Exploring the relationship between restored ecosystem function and species composition: a meta-analysis

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Abstract

The idea that biodiversity confers higher levels of ecosystem functioning has been used as an argument for the conservation of biodiversity, and the relationship between these variables has been well researched. Ecosystem restoration often aims to restore former ecosystem functioning as well as specific species assemblages, not just biodiversity. In many cases monitoring programmes lack funds to measure all these aspects and often assume relationships between these variables; however, these relationships remain largely untested. In this thesis, I undertake the first ever meta-analysis of studies measuring ecological function and species composition in restored sites to test whether such a relationship exists. Bray-Curtis similarity measures were used to compare species composition for each site compared to multiple reference sites. Indicators of ecosystem function were also compared to reference sites, taking into account natural variation within reference sites. A weak relationship between ecosystem function and species composition was found, and it differed between different groups of ecosystem functions. Live plant biomass and structural framework ecosystem functions increased in similarity to reference sites as species composition also increased in similarity to reference sites. Nutrients, soil attributes and interactions between biotic component as well as litter and deadwood production, showed little association with species composition, with levels of ecosystem functioning showing little change as species composition became closer to reference sites. Variables relating to nutrients, soil attributes, and biotic interactions were always similar to intact sites regardless of the degree to which species composition had been restored. Live plant biomass, litter and deadwood production, and framework ecosystem functions, however, often did not reach reference levels of functioning, even when full species composition was restored. This analysis found that overall the shape of the relationship indicates redundancy in species composition, suggesting that increasing similarity in terms of species composition initially increases ecosystem function; however beyond a point, additional similarity does not further assist in the restoration of ecosystem function to reference levels of similarity. The main difference to biodiversity ecosystem function relationships comes with the fact that all ecosystem functions were not returned even when restored sites had similar species composition to reference sites, indicating that something, possibly time, is limiting the return of full ecosystem function to restoration sites. Finally, this research indicates that the relationship between species composition and ecosystem function is not consistent and it would be unwise to use species composition or ecosystem function as proxies for one another.

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Chapter 1 – Measuring ecological composition, structure and function in assessing restoration success

Human society relies heavily on natural resources such as timber, oil, minerals, and many services which are provided by intact ecosystems such as fresh water, pollination, and soil production. If society wishes to continue to extract natural resources, as well as benefit from these services, we must find sustainable ways to extract resources whilst minimising damage and conserving the dwindling remaining intact ecosystems. It is also imperative to repair degradation that has already occurred, as well as that which may happen in the future. Ecological restoration offers a solution to assist with the recovery of degraded ecosystems as well as conserve biodiversity. To achieve this, ecological restoration must not only restore vital functions and processes to ecosystems, but also restore similar assemblages of species than prior to degradation. Research on how species richness relates to ecosystem function is abundant, however, if these patterns also hold true for restoring a specific composition of species is yet unknown.

In this thesis I examine the relationship between ecosystem function and species composition in the restoration of degraded ecosystems. To understand why this relationship is important and how it fits into the context of restoration ecology, as well as broader ecological theory, I will first explain what ecological degradation is, its extent and the development of ecological restoration as a discipline. I will then review how restoration has been assessed with respect to species composition, ecological structure, function, as well as the difficulties that lie in using such standards for success. Finally, I will explore how research on biodiversity and ecosystem function relates to restoration ecology, as well as how meta-analytic techniques are well suited to assist in answering questions on this topic.

What is degradation?

Many definitions exist for the term 'degradation', and even within the world of restoration ecology, the word is not used consistently. For example, Whisenant (1999) considered biophysical degradation to be when ecosystems lose their ability to retain essential resources such as water and nutrients, whereas Harrington (1999) considers degradation as alterations in species present, regardless of their effect on processes.

According to the Society for Ecological Restoration (SER), degraded, damaged, transformed, or destroyed ecosystems are defined depending on the type of change that has occurred (gradual, abrupt, reversible, or irreversible) (SER 2004). Throughout this thesis, I classify degraded or damaged ecosystems as a deviation from an intact ecosystem to a point at which it can no longer recover without human assistance (either through having to remove the degrading processes before recovery can occur, or actively assisting in the recovery itself). This is differentiated from a short-lived disturbance event, from which an ecosystem may recover unaided through the process of succession.

Global extent of degradation

As can be expected given the differences in definitions of degradation, the global estimates of the area of degraded land worldwide vary. Oldeman et al. (1991) estimated that about 15% of the world's soil has suffered from degradation, with the majority of these soils showing water and wind erosion and nutrient depletion. In 2005, the Millennium Assessment Report estimated that 20% of the worlds drylands had degraded soils (MEA 2005). Potapov et al. (2008) estimated that only 23.5% of forests worldwide remain intact, although what he considers 'intact' may not necessarily align with degradation by other definitions. Accurate global estimates are complicated further by difficulties in measuring degradation at such a large scale. Most published figures tend to be ecosystem specific (e.g. only for forests) and many estimates are based on expert opinions rather than empirical estimates. The most recent and comprehensive estimates for worldwide degradation across different land types was made in the State of Land and Water Resources (SOLAW) report by the Food and Agricultural Organization of the United Nations (FAO 2011a). The report categorises land based on the ability of ecosystems to deliver goods and services, as well as the severity of the degrading process. This report estimates that 25% of the world land area is highly degraded (or being degraded quickly) and a further 8% is moderately degraded (FAO 2011a). Although all these above estimates may differ, they all indicate that a large proportion of the worlds ecosystems are either already degraded or at risk of becoming degraded.

In addition the State of the World's Forest Report in 2011 has indicated that the worldwide rate of deforestation has slowed between 1990-2000 and 2000-2010 (FAO 2011b). Even with current levels of degradation slowing and reversing in some areas, there is still considerable scope for improvement in terms of restoring the world's ecosystems. Indeed, the SOLAW report estimated that despite high degradation worldwide, 10% of the land is considered to be 'improving' or reversing degradation (FAO 2011a). Restoration is not just necessary as a channel through which to conserve biodiversity, but is also necessary to human society as we rely heavily on the goods and services provided by intact ecosystems.

Restoration ecology

The practice of restoring ecosystems is not new. Activities such as rangeland improvement and erosion control have been practised by agriculturists for centuries. The field of ecological restoration first received widespread recognition in the 1980s, and since that time its definition and goals have seemingly changed several times. Some early restoration was considered to be the return to pre-disturbance conditions in regard to certain characteristic species being present (Whisenant 1999). Bradshaw (1996) also recognised that perhaps this early form of restoration should be referred to as 'habitat' restoration, rather than 'ecosystem' restoration which, implies incorporating the fundamental processes by which ecosystems function. Currently, the most widely accepted meaning of ecological restoration is defined as "the intentional activity that initiates or accelerates the recovery of an ecosystem with respect to health, integrity and sustainability" (SER 2004).

Since the 1980s, restoration ecology has a matured as a discipline of research-based applied science with a broadening ecological and conceptual framework (Hobbs & Harris 2001; Young et al. 2005). Since the early 1990s the number of published papers focused on ecological restoration have steadily increased and, as of 2010, form approximately 5% of all ecology articles published (Young et al. 2005; Brudvig 2011). Restoration research is deeply rooted in ecological concepts such as competition, succession, niche theory, recruitment, facilitation and mutualisms (Young et al. 2005). Restoration studies provide an opportunity to inform ecological understanding by providing a platform to test theories using manipulative experiments in natural ecosystems (Bradshaw 1984).

Understanding the dynamics of plant community development has considerable ramifications for the efficacy of applied restoration projects. This knowledge can guide how best to assist ecosystem recovery through an appreciation of the effect of restoration actions on the trajectories and endpoints for communities. Theories on succession and state-transition models dominated early restoration research (Milton et al. 1994; Young et al. 2001). These models appealed to restoration practitioners as they assume a predictable pathway along which the community will develop on its way back to pre-disturbed state. Ecological thresholds, which limit ecosystems passing from one state into another, have been explored through theories about ecosystem stability and resilience to disturbance (e.g. Holling 1973). Observation of restoration projects that seem to be 'stuck' at a certain successional stage has led to the inclusion of these thresholds concepts into restoration ecology(Milton et al. 1994; Whisenant 1999). Assembly theory and alternative stable states have also added to ideas about plant community development in the process of restoration. Assembly theory, which stems from island biogeography theory (MacArthur & Wilson, 1967), considers the restrictions and constraints that limit which species end up in certain communities from the larger species pool (Keddy 1999). Alternative stable state theory suggests that multiple endpoints with different species compositions may result for any community (Beisner 2003).

One particularly important area of research area that restoration ecology is well placed to inform and vice versa, involves theories on the relationship between biodiversity and function (Cortina et al. 2006). This area of research has continued to receive a large amount attention over the past few decades, as it is explores a question at the heart of biological conservation, "is biodiversity important for the functioning of ecosystems?" (for reviews see Schwartz et al. 2000; Schmid et al. 2009). Biodiversity and function relationships are frequently examined by exploring changes in ecosystem function as the numbers of species within an ecosystem are varied experimentally (Naeem et al. 1995). Restoration ecology offers a novel opportunity to examine this relationship, by monitoring how ecosystem function changes in large-scale field experiments where species increase as the ecosystems is restored.

Restoration goals and measurements of success

Restoration ecology has been criticised for being too concerned with the past and "at best a fiction and at worst motivated by a particular dominant cultural perspective" (Davis 2000). Some have argued for a shift away from the 'past-orientated and idealistic' restoration paradigm (Choi 2007). Instead, Choi (2007) suggested that restoration ecology goals should focus more on the functioning of ecosystems rather than resembling a past state.

Ehrenfeld (2000) described four main routes which led to the development of restoration ecology goals. The first originated from conservation biology goals with an emphasis on threatened species or communities. The second stemmed from geography and landscape ecology with an emphasis on landscape scale ecosystem management. The third came from wetland management and centred on restoration of an ecosystems functions and services. The fourth comes from attempts to manage extremely degraded or toxic land caused by extractive activities such as mining, and focuses on stabilisation of soils and halting further degradation. With such different themes, it is unsurprising that forming universal goals for restoration projects is difficult.

Three different levels of restoration goals were suggested by van Diggelen et al. (2001), which were dependent upon the ambitions of the individual projects. The first level, 'reclamation', involves increasing the biodiversity in highly degraded sites. The second level, ‘rehabilitation’, involves restoring important functions and services, and the third level, ‘true restoration’ combined the first and second levels aiming to reinstate a former functioning ecosystem as well as its components.

Whether restoration focuses on species, ecosystem services, or ecosystem functions, all have their own advantages and disadvantages (Ehrenfeld 2000). For example, a focus on one species can lead to achievable goals and outcomes, but may be to the detriment of other species (Ehrenfeld 2000). Using ecosystem functions alone as a goal can lead to ecosystems that can be very different from pre-degradation states and often maximising one service can lead to declines in some species and/or other services (e.g. restoring for timber production might be to detriment of shrub species). Restoring for ecosystem functions can not only provide important services for humans such as clean air and water and, but can also help with the conservation of biodiversity. One of the main criticisms of using function-based goals for restoration is that poor definitions of what constitutes an ecosystem processes and functions exist (Goldstein 1999). Another problem concerns the variability and heterogeneity in these process and functions even within ‘natural’ ecosystems (Ehrenfeld 2000).

The Society for Ecological Restoration (SER) suggests that goals or targets should be based on the definition that: “an ecosystem has recovered – and is restored – when it contains sufficient biotic and abiotic resources to continue its development without further assistance or subsidy. It will sustain itself structurally and functionally. It will demonstrate resilience to normal ranges of environmental stress and disturbance; it will interact with contiguous ecosystems in terms of biotic and abiotic flows and cultural interactions” (SER 2004).

Once restoration goals have been set, assessing their success provides another challenge to restoration ecology. The SER definition requires “sufficient biotic and abiotic resources” to be able to “sustain itself structurally and functionally”, “demonstrate resilience” and “interact with contiguous ecosystems”. None of these are sufficiently well defined to allow measurement. The SER goes further to define nine attributes of restored ecosystems that give more guidance on to how one could assess whether an ecosystem has been restored. The nine ecosystem attributes of a restored ecosystem are:

1. Characteristic assemblage of species that provide appropriate structure.
2. Consists of indigenous species.
3. All functional groups necessary.
4. Physical environment capable of sustaining reproducing populations of species necessary for continued stability or development.

5. The restored ecosystem apparently functions normally for its ecological stage of development and signs of dysfunction are absent.
6. Suitably integrated into larger ecological matrix, interacts with abiotic and biotic flows and exchanges.
7. Potential threats to the health and integrity of restored ecosystem have been eliminated or reduced.
8. Sufficiently resilient to endure normal periodic stress events that serve to maintain the integrity of ecosystem.
9. Self-sustaining to the same degree as its reference ecosystem and has the potential to persist indefinitely under existing environmental conditions.

The first three points could be placed in a single category of composition and structure. Attribute four, five, six, eight, and nine are related to how the ecosystem functions, is self sustaining and resilient. Structure, composition, and function are also suggested by other authors as components that should be measured for restoration success (Hobbs & Norton 1996; Higgs 1997; Ruiz-Jaen & Aide 2005). All of the attributes proposed by SER, however, are vague on definitions and challenging to assess. A few other suggestions include measuring vigour, durability, and resilience (Higgs 1997; Rapport et al. 1998). Difficulty arises when trying to find methods to measure these attributes in ways that are cost effective and simple enough for restoration practitioners to realistically implement. Measuring ecosystem composition, structure, and certain functions is well established in ecology, though ways in which to measure vigour, durability, and resilience are less clear.

Reference sites

In order to be able to measure how well a site has been restored in terms of species composition and functional attributes, it must be compared to a reference site. The selection of appropriate reference sites is an ongoing issue in restoration ecology (White & Walker 1997). Few sites have adequate data concerning pre-degradation conditions, so often another site that represents a similar habitat is chosen. It is impossible to find a reference site that represents an exact match and often appropriate reference sites may be located away from restoration sites when widespread degradation and land-use change has occurred. This is problematic considering these sites may differ in soils, climate, biogeography and history (Beauchamp & Shafroth 2011). There are also cases where ‘natural’ and undisturbed reference sites do not exist due to a long history of human disturbance and manipulation. So the best approach is to choose multiple sites that best represent what the ecosystem may have resembled pre-degradation and define a suitable range of variability for parameters monitored in restoration sites (Holl & Cairns 2002).

Even within a reference site, high levels of variability in both species composition and ecological processes may occur (White & Walker 1997). Sites may vary spatially, over environmental gradients, as well as temporally through seasons, long-term climatic trends as well as through disturbance and succession (White & Walker 1997). This further highlights the need for multiple reference sites to try and encompass natural variation, as well as the need to sample reference sites across sufficient scales (Holl & Cairns 2002). When comparing restored sites to reference, it is important to always consider this, for example regarding restoration sites as recovered if the measurement of processes within levels of variation of reference sites, rather than simply reaching the mean level (Morgan & Short 2002).

Ecological composition, structure and function

Ecological/species composition refers to the make-up of the assemblage of species within the ecosystem, and pertains not only to the species present, but also their relative abundances. However, often only aspects of composition like species richness, rather than information on the abundance of each species, are measured and used inappropriately as proxies for species composition (Ruiz-Jaen & Aide 2005)

Another commonly used term in restoration ecology is ecological structure. However, clear definitions do not exist for this term. In some cases, ecological structure refers to the make-up of species present (Ehrenfeld 2000), which is what I refer to as species composition. The term ecological structure has also been referred to as the physical biological components such as stem density, tree height, canopy cover and occasionally even biomass and leaf litter (Ruiz-Jaen & Aide 2005). These attributes are, however, often also considered ecosystem functions by others (Schwartz et al. 2000). I believe that it is more sensible to place these into the latter category as all of these can be independent of the species composition themselves, serve functions within the ecosystem such as providing habitats, changing water infiltration rates, microclimates, driving decomposition, and carbon and energy accumulation. Despite these confusions, inconsistencies and overlaps, the term ecosystem structure, especially coupled with ecosystem function, continues to be pervasive in the field of ecology.

There is no lack of recognition that the ways in which ecosystems function and the processes that occur within such ecosystems are vitally important when attempting to understand or restore them (e.g. Bradshaw 1996; Ruiz-Jaen & Aide 2005; Grant et al. 2007).

Despite this recognition, the field of research continues to suffer from vagueness in defining what constitutes an ecosystem function or process (Ehrenfeld 2000). Ecosystem functions have been loosely defined as factors which "cause an ecosystem to be self-renewing" (SER 2004) or "changes in energy and matter over time and space through the interplay of biological activity and abiotic factors" (Montoya et al. 2012).

This non-unified definition, however, has not stopped research into how ecosystems function. Another issue comes with the interactive effect of ecosystem composition and structure with function. When these relationships are explored, ecosystem functions are normally depicted on the y-axis, although it has also been recognised that function can be a result of composition and structure as well as a causative factor (Ehrenfeld 2000).

Although there is no clear definition of ecosystem function – there appears to be agreement from many authors on particular attributes that are considered indicators of ecosystem functioning. Some of the most common attributes considered to be ecosystem functions are biomass, productivity, nutrient cycling and storage, decomposition and structural aspects of soil and ecosystems (see Appendix I for examples of attributes considered ecosystem functions by various papers).

Attempts to group ecosystem functions have been made. Ruiz-Jaen & Aide (2005) combine ecosystem functions into 'biological interaction', 'nutrient pools' and 'soil organic matter'. However, they also grouped vegetation structure (cover, density, biomass, height and litter) separately, though all of these have been considered ecosystem functions by other authors (Appendix I). Ehrenfeld (2000) tended to group ecosystem process and function into three main groups – 'material flows', 'physical elements' and 'biological structure'. 'Material flows' comprises energy flow (so functions to do with the fixation of solar energy and accumulation of biomass) as well as flows of nutrients and water. 'Physical elements' have more to do with physical aspects such as disturbance regimes, soil formation and landscape structure. The third grouping, 'biological structure', included any biological aspects such as interactions between organisms.

The main ecosystem functions that have been studied in restoration ecology include biomass, nutrient pools and nutrient cycling, leaf litter accumulation, structural aspects and biotic interactions. Broader groupings used within this study are: 1) nutrient pools and cycling '*nutrients*', 2) biomass and productivity '*live biomass*', 3) soil characteristics '*soil*', 4) litter, deadwood and decomposition 'litter', 5) structural biological characteristics '*framework*', 6) interactions between species and/or environment '*biotic interactions*'.

Detailed explanations of these groupings will be further discussed in the Methods section of Chapter 2.

Relationship between species composition and ecosystem function

Much research has been undertaken investigating the relationship between biodiversity and ecosystem function (BEF) (for reviews see Schwartz et al. 2000; Schmid et al. 2009). These studies have mainly been concerned with what happens in ecosystems when species are lost and certain hypotheses have been used as arguments for the importance of maintaining high levels of biodiversity. The main hypothesised BEF relationships are presented in Figure 1 but can be further condensed into three categories 1) that biodiversity confers stability, 2) that many species are redundant and 3) that impacts are context dependent and therefore unpredictable (King 2009). Some empirical evidence for the shape of the relationship between ecosystem functioning and biodiversity has been found in support of redundant, positive as well as idiosyncratic BEF models (Schwartz et al. 2000).

The hypotheses falling into the first category all propose that higher levels of biodiversity mean higher levels of ecosystem function (linear, keystone and to an extent rivet from Figure 1). Positive relationships between biodiversity and ecosystem functioning have been demonstrated, though the mechanism behind this is unknown (Loreau et al. 2001). Two proposed, and not necessarily mutually exclusive, explanations are ‘niche complementarity’ and ‘dominance’ (Loreau et al. 2001). Niche complementarity proposes an emergent property whereby species interact together such that the sum of their effects on ecosystem function is greater than singularly, so that with greater biodiversity comes more complimentary interactions and higher overall function (Loreau et al. 2001). Dominance however, suggests that some species contribute more to ecosystem functioning than others, so with higher numbers of species, the mix is more likely to contain these ‘dominant’ species and so functioning is higher (Loreau et al. 2001).

Hypotheses about redundancy (the second category) suggest that species are often so similar to one another in terms of their roles in the ecosystem that as long as major functional groups are present, a loss of individual species may have little effect on ecosystem functioning. The rivet hypothesis also has elements of redundancy, as the loss of species may have little effect on functioning, although only up until unknown tipping points, where are large impact may be seen. The implications for conservation biology if this relationship is found to be consistently true are substantial (Schwartz et al. 2000). It would mean that ecosystems may lose some species without depreciable effects on the systems functioning. A review of expert opinions on the relationship between biodiversity and ecosystem functioning revealed that the redundancy relationship were the most expected type of relationship for most types of ecosystem processes (Schläpfer et al. 1999). Even if the redundancy relationship were universal, we do not know at what point the small incremental losses in ecosystem function would have ramifications. Another argument for the conservation of species, given a certain level of redundancy is that higher levels of biodiversity are needed for ecosystem multifunctionality (Sanderson et al. 2004). This states that the species needed to sustain one function may differ from the species needed to sustain another different function, so a higher number of species overall is required to maintaining multiple functions within an ecosystem. Hector & Bagchi (2007) supported this idea of mulitfunctionality by demonstrating that higher numbers of species were required to maintain multiple functions compared with single processes.

The final third category of hypotheses, simply states that these relationships are very context dependent, variable, and unpredictable. There is a considerable body of literature supporting this 'idiosyncratic' response hypothesis (e.g. Naeem et al. 1995; Slade et al. 2007).

Most recent developments and research into BEF models has shifted its focus from biodiversity measures (using species as the unit of measure) to functional diversity measures (Cadotte et al. 2011). Functional trait diversity, the diversity of different traits within a community, has the potential to have a much more meaningful role, as the causal relationship to ecosystem function is more obvious (McGill et al. 2006). Functional diversity is showing promise as a new measure of true biodiversity and being successfully incorporated into many field of ecological research (Reiss et al. 2009).

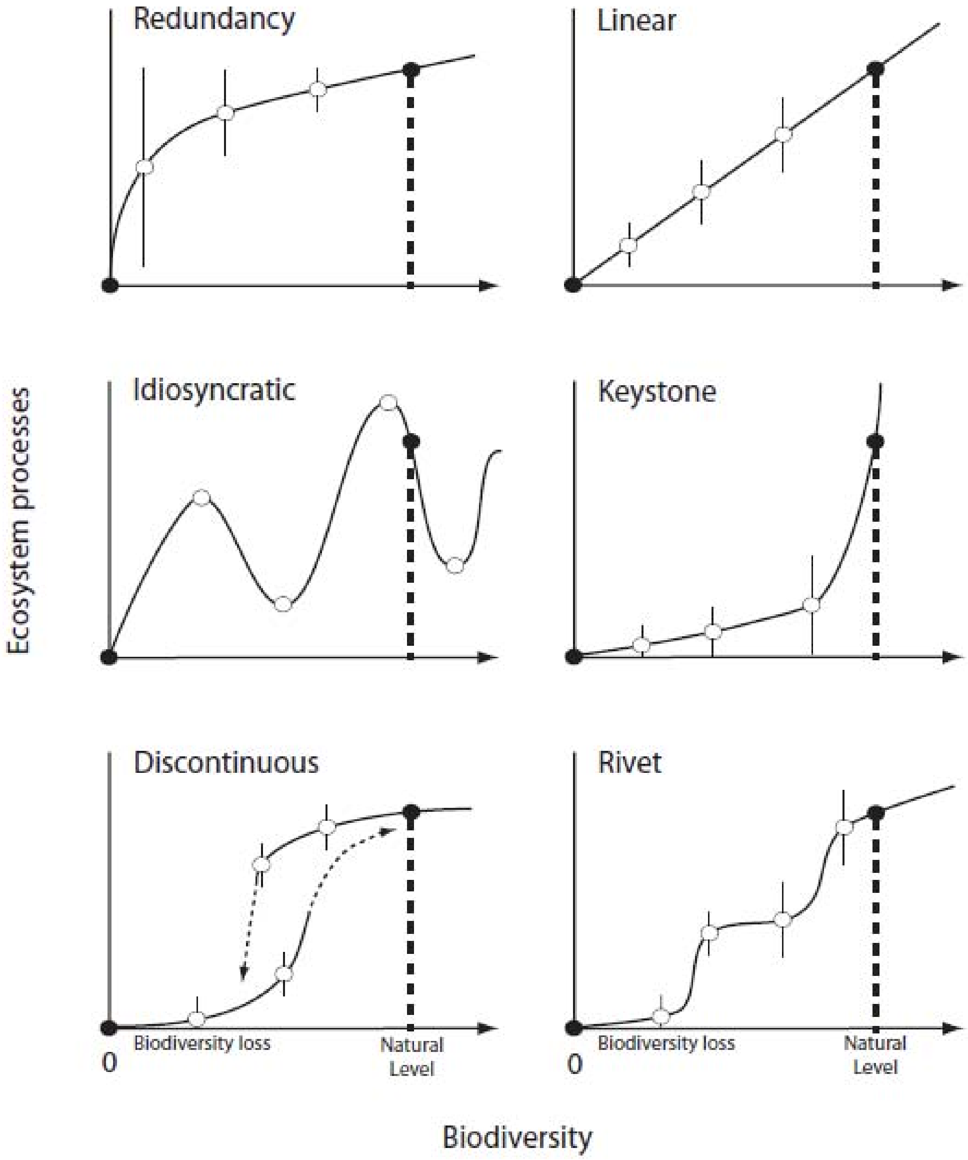


Figure 1. Graphical representation of hypothetical relationships between biodiversity and ecosystem functioning (reproduced from King 2009).

Restoration and ecosystem functions

Focussing on ecosystem processes and functions is not a new idea and has been suggested as a focal point for more than a decade (Bradshaw 1996). Measurement of restoration success, however, still mainly focuses on restoring species and communities, though recently there appears to be a shift towards evaluating ecological processes as well (Ruiz-Jaen & Aide 2005).

The relationship between restoring structure and function was first visually depicted by Bradshaw (1984) (Figure 2a). Although Bradshaw (1984) called the x axis 'structure' it represented species and complexity. Since then, all restoration biodiversity ecosystem function models (RBEF) for restoration have labelled that axis 'biodiversity'. These RBEF models have taken a few different forms since their introduction into restoration ecology. Some modifications include substituting 'structure' for 'biodiversity' (Figure 2b) as well as changing the shape of this curve to a asymptote with function restoring before biodiversity rather than a straight line relationship (Figure 2e, Naeem 2006). There has also been recognition that sometimes even when systems are degraded they are in fact managed for a certain ecosystem function, for example agricultural lands managed for productivity. In these cases, the degraded state need not necessarily be one of lower function, but could be of higher functioning than the original ecosystem (Figure 2c, Naeem 2006; Jelinski et al. 2011). It has also been proposed that there may be sudden jumps in function as thresholds are overcome (Figure 2d, Whisenant 1999). Even though restoration projects are perfectly placed to be able to examine BEF relationships, only a few studies have specifically tested whether these relationships hold up in specific restoration case studies (e.g. Maestre & Cortina 2004; Jelinski et al. 2011).

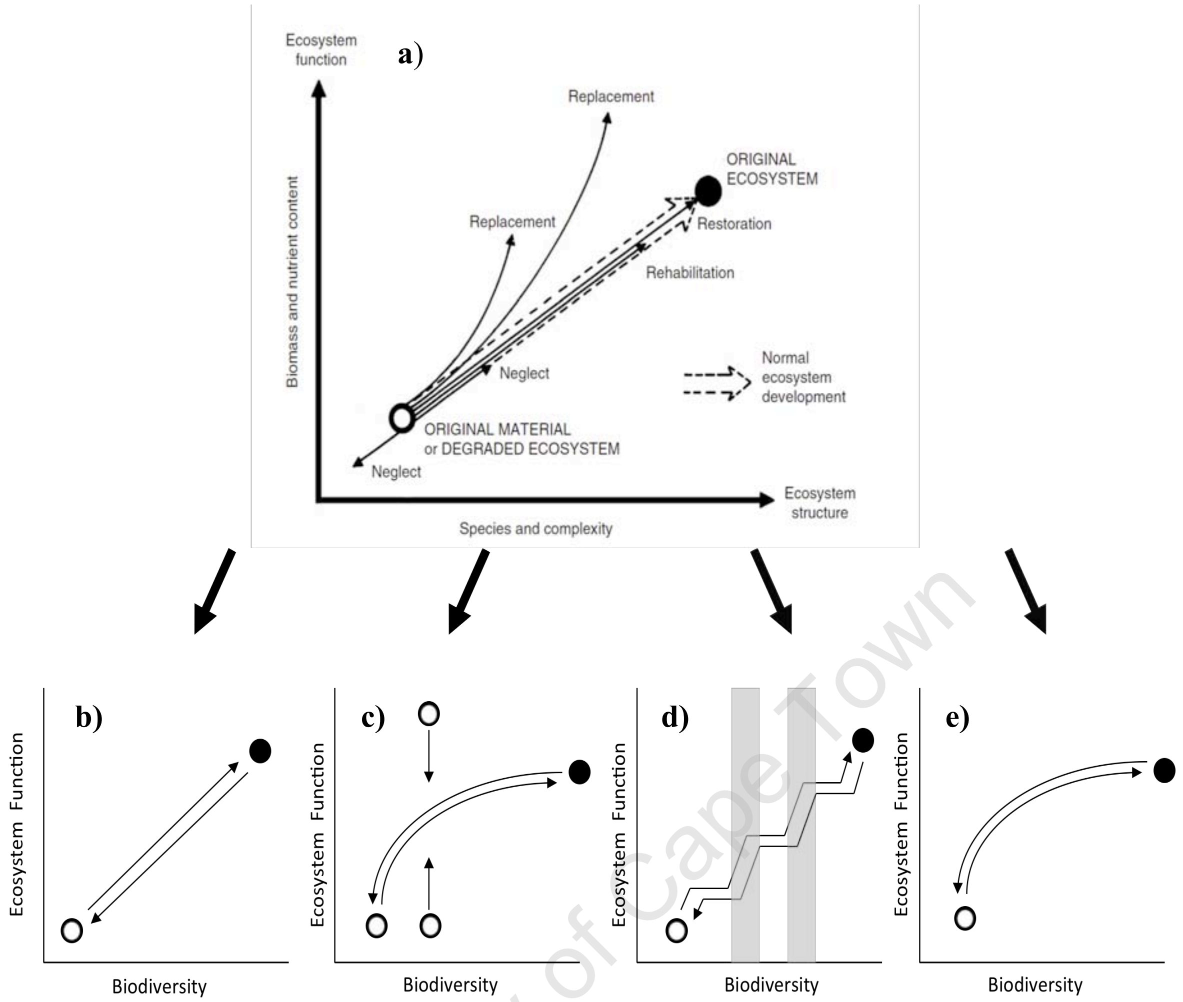


Figure 2. Graphic representation of the structure-function model a) originally from Bradshaw 1984 taken from Cortina et al. 2006). Lower graphs show alternative derivatives of the model including b) substituting biodiversity for structure, c) managed systems for higher or lower function, d) including thresholds or e) redundancy (adapted Whisenant 1999; Naeem 2006 and Jelinski et al. 2011).

Moreno-Mateos et al. (2012) reviewed case studies of wetland restoration projects examining the recovery in terms of structure and function. They focused on measures of structure (which they defined as abundance, species richness, density) as well as biogeochemistry (including nutrient cycling) in restored compared with remnant sites. This was one of the largest attempts to look at restoring structure and function together and they found that function was restored to on average 77% of the reference system (compared with 74% for structure). These numbers are not directly comparable as structure and function were not necessarily always measured in the same sites.

Rey Benayas et al. (2009) looked at paired measurements for function and biodiversity in restored sites compared with remnant sites. In this study they found what appeared to be an asymptotic relationship between restoring ecosystem services and biodiversity (suggesting redundancy), whereby function was restored closer to reference levels than measures of biodiversity. This was however for ecosystem services (e.g. timber production) as opposed to a range of ecologically meaningful processes (e.g. biomass accumulation, biotic interactions, water retention).

Biodiversity, measured by species richness or biodiversity indices only gives a partial picture of the ecosystem. Most restoration goals encompass restoring species ‘composition’ not just species richness. Not only does restoring composition insure that a similar number of species is restored, but also that the assemblage is one that is both adapted to that environment and contains a mix of species that is known to support a fully functioning ecosystem. However, the relationship between restoring an ecosystem in terms of composition and function is untested.

Meta-analysis

Manipulative ecological studies are often highly constrained in the scale and replication of the experimentation for logistical and economic reasons. This is also the case in restoration ecology, where often only a few sites are studied at a time due to the nature and scale of the restoration projects. Much ecological theory (and ecological restoration theory), however, requires testing across large scales, different ecosystem types and ecosystems in order to understand the generality of any pattern. Meta-analyses provide a useful tool for testing such theories and relationships by synthesising data and results from multiple studies. Further discussion on meta-analytic techniques is included in Chapter 2.

The number of restoration studies is increasing in the scientific literature (Young et al. 2005; Brudvig 2011). In addition, restoration studies, even if not testing specific theories themselves, have often collected adequate data, and provide a novel way, to test large-scale ecological questions using meta-analyses. In this thesis, I explore the relationship between ecosystem function and species composition, using such data, across a range of restoration studies using meta-analysis techniques.

Chapter 2 – The relationship between restored ecosystem function and species composition: a meta-analysis

Introduction

Restoration is one of the most common management practices used to improve land that has been damaged through human activities, and has given rise to the fully fledged discipline of restoration ecology, which attempts to understand the patterns and processes that come out of this practice. The central goals in restoration are firstly to increase the biodiversity or species richness of a site and, secondly, to restore a particular set of attributes including characteristic assemblages and ecosystem functions (SER 2004). Although these goals are often complementary, the relationship between the two may not be straight forward or linear, which may have far reaching implications (Schwartz et al. 2000).

Previous research focusing on the relationship between biodiversity and ecosystem functioning (BEF) has found that the level of biodiversity can affect the functioning of ecosystems (Balvanera et al. 2006; Cardinale et al. 2006). For example, research by Schmid et al. (2009) synthesised results from two separate meta-analyses together with expert reviews and suggested that there was considerable heterogeneity in BEF relationships, although certain factors repeatedly emerge as having a large influence. These include the type of ecosystem in which the restoration had occurred, the level at which the response is measured (ecosystem, community or population) as well as the different groups of ecosystem function under consideration. Linear, redundancy (saturating/asymptotic) and idiosyncratic curves appear to be the most commonly demonstrated relationships between BEF (Schwartz et al. 2000; Schmid et al. 2009).

If species redundancy in ecosystem function is widespread, then this may imply that ecosystem function could be achieved through a variety of different combinations of species, not necessarily only the composition of the previously intact site (or reference site). This however, would not assist in reaching goals of restoring a similar composition. If a linear relationship exists, it would suggest that full species composition must be required for full ecosystem function to be restored. Restoration monitoring programs are often limited in funds to measure multiple ecological processes as well as species composition, so understanding how these variables relate to one another is crucial to try and minimise monitoring costs and maximise efficiency.

Many restoration projects aim to restore characteristic assemblages, although many only measure species richness, overall abundance, or biodiversity indices rather than species composition (Ruiz-Jaen & Aide 2005). These metrics are easy to understand and analyse as they each present a single metric for each site. However, these metrics do not incorporate the species identity and so cannot actually inform practitioners whether or not the site has been restored in terms of species composition. Multivariate statistics, on the other hand, are well suited to answering such questions, since they take into account which species are present as well as their relative abundances. Using multivariate similarity indices allow species composition to be compared between restored and reference sites to assess the success of restoration efforts. Despite the obvious theoretical benefits of having multiple reference sites for comparing restoration success (see Chapter 1) many studies only use one reference site, or have none at all (Ruiz-Jaen & Aide 2005). Given the inherent variability in ecosystems, lack of multiple reference sites means it is impossible to fairly assess whether or not the sites have been restored to levels that are within the realms of variation for intact sites.

This study aims to explore if a consistent relationship exists between restoring species composition and ecosystem function, and what factors may influence the nature of this relationship. This kind of question cannot be feasibly answered in a single experimental study. The level of replication of restoration sites, as well as appropriate reference sites required make it impossible. However, because many restoration projects have carried out research around similar issues, the published literature evaluating restoration effort provide an extensive pool of information that can be tapped into in order to address large-scale questions such as these.

Meta-analytic techniques have developed to allow synthesis of independent studies, avoiding some of the statistical flaws associated with traditional 'vote counting' procedures, as well as providing a more objective and defensible method than narrative reviews (Ainsworth et al. 2007). Though developed for the use in other disciplines, meta-analytic techniques have been adapted for ecological questions and their use is growing (Nakagawa & Santos 2012). These techniques allow the discrimination of overall effect from variation between studies and other factors, which is particularly useful when trying to generalise across inherently variable ecosystems.

Very few individual studies actually measure and report species composition and ecosystem function, so regardless of other drawbacks, a qualitative review of the findings of these studies would not be particularly useful. A great deal more studies, however, have collected data that could be used to tackle questions regarding species composition and ecosystem function. For this reason, I used primary data from restoration research articles and quantitatively analysed the relationship between ecosystem function and species composition.

If species redundancy exists, and full complement of species on is not required for ecosystem functioning, then ecosystem function should return more readily, or be closer to being returned, than species composition through restoration. The way in which restoration is carried out, as well as the functions and the type of ecosystem studied, could alter patterns as the restoration may target certain functions or some ecosystems/functions may be simpler and easier to restore. From these ideas the following hypotheses were generated and tested:

1) That ecosystem function is restored more often to, or closer to, the within the range of reference sites than species composition, and that the restoring of these variables is not equal between ecosystem functions, restoration types (active or passive) or the ecosystem type in which the study occurs
2) That a relationship exists between species composition and ecosystem function in restoration sites. Variation in this relationship can be explained by ecosystem functions, restoration type and ecosystem types.

To my knowledge this study represents the first attempt to explore the relationship between restoring species composition and ecosystem function across multiple studies. This research explores an important question for restoration ecology that has implications for the way in which restoration success is assessed. This study also allows new insights into BEF research to be derived using a novel technique examining restoration studies.

Methods

Literature search

A literature search was conducted on 26 September 2012 in Web of Knowledge (Thomson Reuters Web of Knowledge) using the terms (RESTOR* OR REHABILIT* OR REFOREST*) AND (ECOLOG* OR ECOSYSTEM OR ENVIRON*) AND (FUNCTION* OR PROCESS* OR SERVICE*) AND (COMPOSITION OR BIODIVERSITY OR DIVERSITY). The first two categories of terms were chosen to attempt to encompass a range of ecological restoration studies, which are sometimes referred to with different names. The second and third categories of terms attempt to refine the search to those papers which measure some aspect of ecosystem function or processes. The term SERVICE* was also included to refer to ecosystem services, which depending on the definition, can also include important ecosystem functions and are the focus of much recent research (MEA 2005). The final term was used to include studies which reported measurements on species composition. BIODIVERSITY OR DIVERSITY were also included as often composition is measured (in terms of species and abundances), but the data were converted into biodiversity metrics for simplification.

Resulting papers were first refined in Web of Knowledge to exclude non-English papers and papers outside of 'science technology' research domain. Papers were further narrowed down by including only relevant research areas (environmental sciences ecology, biodiversity conservation, zoology, agriculture, entomology and plant science). The resulting papers were further refined through a process of first examining titles for relevance, then by abstracts and the finally the reduced number of papers were read in full (as suggested in Pullin & Stewart 2006). At the first stage, examining titles, the criteria for inclusion were broad and any paper pertaining to the restoration of ecosystems was retained. Restoration can either be active, for example planting seedlings lost from the system, or passive – where the degrading/disturbing pressure is removed and ecosystem left to recover on its own, for example cessation of intensive grazing regimes. Abstracts of the reduced list were read and retained if they met the criteria of including ecosystems under restoration (active or passive) and measured some aspect of biodiversity (composition, biodiversity and species) together with some aspect of ecosystem function in both restored and reference sites. When it was unclear which variables had been measured, or if a reference site was used, the paper was also retained. Finally full papers were examined to make sure the final set only included papers that measured both the species which were present and their abundances (even if only condensed metrics were presented in paper) together with at least one ecosystem function in both restored and multiple reference sites.

Extracting data

Authors of the final set of papers were contacted for raw data regarding the abundance, cover or biomass of each individual species within each plot/site to calculate a measure of species composition and for measurements of ecosystem function within each plot/site. For papers where authors could not be reached, attempts were made to extract adequate data from papers/appendices/supplementary material. If adequate data could not be obtained, these papers were excluded from the analysis.

Groupings of data

Measurements of ecosystem function varied across the studies, which is unsurprising given the different systems, scales, and budgets of the different restoration projects. Each measure is an indicator of overall ecosystem functioning and it is assumed that each study had chosen sensible indicators for the system under consideration. As it would not be possible to analyse each measure, they were categorised into broader types of ecosystem functions. These categories were formulated based on the ecosystem functions measured in the final cut of papers and literature reviewed in Chapter 1 (see Appendix Table A1). Not all groups in Table A1 were measured in the final subset of studies used, and also since many of these are closely related to one another, they were combined into the broader categories explained below.

The category *live biomass* includes measures of live plant biomass or productivity, which were grouped together as they represent the ability of the ecosystem to harness solar energy and accumulate biomass. Biomass of soil fauna, or root structures were not included in this category, as they serve different functions, they were included in other categories (see later). *Biotic interactions* relate to interactions that enable the ecosystem to reproduce and sustain itself. These include pollination, animal facilitated seed dispersal, seedbank composition or germination as well as measures of biomass of soil biota such as earthworms, bacteria and fungi. The *litter* group comprises measures of leaf litter and other dead plant material such as deadwood logs. These were distinct from live biomass as they relate to the intrinsic accumulation of organic material (and in turn, the decomposition and cycling of nutrients), as well as providing habitat for many faunal species. *Nutrients* include both measures of nutrient pools in the soils as well as indicators of nutrient cycling. Sometimes these were considered to be separate ecosystem functions (Ruiz-Jaen & Aide 2005), however, nutrient pools are often measured as indicators of nutrient cycling, and only one of the chosen studies actually measured nutrient cycling. Measures in the category *soil* include attributes related to soil temperature, stability, texture, and water retention. The final category *framework* relates to structural characteristics of the plant community such as tree height and cover that provide habitat structure within the ecosystem, this includes measurement of fine root structures.

The ecosystem type of each study site was also assigned and were grouped into five different ecosystem types based on information provided in each paper. The groups were *forest*, *grassland*, *shrubland*, *wetland* and *woodland* and these were the same for each paper.

Each site was also assigned a restoration type. Sites which had undergone active intervention such as planting or seeding were assigned to the category *actively restored*. Sites where the degradation process had been halted or removed, and sites then left to recover on their own were assigned the category *passively restored*.

Species composition and ecosystem function metrics

Bray-Curtis similarity indices are the most widely used in ecological studies to compare species composition as they have a number of qualities which make them numerically appropriate for comparing ecological communities (Clarke & Warwick 1994). The first quality is that if two samples have no species in common they have a similarity of 0%, and if they are identical have a similarity of 100%. The second is that it can accommodate different measures of species abundance (e.g. counts, biomass, density). Thirdly, Bray-Curtis ignores “joint absences” i.e. does not consider samples similar because they both lack a certain species.

To compare species composition between restored and reference sites, data for each species in each site were used to construct a Bray-Curtis similarity matrix in PRIMER v. 6 (Clarke & Gorley 2006). Data were squared root transformed in order to down-weight the influence of over-abundant species to allow the less abundant species to play a role (Clarke & Warwick 1994). The mean similarity within reference sites was calculated as the mean of all pairwise similarity measures between reference sites. This is henceforth called SC Sim_{REF}. The mean similarity of restored sites to reference sites was calculated as the mean of pairwise similarity between each restored sites and each of the reference sites. This is henceforth called SC Sim_{REST}. Using both these mean Bray-Curtis measures form the basis for comparing how similar the restored sites are to reference sites. Using the mean similarity between restored sites and reference sites alone is problematic because it is not comparable between different studies, because the variability between reference sites will likely differ between different ecosystems with some ecosystems being more inherently more heterogeneous than others. Failing to account for variation between reference sites, would mean that similarity in species-rich or heterogeneous ecosystems are likely to be underestimated because obtaining high values of similarity is more difficult in such systems.

Similarly, within every study, the mean for each different ecosystem function measure was calculated for each of the reference sites. The similarity between each possible pair of reference sites was calculated by dividing the smaller of the two means by the larger. This is referred to as EF Sim_{REF} and represents how similar reference sites are to one another. For each measure of ecosystem function within a site, the similarity of the restoration site to each reference site was calculated by dividing the smaller of the two means by the larger. This number is referred to as EF Sim_{REST}. These metrics gave a number between 0 and 1. To make this comparable to the species composition metrics that were out of 100 (as Bray-Curtis measures are out of 100), the number was multiplied by 100. These two mean similarity measures form the basis for comparing how similar the restored sites are to reference sites in terms of ecosystem function.

Response ratios

The most commonly used effect size measures in ecology and evolution is the response ratio ln(RR) (Nakagawa & Santos 2012). In this study, the response ratio was modified to account for the different types of metrics used (similarity indices) as well as the comparison of one restored site to multiple reference sites. The ln(RR) is the natural-log of the ratio of the means of a treatment group compared to a control or reference group. In this case is it the mean similarity of restoration sites to mean similarity of reference sites.

$$ln(RR) = \ln(REST/REF)$$

In this study REST and REF are the mean similarity between restored sites and reference sites, or among reference sites. Meta-analysis also traditionally assigns a weight to each ln(RR) which is the inverse of its sampling variance:

$$\hat{\sigma}^2\ (\ln(RR)) = \frac{(SD_{REST})^2}{N_{REST}Sim_{REST}^2} + \frac{(SD_{REF})^2}{N_{REF}Sim_{REF}^2}$$

Where *SD* is the standard deviation and *N* the sample size. This works to down weight studies with larger variances. However, the way in which the Sim_{REF} and Sim_{RES} are calculated in this study already takes into account the variation within reference sites. Therefore, calculating variance for each measure was not considered necessary in this study as it would only represent variation in reference measures, and there is none in the single restored site measure.

The response ratio is often preferred over other effect size measures in ecology as it is a meaningful way to summarise the difference between an experimental and control groups compared with less intuitive metrics as it provides a ratio (Hedges et al. 1999). Another advantage of the response ratio in that it linearises data, by treating changes in the numerator similar to changes in the denominator (Hedges et al. 1999). The response ratio also has an approximately normal distribution allowing for more conventional statistics (Hedges et al. 1999).

The ln(RR) cannot, however, accommodate zeros in either the numerator or denominator, however, these zero values are meaningful (representing for example no restoration of a particular ecosystem function at a restored site) and their inclusion is therefore important. This problem has been overcome by adding one to both the numerator and denominator (e.g. Moreno-Mateos et al. 2012). Adding one to both sides of the ratio, importantly, cannot change whether or not a site is considered restored (ratio greater than 1), however, adding smaller numbers also runs the risk of giving undue influence to these small numbers.

A possible problem with the use of the ln(RR) in study designs with multiple groups compared to the same control group (in this case reference sites) is that the ln(RR)s are not independent of one another (Gurevitch & Hedges 1999; Lajeunesse 2011). This problem can be avoided if the groups are separated by mutually exclusive moderator categories in the analysis (e.g. different ecosystem functions), and so are not pooled together in the analysis (Lajeunesse 2011). Another way to account for this non-independence within studies is to include another moderator category that separates the measures as a random factor in the analysis (in this case study or ecosystem functions) (Gurevitch & Hedges 1999).

The ln(RR+1) was calculated for each site for both species composition and ecosystem function. If a paper measured more than one ecosystem function of the same category, then the mean response ratio was used rather than each measure separately. This was done after response ratios were calculated, as response ratios are then all on the same scale.

The novel approaches employed in this study to calculate the values for ecosystem function and species composition were necessary because this study differs from most meta-analyses which compare the mean of one group to the mean of a control group. Although this conventional approach would have been possible for ecosystem function, it would not have been possible for species composition given the nature of similarity metrics (only one value for a comparison between two sites rather than a ratio with a value for each site and set of reference sites separately). It was desirable to use the same metric for both ecosystem function and species composition. Different metrics would bias the results, as it would be easier to restore a site to within the variation of a set of reference sites than to the mean of those reference sites. Other alternatives would be to use metrics such as species richness or biodiversity indices. However, as discussed in the introduction, these measures are not well suited to answering questions about species composition as they overlook a lot of the necessary detail and can produce misleading results. In addition, traditional RR only considers sampling variance in the weighting. In the case of restoration we are also interested in the level of natural variation within reference sites.

Analysis

To graphically illustrate the distribution of the data, values were transformed to positive numbers between 0 and 100 to be more intuitive to understand. This was done by taking the exponent of the ln(RR). Numbers above 100% were assigned the value of 100 (as they can be considered restored). For the rest of the analyses, the ln(RR+1) data were used.

For each sample (n = 557) the number with ln(RR+1) above zero for each ecosystem function and species composition were calculated. To explore whether full restoration differed between ecosystem function or species composition, the number of samples that were either restored or not for these two variables was calculated and analysed using chi-squared contingency test. Whether or not the pattern of ecosystem function restored or not was consistent across ecosystem functions, restoration types or ecosystem types were also explored using separate contingency tests. The same tests, examining whether or not species composition was restored were also conducted.

For each sample, whether or not ecosystem function or species composition was closer to being fully restored (i.e. which variable had ln(RR+1) closer to 0) was determined. These data were then compared to a random 50:50 expected ratio with a chi-squared goodness-of-fit test. The 50:50 expected ratio was used as this is what would be expected if species composition and ecosystem function returned equally. To then see if any pattern differed across ecosystem functions, restoration types or ecosystem types, contingency tests were again employed.

General linear mixed models were fitted to the data using the lme4 package in R (R Core Development Team 2013). The initial model used the ecosystem function response ratio as the response variable and species composition as a fixed explanatory variable. Two random terms, study and ecosystem function type, were also included to account for non independence of multiple samples for each site measuring different ecosystem function types and also because there were often multiple sites from each paper. The second model explored whether ecosystem function type, restoration type or ecosystem type influenced this relationship. Factors were added one at a time and their influence on corrected Akaike Information Criterion (AICc) recorded. The AICc trades off the amount of variation explained by the new addition with the number of parameters and corrects for small sample sizes. This is done by penalising for the addition of new factors such that models with the least and most influential factors have the lowest AICc. Factors that lowered AICc by more than two compared with base model were included in further models (Schwarz 2011). The final model chosen was the one with the lowest AICc value. If models provided equally low AICc values (within 2 units or each other), then the simplest one was chosen. Models that included ecosystem function type were compared to Base Model 1 (included species composition as a fixed factor and study as a random factor). Models that did not include ecosystem function type as a fixed factor were compared to Base Model 2 (with ecosystem function also included as a random factor). This was done to account for possible influence of non independence from multiple points from the same site of different ecosystem function types.

The models were fitted with the maximum likelihood (ML) criterion to allow comparison using AICc, but to obtain parameter estimates the models were refitted with restricted maximum likelihood (REML) criterion (Bates 2011). Model fit was assessed visually using the residual and q-q norm plots. The significance of the main effects in models were examined using Type III F-tests. These tests examine the significance of each term after controlling for all other terms within the model, which is important considering the importance of lower-order terms (such as species composition) in the model.

What constitutes the appropriate denominator degrees of freedom in general linear mixed models, is often debated and although some argue F-tests should not be used, others have come up with methods to allow p-value calculation (see online discussion at http://rwiki.sciviews.org). The Kenward-Roger approximation was used to estimate the denominator degrees of freedom and calculate p-values (Halekoh & Hojsgaard submitted). The deviance explained (%) by each main factor were derived by the sum of squares of a fixed effect divided by the sum of squares total (Tremblay 2013). Significant differences in interactions were explored by re-running models for subsetted data for each different group. Significant differences in main effects were explored by assessing the overlap of confidence intervals with zero. Confidence intervals were calculated using Markov chain Monte Carlo (MCMC) procedures (Baayen 2012).

It is also possible species composition is more variable at reference sites than ecosystem function is, or vice versa, which may therefore influence the ease of that attribute being classified as restored. Also, if for example, reference sites are highly variably in their ecosystem functions, then it might make it more likely that the restored site will be restored to within that range. However, if there is very little variation between reference sites, then it might make that attribute harder to be restored within those narrow bounds. To test if the mean level of similarity between reference sites was different for species composition or ecosystem function, general linear models were run. The response variable was the mean similarity within reference sites, Sim_{REF}, and the explanatory variable the type of measure (ecosystem function or species composition). To see if the mean level of reference similarity for ecosystem function depended on ecosystem function type or ecosystem type, models with each of these and their interaction were also run. This was also done for species composition to see if ecosystem type influenced the mean level of similarity within reference sites. Ecosystem function type was not included as it does not make logical sense that the type of ecosystem function measured could affect species composition. Similarly the restoration type was not included in either test as these are applied to the restored sites and not reference sites, so their inclusion is illogical. As with other models appropriate model fit was assessed visually using the residual and q-q norm plots.

Results

Literature search

The literature search resulted in 4072 papers. Refining these based on language, research domain and areas resulted in 3204 papers. Filtering based on the relevance of titles left 707 papers, and after reading their abstracts a total of 155 papers were shortlisted. Once these papers were examined in full, 67 papers with suitable criteria remained and attempts were made to contact authors for data.

The authors of twenty-three studies were able to provide data; of which 20 could be used (the other three either did not have multiple reference samples or adequate data to form Bray-Curtis similarity measures). An additional five papers provided enough data (in papers/appendices/supplementary material) to construct species incidence data for each site. Details of the papers used for the final analyses are provided in Appendix II. These papers came from multiple countries and ecosystem types. Most studies dealt with vegetation species composition, and five concerned invertebrates. *Nutrients* and *framework* were the most commonly measured ecosystem functions (Appendix II). A total of 557 samples from 237 sites were calculated. Samples sizes for each of the categories used in the analyses are provided in Appendix III.

Relationship between species composition and ecosystem function

Figure 3 shows the distribution of data when numbers were calculated as a percentage of the reference site similarity (with zero indicating no similarity and 100% meaning within the range of variability of reference sites). There was substantial variation, but the majority of points are clustered along the 100% ecosystem function line or above the 1:1 diagonal (74%, Figure 3). This indicates that in restoration sites ecosystem function was more often similar to reference sites than was species composition. Even at extremely low similarity to reference sites for species composition, there were sites with ecosystem function restored. However, there were also samples with species composition similar to reference sites which had low similarity in terms of ecosystem functioning to reference sites.

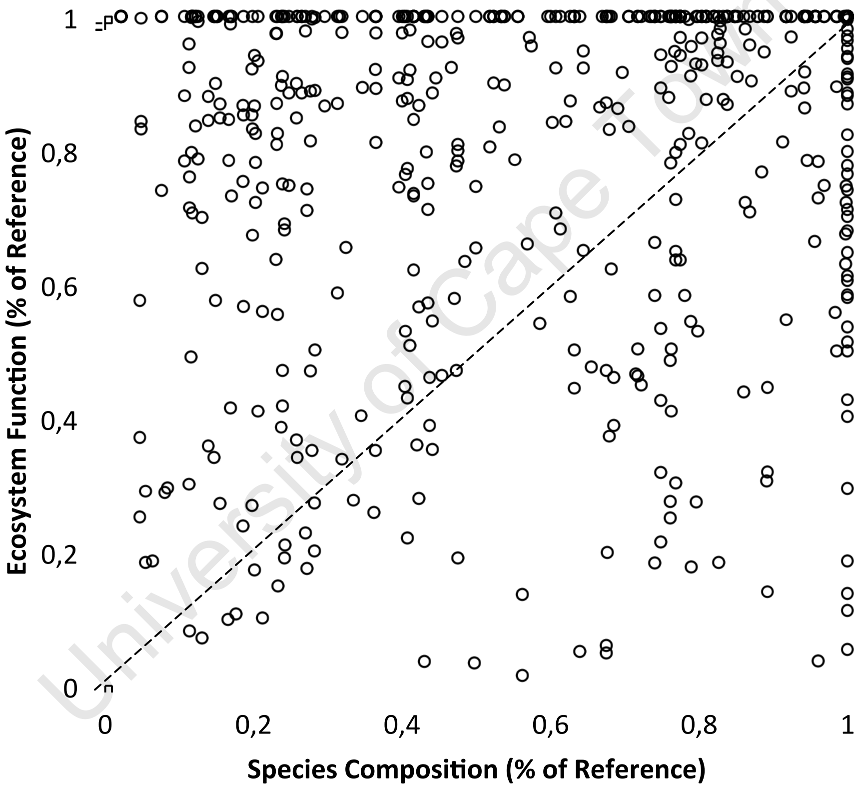


Figure 3. Relationship between ecosystem function and species composition in 557 samples from 237 restoration sites as a percentage of how similar each sample it to their reference sites. Ecosystem function and species composition are calculated for each site by taking the mean similarity to multiple reference sites divided by the mean similarity within those reference sites. Any samples within the range of variability of reference sites (ratio >1) were converted to 100% and any site with undefined ratio due to presence of zeros was converted to 0%.

Descriptive statistics

The number of samples that had ecosystem function restored ($\ln(RR+1) \geq 0$) or not ($\ln(RR+1) < 0$) depended on whether or not species composition had also been restored (Table 1a). When species composition was restored, there was a higher than expected number of samples with ecosystem function also restored, indicating that species composition and ecosystem function are not independent of one another. When the analysis was separated into ecosystem function types, the number of sites with ecosystem function restored or not, differed between ecosystem function types (Table 1a). *Nutrients* and *soil* had greater than expected numbers of samples with ecosystem function restored, whereas *live biomass* and *framework* had less than expected. When the sites are broken down into restoration type, passively restored sites had a slightly higher, and actively restored slightly lower, than expected number of sites with ecosystem function restored. There was no significant difference between different ecosystem types. There were differences in the number of samples with species composition restored between ecosystem function types (Table 1b). *Live biomass* had a higher than expected number of samples with species composition restored, whereas *framework*, and *soil* had a lower than expected number. There was no difference between restoration types. *Grassland* and *woodland* had a higher, and *forests*, *shrubland*, and *wetlands* had a lower than expected number of samples with species composition restored.

There were significantly more samples (74%) with ecosystem function closer to being restored than species composition (Table 1c). This pattern, however, was not consistent between ecosystem functions or restoration types (Table 1c). *Live biomass*, *litter*, and *framework* all had lower than expected number or sites with ecosystem function greater than species composition, whereas *nutrients* and *soil* had a greater number than expected. There was no difference in the pattern between ecosystem types.

Table 1. Number of samples from restoration sites with a) ecosystem function b) species composition restored or not, or c) ecosystem function or species composition being closer to restored for each category of ecosystem functions, restoration types and ecosystem types. Chi-squared contingency tests were performed within each category, testing whether the pattern of a) ecosystem function being restored, b) species composition being restored or c) ecosystem function being closer to being restored than species composition was consistent among categories.

a)	**Category**	**Eco. function restored**	**Eco. function not restored**	**% restored**	**χ^2**	**d.f.**	**p**
Species Composition	Restored	45	36	56	10.0	1	0.002
	Not restored	176	300	37			
Ecosystem Function Type	Live biomass	24	53	31	50.5	5	<0.001
	Biotic interactions	19	42	31			
	Litter	21	43	33			
	Nutrients	65	55	54			
	Soil	69	51	58			
	Framework	23	92	20			
Restoration Type	Active	145	254	36	6.5	1	0.011
	Passive	76	82	48			
Ecosystem Type	Forest	59	88	40	9.0	4	0.061
	Grassland	63	76	45			
	Shrubland	22	40	35			
	Wetland	11	6	65			
	Woodland	66	126	34			

b)	**Category**	**Sp. comp. restored**	**Sp. comp. not restored**	**% restored**	**χ^2**	**d.f.**	**p**
Ecosystem Function Type	Live biomass	3	15	23	19.8	5	0.001
	Biotic interactions	2	14	23			
	Litter	12	62	19			
	Nutrients	20	106	17			
	Soil	5	103	7			
	Framework	9	112	8			
Restoration Type	Active	52	347	13	2.6	1	0.108
	Passive	29	129	18			
Ecosystem Type	Forest	10	152	7	28.1	4	<0.001
	Grassland	36	103	26			
	Shrubland	2	46	6			
	Wetland	0	5	0			
	Woodland	31	172	16			

Table 1. continued

c)	**Category**	**Sp. comp. closer than eco. function**	**Eco. function closer than sp. comp.**	**% eco. function closer then sp. comp**	**χ^2**	**d.f.**	**p**
	All samples	147	410	74	124.2	1	<0.001
Ecosystem Function Type	Live biomass	36	41	53	68.8	5	<0.001
	Biotic interactions	19	42	69			
	Litter	28	36	56			
	Nutrients	16	104	87			
	Soil	7	113	94			
	Framework	41	74	64			
Restoration Type	Active	85	314	71	18.7	1	<0.001
	Passive	62	96	61			
Ecosystem Type	Forest	42	105	71	4.7	4	0.325
	Grassland	40	99	71			
	Shrubland	16	46	74			
	Wetland	1	16	94			
	Woodland	48	144	75			

Modelling the relationships between ecosystem function and species composition

The data transformed into ln(RR+1) for analysis are presented in Figure 4. Here, samples above zero on either axis represent the restored site being within the range of variability of reference sites, with the more positive being more similar to the range of reference sites, than the reference sites to themselves. Samples equal to or above zero on the y-axis have ecosystem function restored and samples equal to or above zero and the x-axis have species composition restored. Samples equal to or above zero for both axes are considered restored both in terms of ecosystem function and species composition. There is a large cluster of samples around the origin, indicating that many of the samples were within reference range for both ecosystem function and species composition.

To test if there was a consistent relationship between ecosystem function and species composition, the base model was examined. The line in Figure 4 is the model output with both study and ecosystem function type as random terms. The intercept of the line represents the level of ecosystem function when species composition is, on average, fully restored. In this case, the intercept is negative (i.e. not fully restored), and the relationship is positive, showing that as species composition increases, so does ecosystem function. This relationship was significant but only explained a small amount of the modelled deviance (Table 2). The random terms in the model, study and ecosystem function type explained 17% and 12% of the deviance in the model respectively. When the model output is converted back into positive values between 0 and 100, it can be seen that the relationship is a positive saturating curve (Figure 5). Although the intercept is still lower than 100% on the ecosystem function scale, the upper 95% confidence interval does incorporate the origin.

The inclusion of ecosystem function type improved the fit of Base Model 1 and lowered the AICc, however, ecosystem type or restoration type did not improve the fit of Base Model 2 (Appendix IV). Three models had similarly low AICc values (Appendix IV), however, the two larger models also included non-significant terms, so the model containing only species composition, ecosystem function and their interaction was chosen. All factors within the model were significant (Table 2). The random term, study explained 11% of the deviance in the model. Ecosystem function as a factor explained the most deviance in the model followed by the interaction with species composition. The interaction between ecosystem function type and species composition was explored by plotting the model outputs for each function using the intercept and slope estimates from the model (Figures 6).

Differences in the relationship between ecosystem function and species composition for each ecosystem function type are presented in Figure 6. *Nutrients* had a positive intercept, indicating that this ecosystem function is generally restored when species composition is also restored. The intercepts for *soil* and *biotic interactions* were not far from zero, whereas *live biomass*, *litter*, and *framework* were more negative, indicating that even with fully restored species composition, ecosystem function was, on average, not restored. These latter three ecosystem functions also show high levels of variation and some of the lowest levels of ecosystem function, especially at higher levels of species composition. When the MCMC 95% confidence intervals are examined, only *live biomass* and *litter* were significantly different from zero (Appendix V). The slope of *live biomass* and *framework* were much more positive, indicating that ecosystem function increases as species composition becomes more similar to reference sites. When each ecosystem function was examined separately, only *live biomass* and *framework* had significant relationships. The confidence intervals of the model output, when transformed into positive number out of 100%, are presented in Figure 7. They show that *live biomass* and *framework* exhibit redundancy relationships, whereas others have very flat relationships, although *biotic interactions* and *litter* were at a much lower level of ecosystem function.

Table 2. Output of the general linear mixed models examined for the relationship between ecosystem function and species composition controlling for the random effects of study and ecosystem function type (Base Model) as well as the model including ecosystem function type and the interaction between ecosystem function and species composition as fixed factors (Final Model). The denominator degrees of freedom were estimated using a Kenward-Roger approximation.

Model and component	F-value	d.f. (numerator, approximated denominator)	p-value	Deviance explained (%)
Base Model:				
Species composition + (study + ecosystem function type)				
Species composition	4.4	1, 227.3	0.036	0.6
Final Model:				
Species composition + ecosystem function type + interaction + (study)				
Species composition	12.6	1, 299.0	<0.001	0.5
Ecosystem function type	7.8	5, 452.3	<0.001	13.4
Interaction	3.6	5, 459.6	0.003	2.3

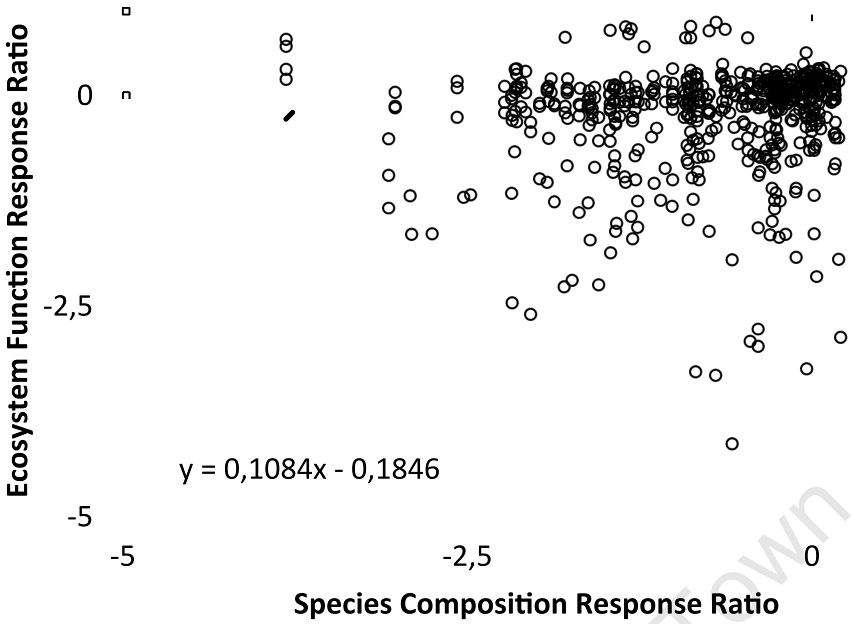


Figure 4. Relationship between ecosystem function and species composition in 557 samples from 237 restored sites. Metrics used are the ln(similarity of restored sites to reference sites +1/similarity within reference sites + 1). The line is the output from a linear mixed model with ecosystem function type and study as random variable.

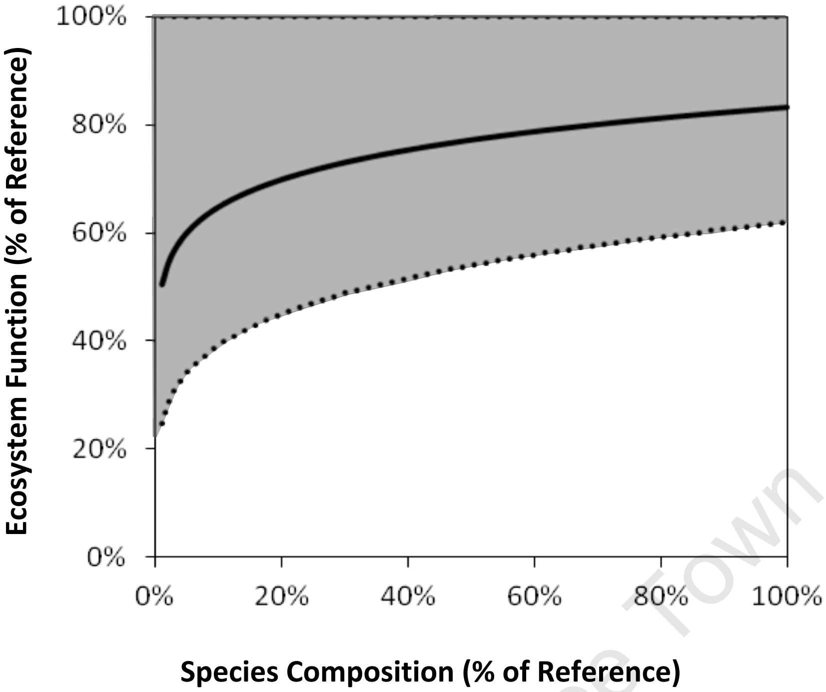


Figure 5. Modelled relationship between species composition and ecosystem function. Values have been transformed into positive values by taking the exponent of both the ecosystem function and species composition values. All values over 100% were converted back to 100% as these are considered restored. The black line is the model output and the grey area represents 95% Markov chain Monte Carlo confidence intervals around model estimates.

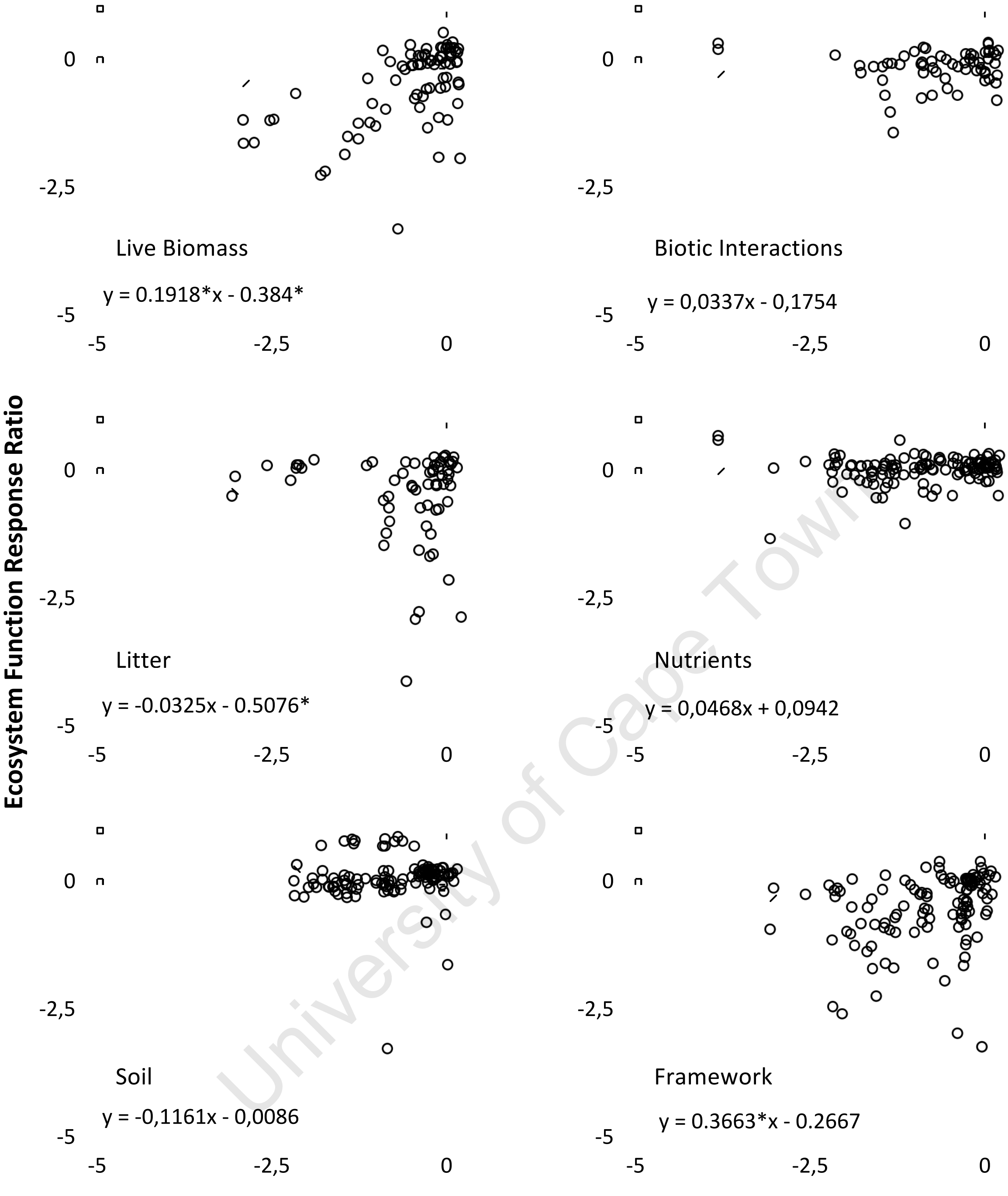


Figure 6. Relationship between ecosystem function and species composition for each of the different ecosystem function types. Response Ratio is the ln(similarity of restored sites to reference sites +1/similarity within reference sites + 1). The line is the output from the full linear mixed model including interactions between species composition and ecosystem function types as fixed variables and study as random variables, for each of the ecosystem function types. * denote significant slopes or intercepts.

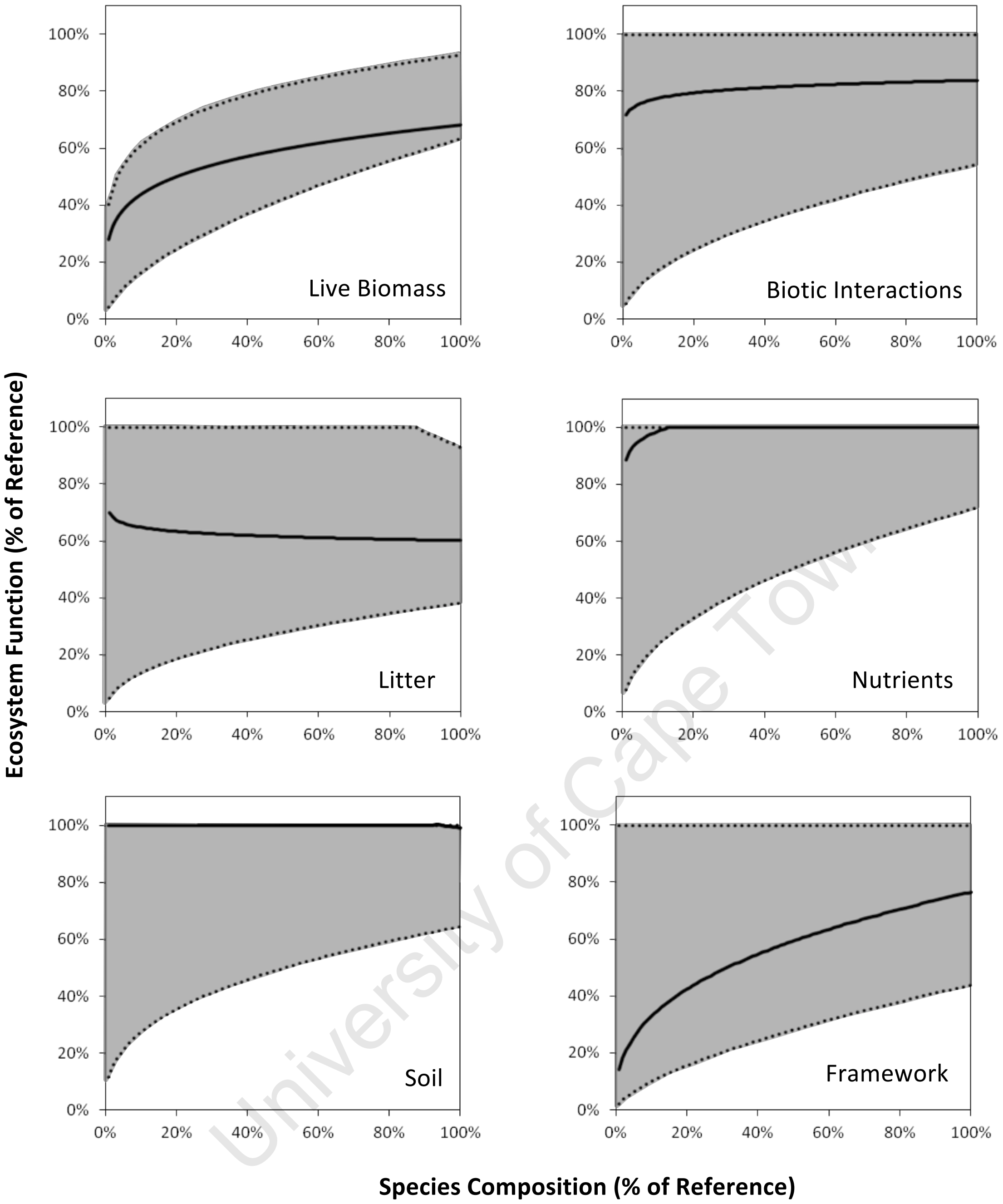


Figure 7. Modelled relationship between species composition and ecosystem function for each group of ecosystem functions. Predicted ecosystem function values have been transformed back into positive values by taking the exponent. All values over 100% were converted back to 100 as these are considered restored. The black line is the model output and the grey area represents 95% Markov chain Monte Carlo confidence intervals around model estimates.

Variation within reference sites

There was much variation within reference sites in terms of both species composition and ecosystem function ranging from 20-100% similarity. The mean similarity of ecosystem function within reference sites was greater than the similarity of species composition within reference sites ($F_{1,98}$ = 50.08, p >0.001, Figure 8). This indicates that reference systems were more variable in terms of species composition than ecosystem function.

Because it is possible that the level of variation within reference sites for ecosystems function could differ with ecosystem function type or ecosystem type, and similarly the level of species composition within reference sites could vary within ecosystem types, these were explicitly tested using general linear models. There was no difference in the variability of ecosystem function between different ecosystem function types ($F_{7, 35}$ = 0.86, p = 0.544) or different ecosystem types ($F_{7,35}$ = 1.27, p = 0.294). Also there was no difference in the variability of species composition within reference sites between ecosystem types ($F_{7,17}$ = 1.90, p = 0.132).

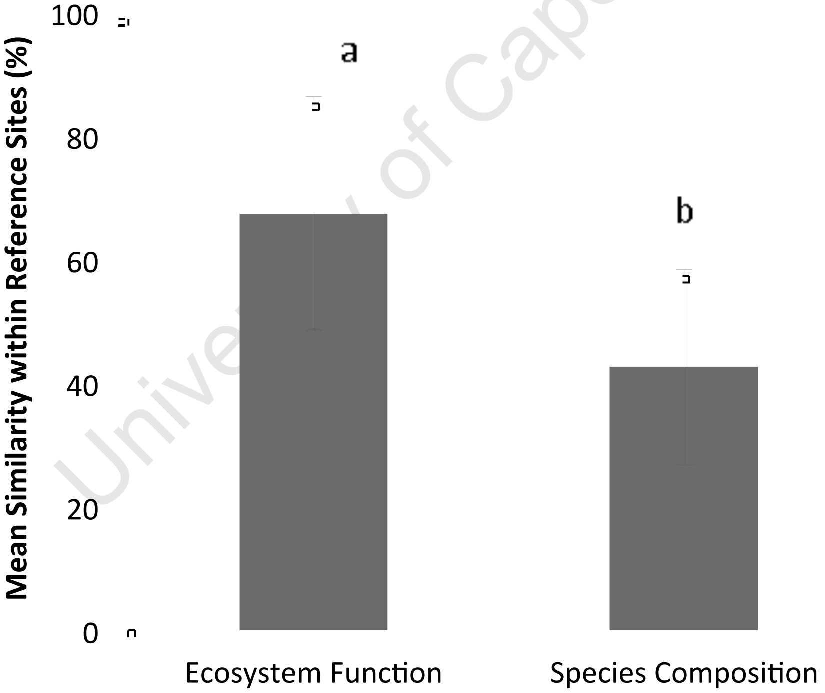


Figure 8. Mean similarity in ecosystem function and species composition within reference sites from each of the 25 papers used in the meta-analysis. Similarity for ecosystem function is the mean ratio of pairwise ratios of each reference site to each other and for species composition it is the mean of pairwise Bray-Curtis similarity measures with a study or group of reference sites within the study. Significant differences ($p < 0.05$) were detected using a general linear model and are denoted by different letters

Discussion

Ecosystem function was more often restored, and more often similar, to reference levels than was species composition. The combined dataset revealed that there is an overall positive relationship, however, it was weak and showed little consistency among different types of ecosystem functions. Only two ecosystem function types, *live biomass* and *framework*, showed strong positive relationships with species composition. Even when species composition was restored to reference levels of similarity, *live biomass* and *litter* ecosystem functions were not.

The shape of the overall relationship between ecosystem function and species composition closely resembles an asymptotic (redundancy) BEF relationship. However, instead of reaching full ecosystem functioning and levelling out, it plateaus at a sub-reference level of similarity. This suggests that increasing similarity, in terms of species composition, initially increases ecosystem function. Beyond a point, however, becoming more similar to the reference site, does not further assist in the restoration of ecosystem function to reference levels of similarity. Although this may seem to be rationale to stop restoration efforts at the point where ecosystem function is no longer increasing, lower number of species may result in lowered resilience of the ecosystem to future perturbations or disturbance (Holling 1973).

The other major difference to commonly reported BEF models, is that almost all BEF models consider ecosystem functioning to be zero when biodiversity is zero (e.g. Schläpfer 1999; Schwartz et al. 2000; Naeem 2006). A zero value for biodiversity/species richness indicates no species present; however, zero similarity (to the reference/s) in terms of species composition does not exclude the presence of other non-native species. Exotic species are capable of increasing ecosystem functions such as biomass, nutrient levels and litter production (Ehrenfeld 2003). Therefore, it is possible that the presence of exotics species in reference sites can lead to non-zero similarity of ecosystem functioning. Additionally, the ecosystem function itself may not degrade beyond a certain point, for instance, the properties of the soil, regardless of any biota, may support a certain level of water infiltration. With certain ecosystem functions, you would not expect an ecosystem devoid of species to retain any residual level of functioning. If there are no species present then there can't be any living plant biomass, litter or deadwood, biotic interactions, or framework components such as plant cover and density.

Differences between ecosystem function types

The shapes of the relationships between ecosystem function and species composition were not consistent among ecosystem function types. Only *live biomass* and *framework* ecosystem functions had positive relationships, indicating that as the species composition similarity to reference sites increased, so did the similarity to reference sites for ecosystem function. Biomass and productivity are often found to have a 'hump' (uni-modal) shaped relationship with biodiversity whereby biomass increases with diversity because of facilitation and niche compartmentality and, then decreases through competition (e.g. Hutson 1997; Gamfeldt et al. 2013). However, a redundancy relationship between biodiversity and biomass are frequently seen. This is possibly because the ecosystems which are often the focus of the study tend to be relatively simple and therefore never get to the stage where the negative effects of competition are observed (Schwartz et al. 2000; Guo 2007). Schmid et al. (2009) found the highest proportion of positive and significant effects of biodiversity in similar types of ecosystem functions. In contrast, the remaining four groups of ecosystem functions, *soil*, *nutrients*, *biotic interactions,* and *litter* all had relatively flat relationships with species composition, indicating they are minimally influenced by the restoration of species composition.

If *soil* and *nutrient* ecosystem functions are not similar to reference sites, then characteristic plants species may not to grow. Whisenant (1999) recognised this and referred to this as an abiotic threshold that limited community development from degraded states back to reference conditions. Due to this threshold, soils are often targeted through active restoration as a priority (e.g. nutrient amelioration or the planting of legumes or soil stabilising plants), which may explain why they appear close to reference conditions even at low species composition. However, even outside of restoration, many experts predicted soil and nutrient functions to have either no relationship with biodiversity, or have almost full function returned with only few species (Schläpfer et al. 1999). Schmid et al. (2009) also found that soil and nutrient ecosystem functions were the least likely to have positive relationships with biodiversity.

Biotic interactions, especially those between soil microorganisms, may also be a prerequisite for effective community development. These interactions can help improve survival and establishment for many species and so restoration of this ecosystem function may happen early on in the restoration process (Harris 2009). Not all interactions would be expected to be restored whilst species composition is still relatively dissimilar to reference sites. For example, interactions that include tight mutualisms, may not be restored until much later when all characteristic species of reference assemblages are present. This reciprocal relationship may explain the observed pattern in this study where by the majority of ecosystem function was restored whilst species composition was still dissimilar to reference sites. However, even once within the range of reference sites similarity, full functioning had still not been resorted. Wright et al. (2009) also identified multiple studies where plant composition had been restored even when the soil microbial community remained dissimilar to reference sites.

Gamfeldt et al. (2013) found that as biodiversity increased so did the probability of deadwood production. However, in this thesis, there was no response of *litter* to increasing similarity of species composition to reference sites. This relationship potentially indicated little response because litter ecosystem functions (compared with deadwood ecosystem functions) were being provided, where as ecosystem function, including deadwood production, which requires mature trees were rarely restored.

Even when species composition was restored to reference levels of similarity, *live biomass* and *litter* ecosystem functions were not. Instances where species composition had been restored, but ecosystem functions were still outside of levels of similarity for reference sites have also been found elsewhere in restoration studies. Craft et al. (1999) found that even after species composition, biomass and certain framework ecosystem functions had been restored in marshes, nutrient accumulation was still not fully restored. Zedler (1993) also showed that although vegetation composition and biomass had been restored to marshes, the height structure of the grass, (important to nesting birds) failed to be restored. Zelder and Callaway (1999) also found a similar lagged response in wetlands where by even after 10 years stem density and width were far from reference conditions. Potentially, these ecosystem functions might therefore, not only rely on the correct species compositions, but may also require them in place for an extended period of time for the appropriate conditions to accumulate. This seems especially likely for certain framework ecosystem functions (i.e. litter, deadwood, live biomass or framework), where only with time can certain tree heights, densities, or cover be provided.

Influence of restoration and ecosystem types

There was no difference in either active or passive restoration in terms of the slope of the relationship, indicating that both types of restoration have similar trajectories with respect to restoring ecosystem function and species composition. However, passive restoration is typically undertaken in ecosystems that have less severe degradation, or do not require physical or vegetation modification to overcome thresholds (Whisenant 1999, 2002). Both passive, and active, restorations were rarely carried out in the same study, this data does not necessarily indicate that passive restoration is as effective as active restoration. Of the two studies that measured both active and passive restoration in the same system, one had both active and passive sites with similar levels of ecosystem function and species composition restored (Forup & Memmott 2005). The other study indicated that active sites were closer to having ecosystem function restored, and passively restored sites were shown to have more variation in ecosystem function, but were slightly closer to species composition being restored (McLachlan & Bazely 2003). These differences were small and there was overlap between samples restored passively and actively. Similarly Morrison & Lindell (2011) found that in situations where passive restoration is not impeded by physical characteristics of the site to be restored, it may provide a more cost effective solution than active restoration.

Surprisingly, this study found little difference between ecosystem types. In other studies, difference between ecosystem types has been a factor that explains much variation in BEF findings (Rey Benayas et al. 2009; Schmid et al. 2009). The only variation between ecosystem types was with the proportion of sites within which species composition restored, suggesting that some ecosystem types are harder to restore. The model in this thesis, however, indicated that ecosystem types did not have a significant influence on relationship between species composition and ecosystem function. Most BEF research studies tend to be carried out where funding exists (i.e. Europe and North America) rather than more uniformly spread across the ecosystem types (Solan et al. 2009). The restoration studies used in this thesis, however, have a different distribution, with the majority conducted in Australia. These differences between my findings and BEF research may have arisen due to the use of biodiversity indicators such as species richness, which may be more influenced by different ecosystem types than species composition similarity indices, which are scaled to levels of reference similarity within the system already.

Reference levels of variation

Rey Benayas et al. (2009) attempted to carry out a similar study by examining the relationship between restoring aspects of biodiversity and ecosystem services also using a meta-analysis of restoration projects. They were unable to account for any variation in the reference systems (due to the small number of studies containing multiple reference sites), which presents a major challenge for interpretation. This makes it more difficult for a site to be considered 'restored' as it needs to reach a specific value for biodiversity or ecosystem function measures, rather than fall within adequate levels of variation. Given that we know ecosystems are inherently variant, this makes it hard for these measures to truly represent the success of restoration projects and biases them towards being considered not yet restored.

The way in which the metrics in this thesis were calculated allowed for the integration of this inherent variation in reference systems to be taken into account. Studies did not have uniform variation in terms of either their species composition or ecosystem function, indicating that there is a need to incorporate this variation when assessing success of restoring these attributes. I also found that this level of similarity within reference sites is lower for species composition than it is for ecosystem function. Low values of similarity between ecosystems for species composition are not unusual and have been documented before (e.g. mean 38% similarity, Beauchamp & Shafroth 2011). The fact that the levels of variation within reference sites were similar across ecosystem types and ecosystem function types indicated that this is not driving any patterns seen in this study.

However, the higher level of variation between reference sites for species composition than ecosystem function, suggests something more fundamental; that similar ecosystem functioning can be achieved through a variety of different species compositions. Ecosystem function was more often restored once species composition was also restored to within the range of reference sites. This suggests that it might be easier to meet restoration goals relating to ecosystem function than species composition. Also, certain ecosystem function, such as *soil, nutrients*, and *biotic interactions* may be restored in a variety of ways rather than only through one type of species assemblage.

Chapter 3 – Broader implications and future research directions

Implication for the practice of ecological restoration

Ecosystem function was more often restored to reference levels than species composition, suggesting it may be an easier goal to meet than both ecosystem function and species composition. Restoring ecosystems for function alone, can lead to novel ecosystems that do not resemble the reference species composition. This may be misaligned with conservation goals, especially if novel ecosystems contain invasive species. This study showed that different types of ecosystem function are more similar to reference sites at different points of species composition reference similarity. This suggests that novel ecosystems containing one group of working ecosystem functions, may not support all other ecosystem functions. This is especially noteworthy if restoration is attempting to re-create/provide a range of ecosystem goods and services to society that were lost through degradation.

This study found that there was an overall positive relationship demonstrated between species composition and ecosystem function, although the relationship was highly variable. The lack of a tight relationship suggests that measurements of ecosystem function and species composition cannot be used as proxies for one another. This highlights the need to measure both aspects when assessing the success of restoration projects.

These results also emphasise the importance of including multiple reference sites with which to compare restoration efforts. The high level of variability in species composition among reference systems, suggests that restoration practitioners need to be more expansive in terms of what they consider a restored assemblage, as well as taking into account the natural levels of variation in reference sites. The high level of redundancy in *soil*, *nutrient* and *biotic interactions* functions suggests that there may also be multiple variations of species composition that can achieve similar levels of functioning. This is particularly important to consider given that under predicted climate change effects, specific assemblages may no longer be able to be reinstated if characteristic species have shifted range or gone extinct (Harris et al. 2006).

The lack of restoration to reference levels for most of the ecosystem functions at restored species composition, suggests that there is something that might be limiting the ecosystems from being restored to full ecosystem function. Given the nature of the ecosystem functions that were not restored, I suggest that this may be a factor of time. Ecological restoration often sets out to speed up the recovery of ecosystems; this study suggests that this may be more successful for certain functions than others.

Tongway (1990) recognised that holistic restoration should not focus solely on any one component as these may be restored at different rates. He suggests that the restoration should rather be deemed successful only once the slowest component has been restored. Aiming to restore multiple ecosystem functions requires a more in-depth knowledge of the system and often requires more complex management (Heneghan et al. 2008). This study represents a step forward in this regard by being able to identify which groups of ecosystem function are generally not restored, even when species composition has been restored to reference levels. Monitoring nutrients, soil attributes and biotic interactions may be necessary in early restoration, as they may limit the ability of the ecosystem to develop. Full restoration success, however, will only really be achieved once all ecosystem functions are restored, which this study indicates is not necessarily attained when species composition is restored.

Implications for the study of biodiversity ecosystem function relationships

Many of the results found in this study supported patterns found in BEF research. The overall relationship showed a typical asymptotic curve and most of the ecosystem functions also had quite a large degree of redundancy in species composition. This study highlighted that at zero species composition similarity to reference sites, ecosystem functioning is not necessarily also at zero similarity to reference sites. This fact is not always considered when depicting BEF models, as they tend to show zero function with zero biodiversity, which as I've discussed earlier, need not necessarily be the case.

The main difference between my results and that of BEF research was in the level of ecosystem function once full species composition had been restored, whereas with BEF research, a 'desired' state is not always defined. When relationships are examined in BEF research they often only consider what happens with increasing biodiversity, rather than comparing to a predefined level of biodiversity. This makes it hard to generalise patterns across ecosystems with different inherent levels of biodiversity or species richness. What might seem like a positive increasing relationship in a simple ecosystem may actually be a redundancy relationship in another, more diverse or species-rich ecosystem, as the former did not have high enough levels of biodiversity/species richness for the curve to asymptote. This also makes it hard to try and determine at which point the loss of species would have a significant effect on ecosystem functioning. This study provides additional insight into this question, in reverse, by examining at which point species composition similarity to reference sites has significant effects on ecosystem function similarity to reference sites. The way in which species composition metrics were calculated in this thesis allows different ecosystem to all be scaled similarly and so comparisons across them are more meaningful. The results suggest that major changes in ecosystem function happen within the first ~20% of species similarity to reference sites being restored. However, the inability of all ecosystem functions to be restored, even at 100% species composition, suggests that there is something more than species composition controlling ecosystem function restoration.

Study limitations and future directions

Most studies I examined in this thesis focused on plant species composition. Although some restoration studies may include measures of other taxa, especially invertebrates, most restoration studies still focus on restoring plant communities (Ruiz-Jaen & Aide 2005). Although plants alone may not provide a full picture of the ecosystem, many previous studies have recognised that plants may be most important to providing and maintaining ecosystem functions within the ecosystem (e.g. expert reviews in Schläpfer 1999) and as a consequence most BEF research also focused on plants (Schmid et al. 2009). As more studies examining other taxa becomes available, it should be explored whether or not incorporating these alters the relationships between species composition and ecosystem functioning. In addition, not all possible groups of ecosystem functions were able to be explored (e.g. water quality, climate regulation, disturbance, invasion resistance, resilience) with the studies that provided data, so once data become available these should also be examined to determine their relationships with restoring species composition.

Further research is needed to explore if and/or how litter, framework and biomass ecosystem functions continue to be restored even after species composition has been restored. As suggested in this Chapter 2 Discussion, it could be a factor to do with community age once composition has been restored. This is easy to envisage in ecosystems such as old growth forests, where deadwood production and extent of leaf littler production may only be at reference levels once the trees are of a certain maturity. In such cases continual monitoring may see these ecosystem functions restored on their own, over time, once composition has been restored.

The published papers used in this meta-analysis do not represent an exhaustive list of all studies measuring species composition and ecosystem function in restoration sites. Only 25 papers of 67 shortlisted were able to be used due to inability to contact authors, authors unwilling or unable to share data, or authors no longer having access to data since publication. It is also possible that some studies did not make it through the screening process, even though they may contain adequate data to allow inclusion in the meta-analysis. This is always a risk with systematic reviews, especially over such a large field of research. In this study I followed procedures outlined by Pullin & Stewart (2006) as they balance the need to be as inclusive as possible, however maintaining practicality, which was very important given the short time frame of this thesis.

As with any meta-analysis, as new studies continue to be published, results of this study should be periodically repeated to ensure its broad applicability.

Conclusion

The overall shape of the relationship examined in this thesis does indicate a degree of redundancy with ecosystem function initially increasing as restored sites become more similar to reference sites, but further similarity in composition does not necessarily confer higher functioning. All ecosystem functions were not returned even when restored sites had similar species composition to reference sites, indicating that something, possibly time, is limiting the return of full ecosystem function to restoration sites. This research indicates that the relationship between species composition and ecosystem function is not consistent and it would be unwise to use species composition or ecosystem function as proxies for one another.

This is a redirection of the current body of BEF work as it answers a more fundamental ecological question of how ecosystem functions are altered in realistic scenarios of change in composition as well as having more practical implication for restoration.

Appendix

Appendix I. Attributes considered as ecosystem functions from various papers as well as broad logical categories.

Category	Ecosystem Function	Paper
Biomass	Above ground biomass	Aerts & Honnay 2011
		Hector & Bagchi 2007
		Hooper & Vitousek 1997
	Below ground biomass	Aerts & Honnay 2011
		Hector & Bagchi 2007
	Biomass	Cortina et al. 2006
		Cuevas et al. 1991
		Ehrenfeld 2000
		Kutiel & Danin 1987
		Loreau et al. 2001
		McNaughton 1977
		Naeem & Li 1997
		Naeem et al. 1995
		Symstad et al. 1998
		Tilman et al. 1996
		Tilman & Downing 1994
		Tilman et al. 1997
		Wardle et al. 1997
	Mass balance	Hobbs & Harris 2001
	Standing crop	Hobbs & Harris 2001
Biotic Interactions	Competition	Ruiz-Jaen & Aide 2005
	Dispersal	Ehrenfeld 2000
	Herbivory	Ruiz-Jaen & Aide 2005
	Mutualisms	Ehrenfeld 2000
	Mycorrhizae	Ruiz-Jaen & Aide 2005
	Organismic interactions	Schläpfer et al. 1999
	Parasitism	Ruiz-Jaen & Aide 2005
	Pollination	Ruiz-Jaen & Aide 2005
	Predation	Ruiz-Jaen & Aide 2005
	Predation/herbivory rates	Ehrenfeld 2000
	Seed dispersal	Ruiz-Jaen & Aide 2005

Appendix I. continued

Category	**Ecosystem Function**	**Paper**
	Succession	Ehrenfeld 2000
	Trophic structure	Ehrenfeld 2000
Litter/deadwood & decomposition	Litter decomposition rates	Ehrenfeld 2000
		Hector & Bagchi 2007
		McGrady-Steed et al. 1997
	Wood decomposition	Hector & Bagchi 2007
	Leaf decomposition	Northington et al. 2011
Disturbance	Disturbance regimes	Ehrenfeld 2000
Energy Capture	Energy flow	Ehrenfeld 2000
	Exergy	Marques et al. 1997
	Fixation	Hobbs & Harris 2001
		Schläpfer et al. 1999
Invasion Susceptibility	Invasion susceptibility	McGrady-Steed et al. 1997
Microclimate	Light at ground level	Hector & Bagchi 2007
	Microclimate	Rey Benayas et al. 2009
Nutrient cycling	Mineral cycling pools	Hobbs & Harris 2001
	Nutrient cycling and storage	Schläpfer et al. 1999
	Nutrient uptake	Northington et al. 2011
	Nutrient cycling	Ehrenfeld 2000
		Finlay et al. 1997
		Maestre & Cortina 2006
		Rey Benayas et al. 2009
Nutrients	Carbon storage	Ehrenfeld 2000
	Extractable nitrogen	Tilman et al. 1996
	Immobilisation	Hobbs & Harris 2001
	Nitrogen use	Hooper & Vitousek 1997
	Nitrogen retention	Naeem et al. 1995
		Symstad et al. 1998
		Wardle et al. 1997
	Nutrient concentrations	Cortina et al. 2006
	Nutrient pools	Ruiz-Jaen & Aide 2005
	Nutrient retention	Ehrenfeld 2000
		Van Voris et al. 1980
	Potassium retention	Naeem et al. 1995

Appendix I. continued

Category	Ecosystem Function	Paper
	Soil total C/N/P	Moreno-Mateos et al. 2012
	Standing stock of nutrients	Ehrenfeld 2000
	Soil Nitrogen	Hector & Bagchi 2007
	Above ground Nitrogen pool	Hector & Bagchi 2007
Organic Matter	Organic matter	Ehrenfeld 2000
	Organic matter	Schläpfer et al. 1999
	Soil organic C/N/P	Moreno-Mateos et al. 2012
	Soil organic matter	Herrick et al. 2006
		Ruiz-Jaen & Aide 2005
Productivity	Above ground productivity	Cuevas et al. 1991
	Primary production	Northington et al. 2011
		Rey Benayas et al. 2009
	Productivity	Bulla 1996
		Ehrenfeld 2000
		Hobbs & Harris 2001
Resilience/Resistance	Resilience/resistance	Ehrenfeld 2000
Microbial activity	Respiration	Northington et al. 2011
		Wardle et al. 1997
	Respiration rate	Moreno-Mateos et al. 2012
	Respiration rates	Ehrenfeld 2000
	C02 flux	McGrady-Steed et al. 1997
Soil Structure	Bulk density	Moreno-Mateos et al. 2012
	Raindrop impact	Herrick et al. 2006
	Soil characteristics	Rey Benayas et al. 2009
	Soil formation	Ehrenfeld 2000
	Soil stability	Herrick et al. 2006
		Maestre & Cortina 2006
Water Capture & Retention	Soil moisture	Moreno-Mateos et al. 2012
	Water and wind erosion	Herrick et al. 2006
	Water flow	Ehrenfeld 2000
	Water infiltration	Maestre & Cortina 2006
	Water retention	Rey Benayas et al. 2009
	Water run-off	Herrick et al. 2006
	Water turnover rates	Ehrenfeld 2000

Appendix I. continued

Category	**Ecosystem Function**	**Paper**
Water Capture & Retention	Water capacity	Kutiel & Danin 1987
	Water catchment and regulation	Schläpfer et al. 1999
Climate Regulation	Climate regulation	Schläpfer et al. 1999
Physical framework	Cover	Ehrenfeld 2000
	Diversity	Ehrenfeld 2000
	Landscape structure	Ehrenfeld 2000
	Percent cover	Naeem et al. 1994
		Naeem et al. 1995
	Species density	Naeem & Li 1997
	Total cover	Tilman et al. 1996
Mineralisation	Mineralisation rate	Ehrenfeld 2000
		Hobbs & Harris 2001
		Moreno-Mateos et al. 2012
Water quality	Water quality	Ehrenfeld 2000

Appendix II. Characteristics of studies used for data analysis. Including country, the type of degradation, restoration type, type of composition measured, number of sites and the different ecosystem functions measured within sites as well as the ecosystem function group they fall into.

Paper	Country	Degradation type	Restoration type	Ecosystem type	Composition measured	No. restored sites	Ecosystem function group	Ecosystem function indicators measured
Andersen et al. 2003	Canada	Peat mining	Passive	Shrubland	Vegetation	8	Litter	Litter depth
							Framework	Vegetation ground cover
Bisevac & Majer 1999	Australia	Mining	Active	Shrubland	Ants	7	Litter	Litter cover
							Soil	Bare ground
							Framework	Plant height
								Vegetation cover
Brown et al. 2005	USA	Contaminated soils from mining	Active	Wetland	Vegetation	5	Biotic interactions	Bacterial biomass
								Fungal biomass
							Nutrients	N mineralisation
								Total soil organic C
Calviño-Cancela et al. 2012	Spain	Clearing & plantations	Passive	Forest	Vegetation	25	Biomass	Biovolume
Emery & Rudgers 2010	USA	Dune removal	Active	Grassland	Vegetation	18	Biomass	Plant biomass
							Nutrients	Soil organic matter
								Soil NH4
								Soil Nitrate
								Soil P
							Biotic interactions	Arbuscular mycorrhizal fungi
Forup & Memmott 2005	UK	Afforestation, agriculture, development	Active & Passive	Shrubland	Vegetation	2	Biotic interactions	Pollen transport
								Flower visitations
Forup et al. 2007	UK	Afforestation, agriculture, development	Active	Shrubland	Vegetation	4	Biotic interactions	Pollen transport
								Flower visitations

Appendix II. continued

Paper	Country	Degradation type	Restoration type	Ecosystem type	Composition measured	No. restored sites	Ecosystem Function Group	Ecosystem function indicators measured
Gibb & Cunningham 2010	Australia	Farmland	Active	Woodland	Beetles	15	Litter	Litter cover
								Logs
								Snags
							Nutrients	Soil C
								Soil N
								Soil P
Good et al. 2012	Australia	Clearing	Passive	Woodland	Vegetation	14	Biomass	Plant biomass
							Litter	Litter cover
							Soil	Bare ground
							Framework	Plant cover
							Nutrients	Soil Al
								Soil C
								Soil Ca
								Soil K
								Soil Mg
								Soil N
								Soil Na
								Soil conductance
Gould 2012	Australia	Mining	Active	Woodland	Vegetation	31	Soil	Soil stability index
							Framework	Plant height
								Patch index
								Canopy volume
							Nutrients	Nutrient cycling index
Herath et al. 2009	Australia	Mining	Active	Shrubland	Vegetation	4	Nutrients	Soil NH4
								Soil conductivity
								Soil N
								Soil organic C

Appendix II. continued

Paper	Country	Degradation type	Restoration type	Ecosystem type	Composition measured	No. restored sites	Ecosystem function group	Ecosystem function indicators measured
Herath et al. 2009 cont.							Nutrients cont.	Soil P Soil K Soil Fe Soil S
Jiao et al. 2012	China	Clearing	Active	Shrubland	Vegetation	5	Soil	Soil structure dispersion Soil bulk density Soil water content
							Framework	Plant cover
							Nutrients	Soil available P Soil available K Soil extractable N Soil organic C Soil total N Soil total P
Lomov et al. 2009	Australia	Clearing	Active	Woodland	Ants	7	Biotic interactions	Ant seed dispersal
Luo et al. 2010	China	Clearing	Active	Wetland	Vegetation	2	Biomass	Plant biomass
Martin et al. 2005	USA	Agriculture	Active	Grassland	Vegetation	3	Biomass	Productivity
							Litter	Deadwood Litter
McLachlan & Bazely 2003	Canada	Clearing	Active & Passive	Forest	Vegetation	28	Soil	Soil moisture
							Framework	Canopy cover
Meers et al. 2012	Australia	Clearing	Passive	Woodland	Vegetation	3	Biotic interactions	Seed bank composition
Miller et al. 2010	Australia	Mining	Active	Shrubland	Vegetation	2	Nutrients	Soil NO3 Soil organic C Soil total N

Appendix II. continued

Paper	Country	Degradation type	Restoration type	Ecosystem type	Composition measured	No. restored sites	Ecosystem function group	Ecosystem function indicators measured
Nakamura et al. 2003	Australia	Clearing & Grazing	Active	Forest	Arthropods	15	Soil	Soil temperature
							Litter	Litter index
								Litter depth
								Debris
							Framework	Canopy height
								Foliage cover
García-Palacios et al. 2011	Spain	Road Development	Active	Grassland	Vegetation	23	Soil	Aggregate soil stability
							Nutrients	Soil N
								Soil organic C
								Soil P
							Biotic interactions	Biological soil crusts
Parrotta & Knowles 2001	Brazil	Mining	Active	Forest	Vegetation	9	Litter	Litter depth
							Framework	Crown cover
							Nutrients	Humus depth
Polley et al. 2005	USA	Agriculture	Active	Grassland	Vegetation	10	Biomass	Plant biomass
Soini et al. 2010	Finland	Peat mining	Passive	Shrubland	Vegetation	1	Framework	Vascular green area
Sonter et al. 2011	Australia	Clearing	Active	Forest	Vegetation	3	Soil	Soil temperature
							Litter	Litter depth
							Framework	Canopy cover
								Tree stalks
								Plant cover
Stefanik & Mitsch 2012	USA	Development	Active	Wetland	Vegetation	5	Biomass	Productivity

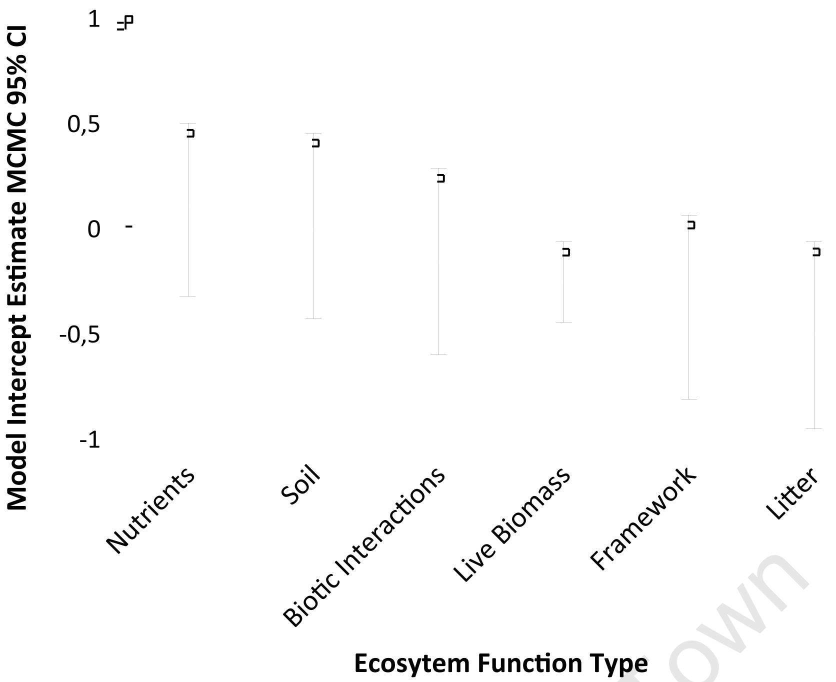
Appendix III. Number of studies used, independent restoration sites and samples for each category included in analysis. There was a total of 25 papers, 237 sites and 557 samples.

Category	Number of studies	Number of sites	Number of samples
Live biomass	7	77	77
Biotic interactions	7	61	61
Litter	8	64	64
Nutrients	10	120	120
Soil	8	120	120
Framework	10	115	115
Active	20	164	399
Passive	7	73	158
Forest	5	75	147
Grassland	4	54	139
Shrubland	8	32	62
Wetland	3	12	17
Woodland	5	64	192

Appendix IV. Corrected Akaike Information Criterion (AICc) for each general linear mixed model examining the relationship between ecosystem function and species composition as well as ecosystem function types, restoration type and ecosystem types including random factors in parentheses. Models with which did not include ecosystem function type as a fixed factor were compared to the Base Model 2, to account for possible influence of multiple ecosystem functions per sites. The model in bold was chosen as final model as it has equally low AICc (within 2 points of one another) as two other models, and contains only significant parameters.

Model	**AICc**
Base Model 1: SC + (Study)	1027
+ EF Type	940
+ EF Type + SCxEF Type	**932**
+ EF Type + Eco Type + SCxEF Type	932
+ EF Type + Rest Type + SCxEF Type	934
+ Eco Type + EF Type + SCxEF Type + SCxBiome	931
+ EF Type + Rest Type + SCxEF Type + SCxRest Type	936
+ Eco Type + EF Type + Rest Type + SCxEF Type + SCxRest Type + SCxBiome	935
Base Model 2: SC + (Study) + (EF Type)	952
+ Rest Type	953
+ Eco Type	951
+ Rest Type + SCxRest Type	951
+ Eco Type + SCxEco Type	951

SC = species composition, EF Type = ecosystem function type, Rest Type = restoration type, Eco Type = ecosystem type



Appendix V. Markov chain Monte Carlo (MCMC) 95% confidence intervals for each intercept estimate from the final general linear mixed model for ecosystem function type. Live biomass and litter categories, where confidence intervals do not overlap with zero, were considered significant.

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