evidence contradicting results found in other studies. Flynn *et al.* (2001) and Cadotte *et al.* (2009) identified PD as the most parsimonious predictor of primary production yet there

was no such relationship in the communities at Silwood Park. The best predictors of production were Rao's Quadratic Diversity and Phylogenetic-Species-Evenness, phylogenetic diversity measures that incorporated phylogenetic evenness. Both studies used data from sown communities where community composition does not follow natural assembly rules. Is it safe to assume that the phylogenetic diversity and soil invertebrate data collected from sown communities are really comparable those found in natural communities? Experiments that manipulate phylogenetic diversity or soil mesofaunal communities may provide further information on the importance of relatedness in the diversity-function relationship.

Despite fairly constant plant species richness (median of six species per plot remained throughout the experiment and following a flood) plant composition varied annually in ambient conditions. We cannot assume that plant communities remain exactly the same year to year, there are community dynamics that come into play (either through abiotic or biotic factors) that results in species losses and gains within these grassland communities. This aspect of community dynamics is sadly missed when studying sown communities. This measure, however, does not account for the identity of species lost or gained. The amount of compositional change was not dependent upon initial plant species richness therefore species-rich communities were not in fact more stable than depauperate ones.

Sown communities generally do not follow natural assembly rules and are artificially maintained, it is worth considering in the light of many of my contradictory results how much of the previous evidence of diversity-function-stability relationships is biased by the controlled nature of experiments. It is also problematic to try to draw general conclusions between experiments using natural communities as there is a level of context dependency. If money, time and effort were no object it would be interesting to run a similar experiment using (a) natural communities; (b) sown communities with the same species richness and composition; (c) sown communities with the same species richness and composition subjected to weeding; (d) sown communities with similar species richness but randomly assigned composition; and (e) sown communities with similar species richness and randomly assigned composition subjected to weeding. Similarly to NutNet, repeating this at multiple locations to identify site dependent factors.

Ecologists need to extend focus to look at how different diversity measures are related in natural, self assembled communities and how those diversity measures can be used in the biodiversity-ecosystem function relationship. Natural communities are complex and contain many confounding factors, but are not without identifying patterns and relationships. My research highlights the context dependency of the diversity-ecosystem function relationship in natural grassland communities.

5.4 Exclusion of species richness in the diversity-function-stability relationships at Silwood Park

With observed and predicted species losses it is imperative we understand how these losses impact ecosystem function and stability (Worm *et al.* 2006, Balvanera *et al.* 2006). Plant species richness is a poor predictor of aboveground plant biomass in grassland communities at Silwood Park. Despite the wealth of evidence from biodiversity-manipulated experiments (e.g. Tilman *et al.* 1997, Fridley 2001, Cardinale *et al.* 2001, Hector *et al.* 2002, Tilman *et al.* 2006) indicating a positive linear relationship between species richness and biomass, a significant relationship was only identified in one of the three years and not overall when all years were analysed together. Stability of production similarly was not dependent upon species richness in any of its forms (constancy, resistance and recovery). Species-poor communities did not experience greater compositional change (therefore stability) than species-rich ones. Not only does this contradict evidence from empirical studies but also from theoretical research (e.g. May 1972, Sinha & Sinha 2006). The importance of richness in community stability may be greatly overstated. My initial results suggest that species losses at Silwood Park would not necessarily have detrimental impacts on compositional stability or aboveground plant biomass production.

Whilst species richness performed poorly in the diversity-primary production relationship it appeared to be a reasonable proxy for more complex diversity measures. Plant species richness in natural grassland communities at Silwood Park strongly correlated with Simpson's D and Berger-Parker Index; as plant species increases evenness increases. Species richness, however, was deemed an "incomplete surrogate" for other diversity measures in a comparison between taxonomic diversity measures across six North American naturally assembled grasslands (Wilsey *et al.* 2005). My results indicated strong positive linear relationships between richness and Faith's PD and Phylogenetic-Species-

Evenness, similar to evidence from natural communities at Jasper Ridge, California (PAE rather than Phylogenetic-Species-Evenness was used) (Cadotte *et al.* 2010). Relationships between richness and diversity metrics were identified during every year of the experiment, allowing me a degree of certainty that they are fairly constant. The differences between my results and previous evidence that species richness is a poor surrogate measure lead me to suspect that taxonomic diversity relationships may be site dependent. We should note it is not advisable to compare diversity measures with species richness in sown communities as the relationship may be an artifact of scientists' choice of sown species.

Rather than species richness, evenness and phylogenetic relatedness were more related to aboveground plant biomass (primary production). Cadotte *et al.* (2012) demonstrated phylogenetic divergence was correlated with greater production whereas my results show the opposite; increased phylogenetic clustering and dominance correlate with increased primary production. Overall plant diversity measures were still weakly correlated with plant biomass.

Plant species richness was negatively correlated (overall and in 2013) with soil mesofaunal biomass. Again, plant species losses may not lead to reduced secondary production. The most parsimonious measure for diversity was phylogenetic-species-evenness. Phylogenetic-Species-Evenness positively correlated with secondary production across the three years and in 2011 and 2012 individually and negatively in 2013. Generally communities composed of more phylogenetically similar species and less even representation (increased dominance) contained greater mesofaunal biomass. Phylogenetic-Species-Evenness is an evenness measure, entirely separate from richness; Phylogenetic-Species-Evenness was one of the few measures not generally correlated with species richness in the grassland at Silwood Park. The best measure therefore for the diversity-secondary production relationship is completely independent of richness. Secondary production, more so than primary production, was dependent upon species relatedness. McIntosh E did not correlate with secondary production at all whereas the phylogenetic measure most similar to it (Phylogenetic-Species-Evenness) strongly correlated with production. For soil mesofaunal biomass it is not a case of species richness rather than the identity of species lost that is more important for functioning. Constancy of secondary production was dependent upon

primary production and as shown earlier primary production is independent of plant species richness.

One of two instances where richness significantly correlated with function was with primary production in 2013. During 2013 the relationship was positive and linear, as the grassland communities at Silwood Park are mature we could posit that improved resource use (niche complementarity effects) was the mechanism behind it (Marquard *et al.* 2009). However, without data on nutrient concentrations in the soil we cannot test this hypothesis. Sampling in 2013 alone would have lead me to agree with findings from Biodepth, Cedar Creek and Jena thus this study highlights the importance of multi-year data-collection. The second instance where species losses or gains could be important was resistance in total soil mesofaunal biomass and mite biomass to a perturbation and constancy and recovery of collembola biomass. Species losses would lead to lower biomass production in mites following an extreme weather event.

Overall richness proved to be an inadequate measure of plant diversity in the diversity-ecosystem function-stability relationship in the natural grassland communities at Silwood Park. Dominance and phylogenetic clustering explained both primary and secondary production more effectively. Dominance and phylogenetic clustering increased as species richness decreased leading me to assume species losses would not necessarily have detrimental effects on the functioning of grasslands at Silwood Park. As ecologists move away from species richness it is critical we understand which aspects of diversity best explain different ecosystem functions and therefore are important in the face of a changing climate.

5.5 Limitations

No experiment is perfect and without fault. Time, money and effort come into play when designing and running a large-scale experiment such as DExtER. The biggest limitation was the fact the experiment was only conducted at Silwood Park. I cannot draw broad conclusions from this experiment but say that my results provide evidence for or against those previous studies. Similarly, plot size and replication was limited by available space at Silwood. With greater plot size (therefore larger communities and potentially larger

richness ranges) we may have seen different results. Given the level of context and temporal dependencies, experiments such as this in natural communities under ambient conditions cannot be truly reproduced. The results may be limited to conditions in 2011, 2012 and 2013 and only at Silwood Park.

It is not an exhaustive study. I looked at a select number of diversity measures, only a couple of functions, and only one type of extreme weather event at a particular level. Even within this limited range I found evidence that the diversity-function-stability relationship is heavily dependent on the diversity measure, differs greatly between primary and secondary productivity, and dependencies vary with different plant community attributes.

It is important to take note that ambient conditions varied greatly from year to year, therefore control conditions were not really "normal" conditions. In 2011 (the first year of the experiment) most of the UK experienced long periods of drought. When soils are dry plants conserve water through stomatal closure, senescence and root dieback (Chaves *et al.* 2003, Faroq *et al.* 2009). This would explain the very low biomass amounts seen in 2011 as plant growth was affected by water limitation. Interestingly the highest species richness values were also found during that year, the naturally occurring drought had negatively impacted biomass and not species richness. Ecologists running the EVENT experiments in Germany circumvent this by having a true control treatment, an "ambient" treatment where monthly average conditions are applied to the plots, and an extreme treatment.

Another limitation is the "extremeness" of the extreme weather event. Whilst it would be considered fairly extreme by UK standards (calculated as 20 years of continuous rainfall in 10 days) it did not impact all aspects of the community. Smith (2011) states for an extreme event to be considered excessive it must evoke an extreme response. Unfortunately the extreme precipitation event did not impact all aspects of the community, time and equipment permitting it would have been better to conduct a range of precipitation extremes.

Lastly unlike experiments using sown communities the DExtER experiment was limited by the natural gradient of species richness. Fortunately across the ~100acres at Silwood Park there was a fair range (4-14 species per m^2) however replication was lower for plots with

either very high or very low species richness. The range observed in my experiment mirrored that of the Biodepth site at Silwood Park therefore should not necessarily greatly impact the results.

5.6 Future Research

The results presented in this thesis only use aboveground plant biomass as a proxy for ecosystem function however in order to compare the results to further research it is important to look at alternative types of function used in the literature. Another widely used measure is nutrient availability and cycling. Soil cores were taken in 2012 and 2013 and stored (either dried or frozen) for nutrient analysis. Sarah Pierce (co-supervised by Dr Tom Bell and Dr Sally Power) will process the samples therefore data to look at the relationship between species richness and an alternative (but widely used) type of function will be available. When using an alternative measure of function will the same diversity-function relationships identified in Chapters 2 and 4 be present in the natural communities at Silwood Park? It could be posited that, as with the different results stemming from the various diversity measures, different ecosystem function types would lead to different biodiversity-ecosystem function relationships. By incorporating another function this experiment could be compared to a wider range of research therefore identifying further differences or similarities in natural communities.

5.7 Conclusions

Despite the limitations associated with the experiment this research identified some very real, justifiable, tangible relationships. Not only do the results not provide further evidence for accepted evidence-based theories, in some cases they directly contradict previous relationships. The main implication of this work is for ecologists to test evidence-based theories in naturally occurring communities. What use is a theory or prediction if it is not tested under natural conditions whereby other factors not considered in our carefully manipulated experiments come into play? Natural communities are complex systems, but as I have shown here they are not completely idiosyncratic. I have provided evidence of strong relationships between diversity, function and stability in natural communities. However in order to do this I had to extend previous definitions of diversity and expand my focus beyond plant-based functions.

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Appendix 1

Appendix 1.1: Interpreting the stability of biomass outputs as it varies with species richness.

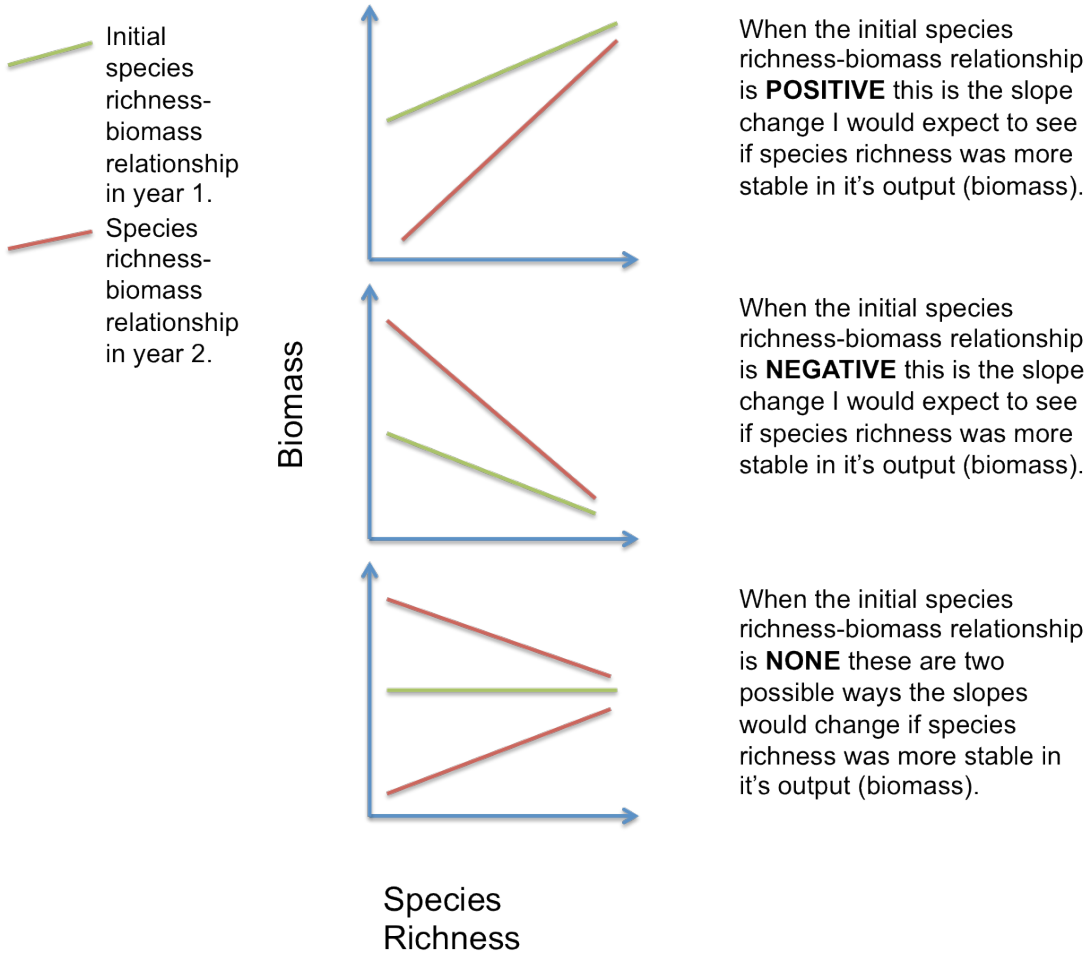


Figure 1A A guide for interpreting how the richness-biomass relationship may change if stability of biomass output varies with richness. Potential scenarios for how the relationships between species richness and biomass might change from year to year or following disturbance if the stability of biomass output is positively correlated with species richness. The greater the distance between the relationship slopes in year 1 and year 2 the greater the variation in biomass output thus greater instability. If the slopes are not significantly different (equal distance between each along the full length of the slope) then stability of biomass output varies independently of species richness. This is not an exhaustive approach

Appendix 1.2 Plant species richness – biomass relationships

Table 1A Percentages of the total variances attributed to random factors in the generalised linear mixed model analysis of the plant species richness and biomass relationships in individual years and when pooling all three years together (overall)

Year tested	Site	Year
2011	62	n/a
2012	68	n/a
2013	51	n/a
Overall	32	37

Appendix 2

Appendix 2.1 Collembola found in samples in experimental plots

Table 2A Mean weights of 30 individuals for each collembolan family identified in experimental plots

Family	Mean weight (μg)	s.d.
Isotomidae	8.876	1.035
Tomoceridae	13.986	0.662
Sminthurididae	3.019	0.058
Sminthuridae	3.004	0.865
Poduridae	7.365	0.999
Onychiuridae	7.347	1.347
Neelidae	9.031	1.366
Neanuridae	7.449	0.098
Katiannidae	3.222	1.185
Hypogastruridae	10.212	2.223
Entomobryidae	5.793	0.757
Dicyrtomidae	3.101	0.801

Appendix 2.2 Mite morphotypes found in samples in experimental plots

Table 2B Mean weights of 30 individuals for each mite morphotype identified in experimental plots

Morphotypes	Mean weight (μg)	s.d.
1	49.562	5.852
2	15.211	2.489
3	26.886	5.671
4	27.736	4.411
5	8.564	1.001
6	11.149	1.032

Appendix 2.3 Relationship between plant species richness and soil invertebrate biomass

Table 2C Percentages of the total variances attributed to random factors in the generalised linear mixed model analysis of the relationship between plant species richness and soil invertebrate biomass. Overall refers to combining across all years (2011-2013).

Invertebrate biomass	Years tested	Site	Year
Total Soil Mesofaunal Biomass (mg/283cm^3)	2011	88	n/a
	2012	75	n/a
	2013	82	n/a
	Overall	39	29
Mite Biomass (µg/283cm^3)	2011	90	n/a
	2012	77	n/a
	2013	83	n/a
	Overall	40	30
Collembola Biomass (µg/283cm^3)	2011	<1	n/a
	2012	21	n/a
	2013	2	n/a
	Overall	5	<1

Appendix 3

Appendix 3.1 Relationships between species richness and other diversity metrics.

Table 3A *Percentages of the total variances attributed to random factors in the generalised linear mixed model analysis of the correlation between plant species richness and diversity metrics during each year (overall includes data pooled from all three years).*

Index	Year tested	Site	Year
Simpson's D	2011	<1	n/a
	2012	52	n/a
	2013	<1	n/a
	Overall	5	4
McIntosh E	2011	<1	n/a
	2012	59	n/a
	2013	<1	n/a
	Overall	16	5
Berger-Parker	2011	<1	n/a
	2012	52	n/a
	2013	11	n/a
	Overall	16	2
Faith's PD	2011	58	n/a
	2012	12	n/a
	2013	47	n/a
	Overall	29	2
Rao Q	2011	<1	n/a
	2012	61	n/a
	2013	22	n/a
	Overall	<1	24
Phylogenetic Species Evenness	2011	10	n/a
	2012	59	n/a
	2013	23	n/a
	Overall	<1	25

Appendix 3.2 Diversity-function relationships using different diversity measures

Table 3B Percentages of the total variances attributed to random factors in the generalised linear mixed model analysis of the relationship between different plant diversity indices and aboveground plant biomass. Overall refers to combining data across all years (2011-2013).

Index	Year tested	Site	Year
Species Richness	2011	54	n/a
	2012	67	n/a
	2013	52	n/a
	Overall	32	36
Simpson's D	2011	56	n/a
	2012	61	n/a
	2013	55	n/a
	Overall	31	38
McIntosh E	2011	54	n/a
	2012	48	n/a
	2013	56	n/a
	Overall	30	39
Berger-Parker	2011	57	n/a
	2012	67	n/a
	2013	56	n/a
	Overall	32	37
Faith's PD	2011	62	n/a
	2012	68	n/a
	2013	61	n/a
	Overall	34	35
Rao Q	2011	58	n/a
	2012	57	n/a
	2013	56	n/a
	Overall	29	37
Phylogenetic Species Evenness	2011	58	n/a
	2012	57	n/a
	2013	56	n/a
	Overall	20	38

Appendix 3.3 Diversity-function relationships using different diversity measures

Table 3C Percentages of the total variances attributed to random factors (site and/or year) in the generalised linear mixed model analysis of the relationship between different plant diversity indices and soil invertebrate biomass. Overall refers to combining data across all years (2011-2013).

Index	Year tested	Site	Year
Species Richness	2011	75	n/a
	2012	71	n/a
	2013	82	n/a
	Overall	39	27
Simpson's D	2011	72	n/a
	2012	71	n/a
	2013	81	n/a
	Overall	38	24
McIntosh E	2011	89	n/a
	2012	77	n/a
	2013	75	n/a
	Overall	40	22
Berger-Parker	2011	87	n/a
	2012	71	n/a
	2013	81	n/a
	Overall	39	24
Faith's PD	2011	81	n/a
	2012	70	n/a
	2013	85	n/a
	Overall	37	26
Rao Q	2011	81	n/a
	2012	73	n/a
	2013	87	n/a
	Overall	42	21
Phylogenetic Species Evenness	2011	88	n/a
	2012	71	n/a
	2013	87	n/a
	Overall	42	20