

THE RECOVERY OF FUNCTIONAL DIVERSITY
WITH RESTORATION: A META-ANALYSIS

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by Sophie Adelaide Hale

University of Canterbury

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Abstract

In light of global change, there is an increasing urgency to successfully harness restoration to safeguard biodiversity and yield resilient and functioning ecosystems. In measuring

5 biodiversity, approaches that incorporate species' functional traits (i.e. measures of functional diversity) are crucial in linking biodiversity with ecosystem functioning in ways richness-based measures alone cannot. However, there lacks a comprehensive global assessment of the effectiveness of restoration in the recovery of functional diversity.

10 I conducted a meta-analysis of 30 restoration projects (freshwater and terrestrial) by extracting species lists from published studies and matching these to publicly available trait data. I compared actively and passively restored sites with degraded and pristine control sites with respect to three key measures of functional diversity (functional richness, evenness and dispersion) and two measures of species diversity (species richness and evenness). I
15 conducted separate analyses for longitudinal studies (which monitored control and restoration sites through time) and space-for-time substitutions, which compared control sites with restoration sites of different ages at one point in time.

Overall, restoration appeared to be effective in space-for-time studies, with restored sites
20 improving across multiple diversity measures over time. However, the studies that were best able to detect a difference (i.e. replicated longitudinal data) did not find sustained benefits of restoration for any measure of functional diversity, suggesting that the positive results found in space-for-time data may have been an artefact of the inability of the study design to control for regional changes across all sites. Further, active measures (i.e. guided recovery) were no

more effective than passive measures (i.e. unassisted regeneration) at restoring species diversity or functional diversity. My findings on differences across study designs explain the variable results found by recent studies that directly measured the response of functional diversity to restoration, as many did not have these controls for temporal changes, whereas the study that did found no long-term effect of restoration. Further to this, functional richness and functional dispersion increased logarithmically with species richness, though this observed relationship was no different than could be expected if assemblages of species had been generated at random. Patterns were consistent across the six taxonomic groups, six ecoregions and two realms (freshwater and terrestrial) included in this work.

10

Based on these findings, I stress the indispensability of including negative degraded controls in ongoing monitoring to distinguish the consequences of restoration efforts from unassisted temporal changes. Additionally, the failure of active restoration to outperform passive restoration suggests that allocating resources towards less intensive measures over larger areas may be a successful strategy to optimise gains for functional biodiversity.

15

Introduction

Environmental change has lead inexorably to the degradation of ecosystems and unprecedented losses of the biodiversity therein (Cardinale et al. 2012). In response to this, ecological restoration is increasingly being harnessed to safeguard species and ecosystems and to the protect the livelihoods that depend upon them (Suding et al. 2015). Restoration seeks to assist the recovery of damaged, degraded or destroyed ecosystems (McDonald et al. 2016). Restoration as a tool has immense potential, however scientists and practitioners have yet to agree on how best to assign suitable restoration targets (Perring et al. 2015), and thereafter how to quantify the success of their efforts (Ruiz-Jaen and Aide 2005). Furthermore, there is a fundamental need to agree upon how to measure biodiversity (Purvis and Hector 2000), so to accurately determine whether restoration targets (and the progress towards them) are actually leading to realised gains for species and ecosystems (Palmer et al. 2005).

Historically, measures of biodiversity have been exclusively taxonomically-based, hence species richness has often been set as an important goal for restoration (Franklin 1993, Gotelli and Colwell 2001). However, it is now widely acknowledged that the functioning of ecosystems (and the resilience of this functioning in light of global change) is pivotal for the persistence of species (Ehrenfeld 2000, McDonald et al. 2016). In recognition of this, biodiversity is increasingly being defined accorded to the differences in functional traits within a community, i.e. functional diversity (Díaz and Cabido 2001, Petchey and Gaston 2006). Functional traits are characteristics that reflect an organism's performance, whether that be the contribution it makes to an ecological function (i.e. an 'effect' trait) or the

response it has to its environment (i.e. a ‘response’ trait) (Lavorel and Garnier 2002, Violle et al. 2007). This shift in focus towards functional traits gives more insight into ecosystem functioning beyond what can be determined from species measures alone (Petchey and Gaston 2002, Diaz et al. 2004, Hooper et al. 2005, Cornwell et al. 2008). The development and improvement of functional diversity metrics has continued in recent years (Villéger et al. 2008, Laliberté and Legendre 2010, Cadotte et al. 2011), and these metrics have been applied in assessing the response of biodiversity to stressors such as land-use change (Laliberté et al. 2010), climate change (Thuiller et al. 2006) and biotic invasion (Funk et al. 2008). This avenue of functional diversity is one with promise, and the inclusion of the characteristics of species that determine their effect on and response to a changing environment has clear benefits for restoration that extend beyond what can be achieved from species’ identities alone (Palmer 2016).

Understanding how functional diversity responds to restoration will also shed light on the drivers of community assembly (Fukami et al. 2005, Funk et al. 2008), particularly the roles of niche differentiation (MacArthur and Levins 1967, Kraft et al. 2008) and habitat filtering (Keddy 1992, Diaz et al. 1998, Mouillot et al. 2007). Understanding whether both, either or neither of these two factors drive the reassembly of restoring communities could reveal whether the target of improving species richness alone would result in expansions (via niche differentiation) or reductions (via habitat filtering) of niche space by default, such that the assembly of communities could be non-random with respect to species traits (Petchey et al. 2007). Increasing richness could expand niche space if, for example, species were only able to colonise if their traits differed markedly from those of the existing community (Fargione et al. 2003). This would result in diverse communities having a greater diversity of trait values than would be expected if species were selected at random from the regional pool.

Conversely, increasing richness would not expand niche space (as much as expected at random) if subsequent species are redundant in their functional roles, for example if environmental filters only allow colonisation by species with a subset of traits (Petchey et al. 2007, Swenson 2011). It has yet to be demonstrated in the context of restoration whether species-based measures sufficiently capture information of functional diversity by default, but the answer to this question requires testing these hypotheses regarding trait diversity during community assembly. Exploring this idea could yield valuable information for scientists and practitioners as they aim to more effectively incorporate functional diversity into the planning and assessment of restoration efforts (Palmer 2016).

In recent years, published studies have begun to explore the response of functional diversity to restoration in different ecosystems and with different focal taxa; however, results have been variable. Restoration was found to yield increases in both functional diversity and species diversity (Qin et al. 2016, Rocha-Ortega et al. 2018), increases in species diversity but not functional diversity (Tullos et al. 2009, Díaz-García et al. 2017), increases in functional diversity despite no change in species diversity (Modiba et al. 2017, Derhé et al. in press), or no significant improvements in either diversity measure (Audino et al. 2014, González-Tokman et al. 2018). Two further studies reported increases in functional diversity with restoration, but did not report the responses of any species diversity measures (Hedberg et al. 2013, Rumm et al. in press). D'Astous et al. (2013) reported increases in both species and functional diversity immediately after restoration, followed by a steady decline in both metrics over time. These results taken together point to a need to explore how aspects of study design may have contributed to generating such variability in the apparent contribution of restoration to functional diversity. Furthermore, the lack of a consistent and generalisable trend in these studies, despite the importance of functional diversity as a predictor of

ecosystem functioning (Petchey and Gaston 2002) and key attribute of restoration success (McDonald et al. 2016), highlights the need for a comprehensive assessment of how restoration is performing in the reinstatement of functional diversity across taxa and ecosystems.

5

In fact, it has been argued that “given the increasing availability of trait data, it would be useful to reanalyse published results to ask whether the traits of restored communities could have predicted their response to environmental conditions imposed by restoration treatments” (Laughlin 2014). Thus, an exciting opportunity to improve future restoration practice exists in
10 conducting a global evaluation of the successfulness of previous restoration projects in recovering functional diversity.

Broadly, the aim of my research is to understand whether restoration benefits functional diversity beyond the goal of simply improving species diversity. The following questions will
15 be addressed: 1) Is there a general relationship between species diversity and functional diversity? i.e. can species diversity serve as a surrogate for functional diversity in restoration monitoring? 2) Does the observed relationship between species and functional diversity differ from what can be expected by chance alone? i.e. as species richness increases, do species
20 tend to be increasingly similar or dissimilar in their traits? 3) Does restoration increase species diversity relative to degraded negative controls, and does any influence increase with time? 4) Does restoration increase functional diversity relative to negative controls, and does this effect change with time? 5) Does the effect of restoration on functional diversity exceed that expected by chance, given any effect of restoration on species richness? 6) Does the
functional diversity of restored sites progress towards that of positive control sites over time,

and is this change faster than in negative controls? 7) Are the above effects consistent across taxa and regions?

To address these questions, I conducted a meta-analysis of previous restoration projects
5 sourced from two meta-analyses that had recently been published when I commenced this research. I extracted data on species responses to restoration and matched these to publicly available trait data across a standardised set of categories. These traits allowed me to calculate indices of functional diversity, and to conduct new analyses on the influence of restoration on functional diversity of multiple taxa across several continents.

Methods

Study selection

5 To source studies for this meta-analysis and constrain its scope, I took advantage of two recent meta-analyses of restoration impacts on communities available at the onset of this research (in early 2016). This approach served two purposes: First, it reduced any potential for me to introduce selection bias via my search criteria, inclusion of studies or delineation of timeframe for inclusion of studies. Second, by analysing studies that tested effects of
10 restoration on species diversity and composition, rather than functional diversity, I avoided the potential for publication bias to lead to studies that only found a significant influence on functional diversity (even though this bias could have influenced changes in richness). By choosing studies with species lists and acquiring my own trait data to match, I was able to standardise that process in terms of the kinds of traits selected. This was therefore an analysis
15 of raw data from a large global dataset, rather than a traditional meta-analysis of effect sizes from studies that already tested the same hypotheses as I do here. I then used studies that directly tested effects of restoration on functional diversity to validate my results (in the Discussion chapter), rather than as part of the analysis.

20 The first of the meta-analyses that served as a data source was Curran et al. (2014), which examined how species richness and composition responded to passive and active restoration. According to this study, passive restoration “relates purely to the cessation of disturbance without any additional remedial human activity,” whereas active restoration “involves a ‘guided recovery’ through targeted human interventions such as vegetation planting (e.g.,
25 with native or exotic species and under mixed or monoculture regimes), animal

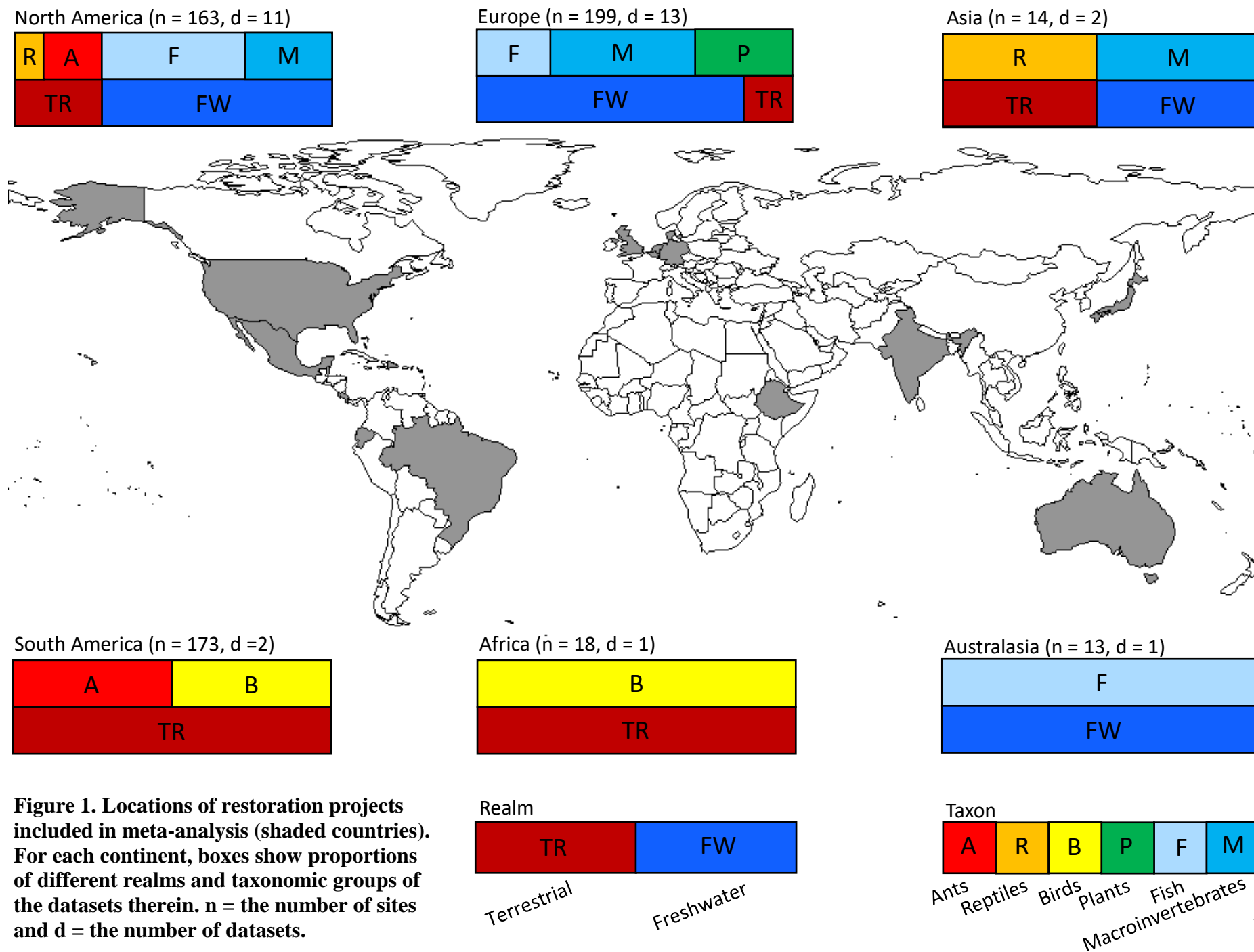
reintroductions, and the storage and replacement of topsoil following surface mining.” Their search began by screening the references of a collection of previous quantitative reviews of restoration ecology and secondary growth literature, limited to studies therein with data available for a secondary growth habitat of known age as well as a comparable old growth habitat. In addition, searches were conducted in Google Scholar and ISI Web of Science, and personal correspondence made to authors of other potentially suitable studies published after 1990. The final analyses of Curran et al. (2014) were conducted on data from 108 studies assembled across terrestrial biomes.

The second source I used was a recent meta-analysis by Kail et al. (2015), which evaluated the effectiveness of restoration in freshwater systems. Their study included data from 64 unpublished projects from three unpublished central European databases as well as 69 peer-reviewed studies assembled via Web of Science and SCOPUS searches. For replicability and verifiability, only the data from published literature were included in my analyses. Their inclusion criteria ensured that retained studies were exclusively from lotic systems, included sufficient hydromorphological and quantitative biological data and stemmed from projects where the overall objective was restoration, rehabilitation or mitigation rather than conventional engineering or flood protection.

Of the studies that comprised these two meta-analyses, datasets were included in my analyses conditional on their passing of the following selection criteria: (1) restoration activities (either passive or active) were intentionally implemented and measured in the study, as opposed to simply comparing between habitat types, (2) at least one unmanipulated (i.e. degraded) control site was included, against which to compare restored sites, (3) collated species lists included at least three different taxonomic families, so as to ensure meaningful variation in

functional diversity and (4) species presence or abundance data were provided for all individual sites across all sampling occurrences. Screening for the first criterion excluded 50 datasets, for the second, 52, and for the third, 20. Of the remaining 55 datasets, site-level species lists were provided in seven of the original publications, so to meet the fourth criterion, authors of the remaining 48 datasets were contacted to obtain full site-level species lists. Seventeen datasets were subsequently excluded either when the authors notified me that the site-level data were not available or if no reply was received. Additionally, eight datasets were excluded for lack of replication (i.e. they sampled only two sites: one unmanipulated control site and one restored site). Site-level species data were obtained for the remaining 30 datasets. Because one of my objectives was to make comparisons across taxa, I only included taxa that appeared in at least two datasets. Consequently, two studies were excluded before final analyses because the focal taxon studied was not addressed by any of the remaining studies. Details of all retained and excluded datasets are listed in Appendices A and C respectively.

Thus, my final analyses were conducted on 28 studies (on the 30 datasets therein) including six taxa: ants, birds, fish, freshwater macroinvertebrates, plants (both terrestrial and freshwater) and reptiles (Figure 1). From here, I extracted data on species responses to restoration for these datasets, then found traits for those species. These traits were then used to calculate different measures of functional diversity for each site in each study. Details of those steps are presented below.



Data extraction and collection – species and site data

I extracted site-level species lists and, where multiple taxonomic groups were sampled within a study, these data were separated by taxon. In the original publications, not all individuals were identified to species level; for simplicity, I will refer to all taxonomic entities from here on as ‘species,’ even if they were reported at a higher taxonomic level (though below I will describe how traits were assigned for these higher-level identifications). For one study, timed counts were reported (all other studies reported abundance or presence-absence data), so I took additional steps to address the inconsistent sampling effort across sites (as detailed for Aerts et al. (2008) in Appendix A). For each dataset I recorded study location, ecoregion (Palearctic, Indo-Malayan, Nearctic, Neotropical, Afrotropical or Australasian) and realm (terrestrial or freshwater), and classified restoration activities as either passive or active and controls as either positive or negative. Passive restoration was limited to cessation of past stressors such as grazing or agriculture and I defined active restoration as any intervention where sites were intentionally physically manipulated to accelerate recovery. Positive controls were reference sites that represent pristine or ‘best attainable’ conditions for a given dataset, and negative controls were unmanipulated degraded sites that were subjected to the same stressors from which restored sites had been liberated. Comparing restored sites against their respective negative controls ensures that any changes over time, in terms of species or functional diversity, can be partitioned into those which can be attributed directly to restoration efforts versus those arising from successional progression or regional (i.e. ‘gamma’) diversity of the study region through time.

Additionally, study design was categorised for each dataset as either longitudinal (sites were repeatedly measured following restoration) or space-for-time (comparisons were made between sites of different times since restoration). Longitudinal studies also measured negative control sites through time alongside restored sites, whereas space-for-time studies compared the restored sites (of various times since restoration) with separate negative control sites. Time since restoration project initiation was recorded for each site (and for each sampling event per site, in longitudinal studies). In space-for-time studies, ages of restored sites were those reported in the original publication, and ages for the negative and positive control sites were recorded as 0 and NA respectively. This means that positive control sites from space-for-time studies were not included in tests of time since restoration effects, because they could not have any time attributed to them. Additionally, as degraded (negative control) sites in space-for-time studies cannot change over time, the effect of restoration age in models of space-for-time data is only able to be compared between active and passive restoration treatments, rather than against negative control sites (as is possible with longitudinal data). In longitudinal studies, restoration age was calculated from sampling dates in the raw data, and a mean value calculated if a range of values were provided. Sampling dates preceding restoration (i.e. where restoration age < 0) were excluded from analyses, because my hypotheses did not include time before restoration, and the negative controls effectively provided a 'before' treatment.

Within each dataset, sites were blocked where necessary, for example if restored sites were paired with control sites and replicated across multiple separate streams. If, following the assignment of sites into blocks, it was discovered that a block within a dataset did not have a negative control site present, the sites within that block were excluded and analyses conducted on sites in blocks that remained in that dataset, so as to adhere to my original

selection criterion that all comparisons (which in hierarchical designs occur within blocks) must include a negative control. I then sought trait data to match the taxa represented in all the 30 datasets of community responses to restoration.

5 *Data extraction and collection – trait data*

Preceding extraction of trait data, I determined six classes of traits with which to measure functional diversity, based on those that are demonstrably important for determining the responses of species to environmental differences and/or their contribution to ecosystem functioning: body dimension, reproduction, dispersal, phenology, habitat preference and feeding.

Body size is correlated with a suite of physiological, metabolic and life-history traits (Woodward et al. 2005), and has been shown to be important for determining species responses to the environment and contributions to ecosystem processes (Larsen et al. 2005), as well as determining interactions among species (e.g. Eklöf et al. 2013) and in turn the stability of food webs (Emmerson and Raffaelli 2004). For this trait, I used measures of mass, body length, and height (in the case of plants), along with size of specific body parts (e.g. wings, tails) depending on data availability.

20

Information about a species' diet can reflect its contribution to important ecosystem functions such as seed dispersal and pollination (Şekercioğlu 2006) as well as decomposition (Botes et al. 2006). Diet has also been utilised as an indicator of species' responses to invaders, and

therefore is important for understanding competitive interactions in communities (Jackson et al. 2016). For my analyses, measures of this trait included dietary preference, feeding strategy, functional feeding group and autotrophy vs. heterotrophy in plants.

- 5 Dispersal ability is fundamental in determining the likelihood of a species to recolonise a restored habitat, and pertains to the resilience potential of a species (Green 2003). It is also important in determining species distributions following disturbance (Moretti and Legg 2009). For this trait, I included data on dispersal type, migratory status, recruitment strategy (for ants) and dispersal agent (for plants).

10

Environmental preferences and abiotic limits determine the inhabitable range of a species, with the importance of these factors being increasingly pronounced in stressful environments (Normand et al. 2009). Abiotic factors interact with biotic factors to determine species coexistence (Holt 2009). Further, taxa with specific habitat requirements are often used as an
15 indicator for environmental change (Moretti and Legg 2009). For this trait, I used a range of traits at different scales, from ecozone and biome to substrate preferences for foraging, as well as moisture tolerance (for plants).

Phenology affects a species' ability to complete its life cycle (Chaine 2010), and thus to
20 persist in degraded sites or recover in restored sites. Particularly in light of altered temperatures and climate regimes, phenological traits can reveal how these changes may affect species interactions if responses are asynchronous between trophic groups (Cleland et al. 2007). For the purposes of my analyses, I utilised data on longevity and life cycle duration, diel activity, and the lengths of breeding or spawning seasons.

Traits pertaining to reproduction included breeding and spawning preferences, clutch size, population size of a mature ant colony and pollen vectors in the case of plants. Egg size and number of offspring are known to play important roles in fitness and survival (Parker and Begon 1986), and characteristics associated with reproduction can be associated with invasion metrics (i.e. the ability of a species to recolonise an area; Hayes and Barry 2008).

These above classes were used as a basis for trait selection across taxa; all datasets incorporated into analyses included at least one trait from each of these classes to standardise information as much as possible across taxa, within data availability limitations. The only exceptions to this rule are the absence of a phenological trait for ant datasets and a dispersal trait for reptiles, as I was not able to acquire full trait information for these classes of these taxa. Where multiple traits were available for the same trait class, these traits were weighted such that each trait class was equally weighted (e.g. three different measures of body size would be each given a 1/3 weighting).

In compiling trait data to match species lists, several sources were used. Where functional data were published alongside original species lists (2 datasets), these were included, provided they fitted into one of the six trait classes and were presented for all species sampled. Where these data were not available or were available for only some of the six required trait classes, trait data were acquired from online databases exclusively (11 datasets) or from these databases supplemented by identification guide books (20 datasets). Of the 30 datasets included in this meta-analysis, I found sources of trait data for 28 of these, extracted full trait data for 24 datasets and extracted the majority of trait data for another four datasets.

Gaps that remained were sourced and extracted by research assistants. Details of the sources of trait data for each dataset are presented in Appendix B (see Tables S9 to S14).

Searches for trait data were conducted firstly on the original published taxa lists and

5 subsequently on lists including verified taxonomic synonyms of those species not found in initial searches. Some of my species data were only identified to higher taxonomic levels, such as Phylum, Order or Family, which would require some aggregation of traits to that level. By aggregating species-level trait data at each taxonomic level up to phylum and recalculating diversity indices at each stage, Mueller et al. (2013) reported significant losses
10 of information when data were aggregated to Class or Phylum level; therefore I excluded taxa entries in original publications identified to higher than Order level. Although Mueller et al. (2013) tested taxonomic sufficiency in freshwater taxonomic groups exclusively, the issue of entries being identified to higher than Order level was limited to freshwater macroinvertebrate datasets, thus the majority of datasets were not affected.

15 If trait data were not available for the resolution at which a taxonomic group was initially reported (e.g., the study identified organisms to species level, but traits could only be found for other species in the genus), trait searches were conducted within the best data source sequentially at higher resolutions as required (up to Order level). In these cases, trait data
20 were estimated by taking a mean of all taxon entries common to the group of the missing entry. Following this, when multiple taxa had their traits estimated at the same, higher taxonomic level, the abundances of these entries were pooled, and their common trait data included only once in analyses. This is because the inclusion of an additional taxon where trait data duplicate data for existing taxa does not make any contribution to functional

diversity (Paynter et al. 2012). Thus, analyses were conducted not on original site-level taxa lists but on the list of functionally unique taxa per site, as limited by trait data availability.

Although it is possible that the inclusion of aggregated data could influence results, previous studies of ecological communities have found results to be robust to data resolution

- 5 (Pakeman 2014), so I decided that the potential drawbacks of including these data were outweighed by the added benefits of their inclusion. Overall, 27.2% of total trait data were estimated at higher taxonomic levels, however the trait data shortcomings were more prominent in some taxonomic groups than others, particularly macroinvertebrates and reptiles (Table 1).

Table 1. The resolution of trait data available for different taxonomic groups. For ants and macroinvertebrates, the ‘Total number of species’ refers to the number of species before aggregation, and ‘Species with estimated trait data’ refers to the number of species that were aggregated in analyses due to sharing trait data with at least one other species. The numbers in parentheses for these groups refer to the numbers of functionally unique species that remained following aggregation. Further details are reported in Appendix A (Tables S1 to S6).

Taxonomic group	Total number of species	Species with estimated trait data	Species with estimated trait data (%)
Ants	118	26 (12)	22.0
Birds	371	59	15.9
Fish	202	3	1.5
Macroinvertebrates	1048	472 (145)	45.0
Plants	450	24	5.3
Reptiles	28	18	39.1

Functional diversity calculations

All calculations and statistical analyses were conducted using R version 3.4.3 (R Core Team 2013). I calculated functional diversity for each site from each dataset using the trait data acquired for the species in that dataset as follows. First, I computed Gower dissimilarity matrices between all species for each dataset using the daisy function in the cluster package (Maechler et al. 2017), and weighted traits such that each trait class was weighted equally even if it contained multiple measures of that trait. Gower dissimilarity matrices were my chosen distance measure primarily because they allow for traits to be weighted by class, as well as allowing the inclusion of mixed variable types (categorical and continuous). I then used the dbFD function in the FD package to calculate indices of functional diversity from the dissimilarity matrices (Laliberté et al. 2014). This function uses principal co-ordinates analysis (PCoA) and uses the axes returned as measures of orthogonal variation in traits with

which to compute functional diversity (FD) measures, which are on the same scale within a dataset. I calculated three different indices of functional diversity – functional richness (FRic), functional evenness (FEve) and functional dispersion (FDis). Functional richness is measured as the convex hull volume of the community in trait space and represents the amount of functional space (i.e. the total range of traits) occupied by species in a community. Functional richness has been shown to contribute positively to ecosystem functioning and stability, as having a greater diversity of traits in a community both increases the partitioning of available resources (Cadotte et al. 2011) and can buffer ecosystems against changeable environmental conditions (Walker et al. 1999). Functional evenness measures the regularity with which species abundance is distributed in functional space, and has been used as an index for functional integrity, with a more even distribution of niches linked to greater response diversity and therefore greater resilience (Schriever et al. 2015). Finally, functional dispersion is the mean distance of individual species to the centroid of all species in the community, weighted by species relative abundances (Villéger et al. 2008, Laliberté and Legendre 2010). An increase in functional dispersion reflects an increase in niche differentiation and therefore lower competition for resources (Derhé et al. in press).

In my calculation of FD indices, I standardised the calculation of functional richness such that it was constrained between 0 and 1. By default, this function corrects for the PCoA axes corresponding to negative eigenvalues that would bias FD estimations by taking a square root of the distances. In the instances where the species-by-species distance matrix could not be represented in Euclidean space, the correction approach described by Cailliez (1983) was applied, such that the smallest possible constant was added to all coefficients in order to eliminate all negative coefficients.

Species diversity calculations

In order to answer questions 1, 2, 3 and 5, species diversity measures were needed. Species richness values per site were taken as the number of species for which I had trait values, and species evenness was calculated as Pielou's evenness (Pielou 1969) using the vegan package (Oksanen et al. 2018). Following this, I removed from all subsequent analysis any sites where less than four functionally unique species were measured, as this did not meet the minimum level required for FD measures to be calculated.

Data analysis and design

Due to differences in the respective assumptions that apply to the interpretation of results from space-for-time and longitudinal study designs (Pickett 1989), my final data were subset by study design in all analyses conducted separately thereafter. Universally across all models, dataset and block were included as nested random variables in that order: dataset to account for inherent differences between dataset locations and researchers, block to control for spatial autocorrelation within studies, when this existed. When there was no non-independence in the design of a study, all sites therein were treated as if in one block. Site was also nested within block for repeated sampling across years in the longitudinal designs. Space-for-time designs by definition do not include repeated sampling; therefore, site was not included as a random effect when evaluating these datasets.

I conducted linear mixed effects models and generalised linear mixed models fit by the Laplace approximation using the lme4 package (Bates et al. 2014). The lmerTest package

was used to estimate degrees of freedom and test hypotheses with Satterthwaite's method of denominator synthesis (Kuznetsova et al. 2017). These models were used to test for effects of restoration treatment, restoration age (i.e. time since the restoration intervention began) and realm (and all two-way interactions) on species richness (Poisson error distribution), species evenness (gaussian error distribution) and all computed FD measures and z scores (gaussian error distribution). Multi-model selection was conducted based on the Akaike Information Criterion (AIC).

Model selection

For each of the models specified below, I first visually assessed data with gaussian errors for linearity and log-transformed variables where this improved linearity. After any required transformations had been conducted, I ran the maximal model with all possible combinations of random effects, including random slopes for the effect of treatment within either taxon or ecoregion. I then selected the combination yielding the lowest AIC as the best random structure. With this random structure, models were run with all possible subsets of fixed effects (and their interactions) and the best model selected based on the lowest AIC value. I tested best-fitting linear (i.e. gaussian) models for homogeneity of variances and normality based on residuals plotted using the ggplot2 package (Wickham 2009) and generalised models for overdispersion by calculating the sum of squared Pearson residuals and comparing it to the residual degrees of freedom. To correct for overdispersion, an observation-level random effect term was included in generalised linear mixed-effects models where necessary (Elston et al. 2001).

Additionally, in all analyses where species evenness was included as a predictor or a response variable, these were conducted after excluding the three studies where original site-level data were presence-absence only (rather than abundance or count data). However, models with functional evenness as a response variable (with predictors other than species evenness) did
5 include these three studies, because changes to evenness in trait space can be attributed both to changes in the evenness of the distribution of abundance among species or changes in the regularity of functional distances among species (Villéger et al. 2008).

Model structure

10

To answer the broad question of how functional diversity responds to restoration, it was important to tease apart and test the relationships that may be driving this response.

Specifically, an increase in functional diversity with restoration could be a direct response, or indirectly driven by an increase in species diversity, which in turn yields a proportionate

15 increase in functional diversity by default.

To distinguish between these possibilities, I first tested the relationship between functional diversity and species diversity (Question 1), supported by additional analyses where I used a null model to determine whether the relationship I observed differed from what would be

20 expected by chance alone. Then, I tested the effect of restoration on species diversity. Finally, I assessed how restoration treatment affects functional diversity, and tested the robustness of this result compared to null expectations.

After initially removing interactions and main effects during model selection, the next step was to collapse the factor levels of restoration such that active and passive were combined into one level (called ‘restored’) and compare the fit of the best models with and without collapsing. Of these, the model with the lowest AIC was used and is interpreted in the text.

5 This did not apply when testing for the effect of species diversity on functional diversity (Question 1 below), as restoration was not included as a factor in these models. When factor levels were collapsed and data were space-for-time, it was not possible to test for a time by treatment interaction; as positive and negative controls are assumed to be unchanging over time in space-for-time substitutions. Thus, with actively and passively restored treatments
10 collapsed together, there is no control temporal trend against which to compare that of the restored sites. Finally, in cases where there was a significant interaction effect between realm and either time or treatment, I tested whether the coefficient for the time or treatment effect in the non-intercept realm was significantly different from zero using a t-test. The above principles were applied throughout my analyses, and the models to test specific questions are
15 described here:

1) Is there a general relationship between species diversity and functional diversity? i.e. can species diversity serve as a surrogate for functional diversity in restoration monitoring?

20 To assess the relationship between species diversity and functional diversity, I conducted linear mixed-effects models for each of FRic, FDis and FEve as response variables. Realm (freshwater vs. terrestrial), the respective measure of species diversity (richness for FRic and FDis and evenness for FEve) and their interaction were included as fixed effects in all maximal models.

2) *Does the observed relationship between species and functional diversity differ from what can be expected by chance alone? i.e. as species richness increases, do species tend to be increasingly similar or dissimilar in their traits?*

5

Several of my focal questions involved tests of how functional diversity responded to restoration. However, after showing that functional diversity is related consistently to species diversity (Question 1), I was interested in whether any effects of restoration on FD were simply consequences of restoration increasing richness and higher richness being associated with higher FD.

10

It could be expected *a priori* that more species-diverse communities will have greater diversity in traits (Mayfield et al. 2010). Therefore, to test how functional richness should increase at random based on the number of species, I calculated z-scores that measured how the observed functional richness values differed from random expectations (i.e. simulated values, see description below) per site, and modelled how these responded to realm, species richness and their interaction as predictors. If the relationship between species richness and z-scores was significant and positive, it would suggest that increasing the number of species is associated with an expansion of niche space greater than could be expected by chance.

Conversely, a negative relationship would suggest that increasing species richness does not expand niche space as much as expected at random, rather that subsequent species are redundant in their functional roles (perhaps due to trait filtering).

15

20

Therefore, to distinguish whether observed changes in FRic were due entirely to changes in species richness, I used a simulation approach to determine how FRic would be expected to change at random with different numbers of species. The simulations iteratively drew species at random from the regional pool (i.e. all species in a study) to generate communities of fixed richness, and then calculated null FRic per random community, against which to compare my observed results. Here I treated as separate ‘sites’ each sample through time in the longitudinal studies. Each site by species matrix (one for each dataset) was randomised using the randomizeMatrix function in the Picante package (Kembel et al. 2010). This function shuffles values (i.e. 1s and 0s, for the presence/absence of species) within rows (sites) whilst holding species richness constant to the initial value of that site. FRic was then calculated for each of 100 iterations per site, to generate a null distribution of expected functional richness for each site, if the species in that site had been drawn at random from the species pool of the study. In all studies where abundance data were provided, site by species matrices were converted to binary before randomisation began. This is because it is difficult to objectively say how abundances should be shuffled in a way that produced a realistic abundance distribution of species (which would not be achieved by shuffling individuals at random across species). For its dependence on species abundances, I therefore did not conduct simulations for FEve, nor for FDis due to the lack of a direct species analog (i.e. FRic had species richness and FEve had species evenness).

With the simulated data, I calculated z-scores per site for how observed FRic deviated from random expectation given the number of species in that site. These z-scores were calculated by subtracting the mean simulated value from the observed value per site and dividing this by the standard deviation of the simulated values. If some of the 100 iterations did not calculate FRic (i.e. because the simulated species richness was too low), the mean simulated value was

calculated from the remaining iterations. This step was only necessary in three of 523 sites (or sampling events of a site, in the case of longitudinal data), and in all cases at least 84% of iterations successfully calculated a functional richness value. To test whether 100 iterations of the null simulation were sufficient, z-scores per site were calculated based on different numbers of iterations and were found to stabilise well before this number (Figure 1).

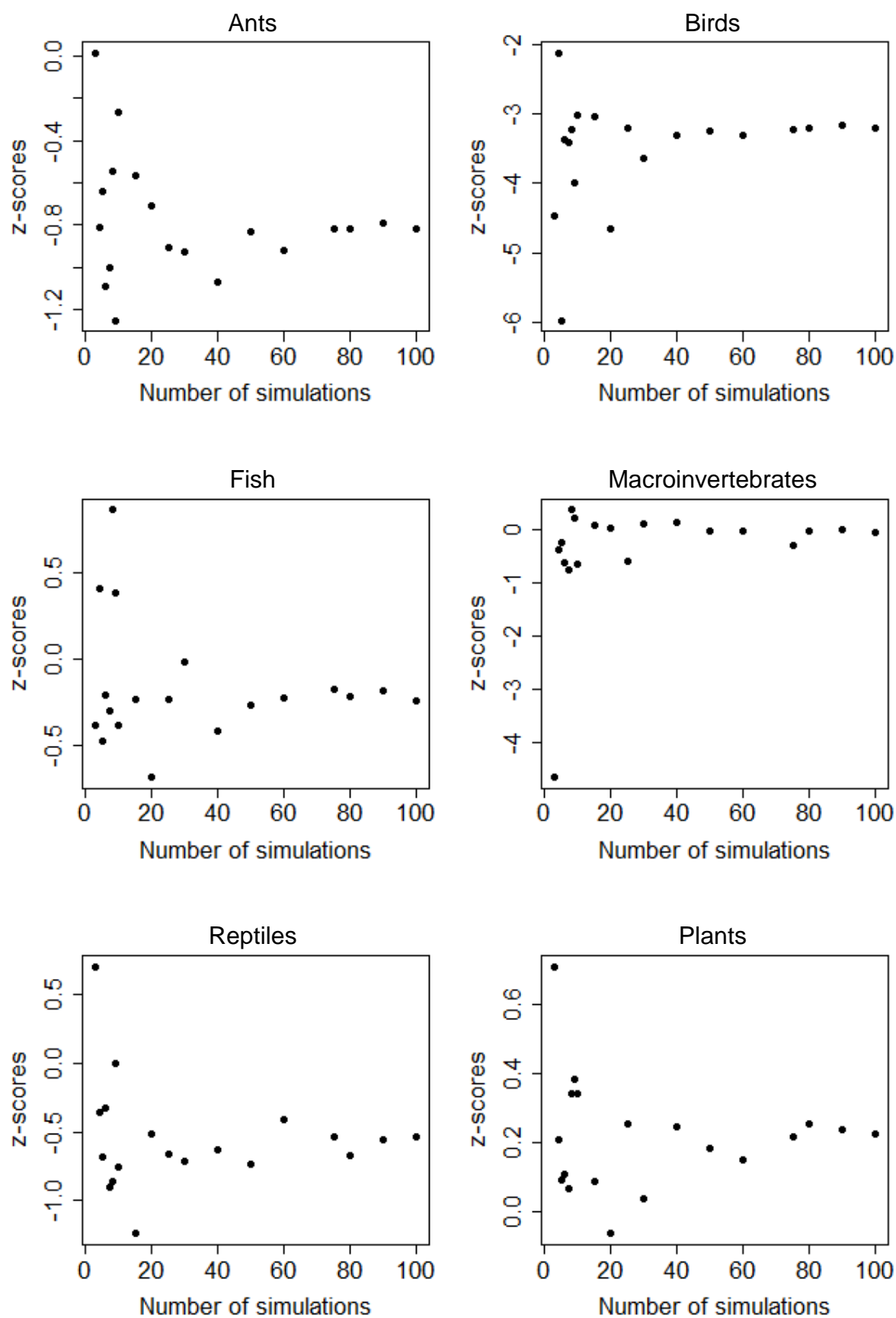


Figure 2. Changes in z-scores with an increasing number of simulations in six randomly chosen sites (one per taxonomic group), up to and including the number of trials executed in simulations (100).

3) *Does restoration increase species diversity relative to negative controls, and does this increase with time?*

To investigate the effect of restoration on species richness and evenness, I conducted Poisson
5 generalised linear mixed-effects models and linear mixed-effects models respectively, with
realm, restoration treatment and years since restoration (and all two-way interactions) as
fixed effects in each maximal model.

4) *Does restoration increase functional diversity relative to negative controls, and does this
10 effect change with time?*

After exploring the above relationships, the final step was to test for an effect of restoration
on functional diversity. To do this, I conducted linear mixed-effects models with FRic, FEve
and FDis as response variables and realm, restoration treatment and years since restoration
15 (and all two-way interactions) as fixed effects in each maximal model.

5) *Does the effect of restoration on functional diversity exceed that expected by chance given
species richness?*

20 Beyond expecting *a priori* that more species-diverse communities will have more diverse
traits, it could be expected that the extent to which observed sites differ from random
expectation (i.e. the extent to which greater-than-random redundancy or trait dissimilarity
occur) differs across restoration treatments. Therefore, to test whether restoration affects
whether functional diversity increases at random based on the number of species, I modelled

the z-scores calculated from the observed and simulated values per site as the response variable (as in Question 2 above) and included realm, restoration treatment, years since restoration and all two-way interactions as predictors.

- 5 *6) Does the functional diversity of restored sites progress towards that of positive control sites over time, and is this change faster than in negative controls?*

To assess whether restored sites move away from the functional diversity of negative controls and toward that of positive control sites, I calculated $FRic_{dist.from.positive}$, $FEve_{dist.from.positive}$ and
10 $FDi_{dist.from.positive}$ by subtracting the respective $FRic$, $FEve$ and FDi values away from the FD value of the corresponding positive control within each block. In cases where there were multiple positive control sites within a block, an average FD value was calculated and used thereafter. Analyses of these additional measures were limited to the subset of space-for-time studies (9 studies) that had positive controls within the same blocks as the restored and
15 negative control sites. In this way, I can ask whether there exists a directed endpoint of functional diversity towards which communities converge, as would be expected based on the functional trait filtering observed by Fukami et al. (2005). Note that Question 7 ('Are the above effects consistent across taxa and regions?') will be answered alongside the above questions.

Results

It is important to note that in space-for-time data, the main effect of restoration treatment (i.e. differences among control, passive and active intercepts) cannot be meaningfully interpreted, as the intercept terms for restored sites are extrapolated beyond the scope of the data; all restored sites have restoration age >0 . Therefore, the main effect of years since restoration in space-for-time studies is used as a proxy for the effect of restoration, with the caveat that this covariate could not be calculated for degraded (negative control) or pristine (positive control) sites (see Discussion for full explanation).

1) Is there a general relationship between species diversity and functional diversity? i.e. can species diversity serve as a surrogate for functional diversity in restoration monitoring?

Sites with higher species richness had significantly higher functional richness in longitudinal studies ($t = 21.613$, $p < 0.0001$; see Figures 3a and 6a), and a non-significant tendency toward higher functional richness in space-for time studies ($t = 2.410$, $p = 0.0591$; see Figure 3b and Table S16 in Appendix D). Longitudinal and space-for-time designs both showed significant positive relationships between species richness and functional dispersion ($t = 2.408$, $p = 0.0169$; $t = 6.197$, $p < 0.0001$ respectively; see Figures 3c, 3d, 6a and 6c). The best-fitting models for FDis in both designs and for FRic in longitudinal studies had species richness log-transformed, indicating that these relationships were saturating.

In space-for-time studies, the relationship between species richness and functional richness varied across taxa and ecoregions (the random slopes for richness significantly improved

model fit), whereas none of these random slopes were retained in the model using longitudinal data. Moreover, when testing for the relationship of species richness with functional richness and functional dispersion, taxon and ecoregion were removed as random effects in model selection, suggesting that the relationship between richness and both functional richness and dispersion were generally consistent across species, locations and biomes.

In longitudinal studies, differences in species evenness across sites were not associated significantly with differences in the evenness of their distribution in functional trait space (Figure 3e; species evenness was removed in model selection). In contrast, in space-for-time data, terrestrial sites had significantly higher functional evenness with increasing species evenness (comparison of slope for effect of species evenness with zero: $t = 2.841$, $p = 0.0049$; see Figure 6d), however freshwater sites showed a non-significant tendency towards lower functional evenness with increasing species evenness (comparison of slope for effect of species evenness with zero: $t = -1.927$, $p = 0.0572$).

Together, these results suggest that as communities increase in the number of species present, the volume of trait space occupied by that community increases. However, the rate at which trait space fills (i.e. the extent to which functional diversity increases in communities with more species) is saturating. In addition, species are on average more distant from the community average (i.e. the centroid in trait space) as richness increases, however this relationship is saturating; thus, traits become increasingly redundant at high richness (species richness was log-transformed in the best-fit models). It is not surprising that functional richness increases with species richness (it may even be an inevitable consequence of the way in which functional diversity is calculated), but this is nevertheless an important prerequisite

for interpreting the following questions. Lastly, having individuals distributed more evenly across different species in a community had inconsistent effects on the evenness of the distribution of individuals across species in terms of their functional traits.

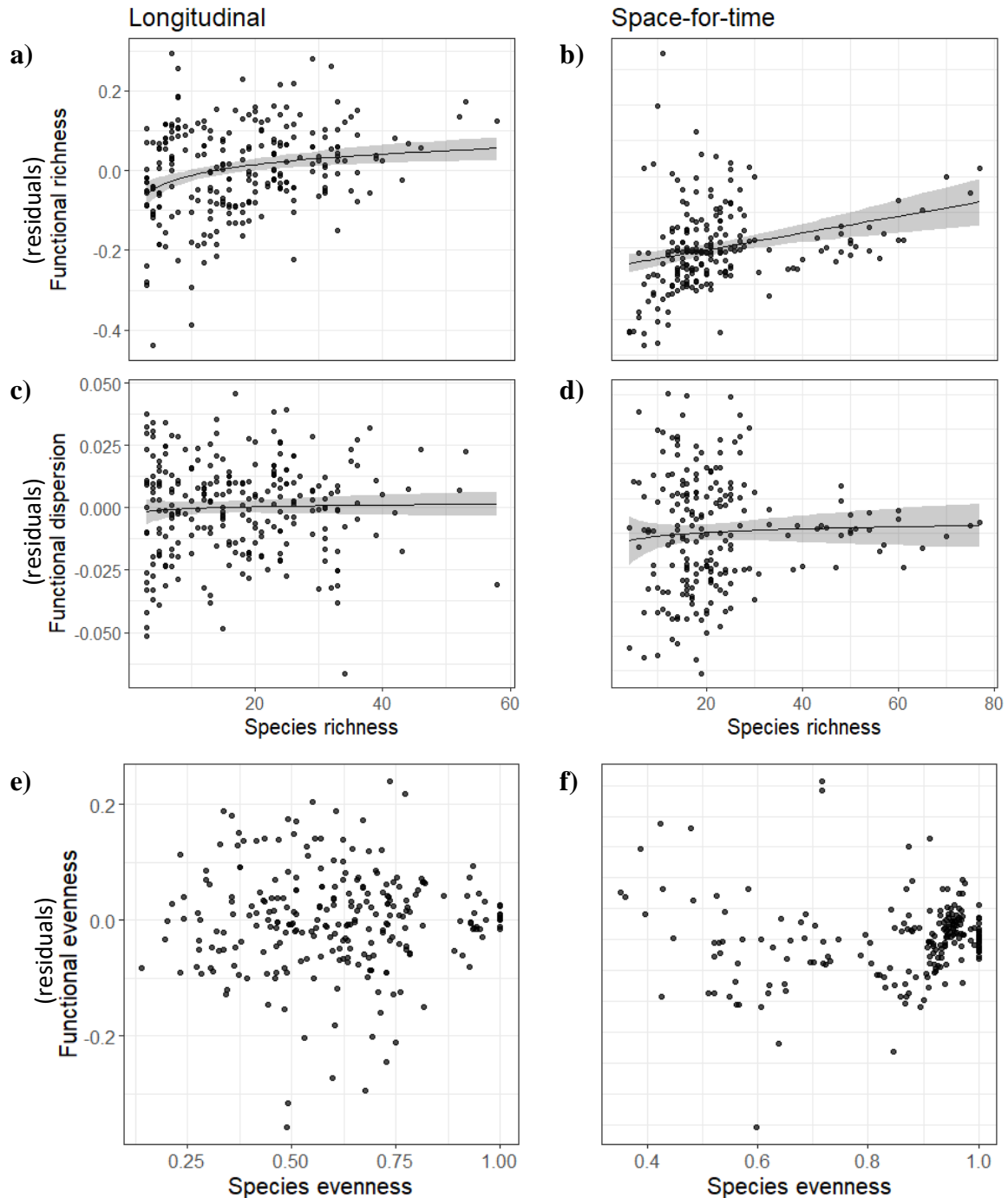


Figure 3. The relationships between species richness and functional richness (a and b), species richness and functional dispersion (c and d) and species evenness and functional evenness (e and f). Data from longitudinal studies are shown in a, c and e; data from space-for-time studies are shown in b, d and f. Plotted values are the residuals having taken into account all random effects in each model (see Table S16 in Appendix D). In models for a, c and d, species richness was log-transformed for linearity. Predicted lines are shown, bounded by 95% confidence intervals, where significant relationships were found.

2) Does the observed relationship between species and functional diversity differ from what can be expected by chance alone? i.e. as species richness increases, do species tend to be increasingly similar or dissimilar in their traits?

5 The accumulation of functional richness with species richness did not differ from what could be expected at random (species richness was removed in model selection in both longitudinal and space-for-time studies). In space-for-time studies, z-scores for freshwater sites tended to be higher than the mean of the null distribution of expected z-scores (intercept estimate: 0.4009), though in terrestrial sites z-scores tended to be lower (estimated mean z-score for
10 terrestrial sites: -0.6981; see Table S17 in Appendix D). Although terrestrial sites were significantly lower than freshwater sites in terms of their z-scores ($t = -3.718$, $p = 0.0003$), the mean z-scores of both realms fell within the range of the null distribution that could have been expected by chance alone. Therefore, the level of functional richness observed in all cases is no different than what could be expected at random, given species richness.
15 Additionally, there were many more terrestrial than freshwater studies with this design (242 vs. 37 replicates, respectively), so inferences about this between-realm difference should be made with caution.

*3) Does restoration increase species diversity relative to negative controls, and does this
20 increase with time?*

The data showed a significant positive relationship between years since restoration and species richness across study designs (longitudinal, $z = 4.265$, $p < 0.0001$; space-for-time, $z = 3.632$, $p = 0.0003$; see Figures 5a, 5b, 6a and 6c and Table S18 in Appendix D). However,

there was no significant interaction between restoration treatment and time since restoration began where this could be detected (longitudinal data: interaction term removed in model selection). Thus, the observed increase in species richness over time occurred in all treatments, i.e. in negative control sites as well as restored sites. The random effect for taxon was retained in the best-fitting models in space-for-time and longitudinal sites, with individual taxon intercepts varying from 2.832 to 3.467 and 1.989 to 2.995 respectively. In space-for-time sites, random slopes for restoration treatment across taxa were also retained, with birds in particular having large differences between active and passive restoration, whereas ants and macroinvertebrates showed smaller effects of restoration type.

In longitudinal studies, passively restored sites were significantly richer in species than negative control sites at the onset of restoration (difference among treatments at intercept: $z = 2.078$, $p = 0.0378$; Figure 6a). However, actively restored and positive control sites were not significantly different from negative control sites in their species richness ($z = 0.825$, $p = 0.4095$; $z = -0.647$, $p = 0.5175$ respectively). In longitudinal studies, species richness was lower in terrestrial than freshwater sites ($z = -2.607$, $p = 0.0091$), but this difference diminished over time as terrestrial sites increased in richness more rapidly than freshwater sites with increasing time since restoration (realm * time interaction: $z = 2.460$, $p = 0.0139$). However, there were many more freshwater than terrestrial studies with this design (239 vs. 18 replicates, respectively) and, in terms of treatment, a greater number of actively than passively restored sites (116 vs. 6 replicates, respectively), so inferences about these differences should be made with caution.

In space-for-time studies, actively restored terrestrial sites were significantly richer in species than terrestrial negative control sites ($z = 3.769$, $p = 0.0002$; Figure 6c), although this relationship was not observed in freshwater sites (comparison of fitted mean with zero: $z = -1.218$, $p = 0.2231$), nor in the terrestrial sites that underwent passive restoration measures (terrestrial, comparison of fitted mean with zero: $z = 0.568$, $p = 0.5703$; no freshwater sites were passively restored). Additionally, space-for-time data showed a significant and positive interaction such that the benefits of active restoration were greater in the terrestrial realm (interaction: $z = 6.705$, $p < 0.0001$). In this design, the positive relationship of time with richness was driven by freshwater sites alone (terrestrial, comparison of fitted mean with zero: $z = 0.749$, $p = 0.4538$), and there was a significantly negative interaction such that the effect of time and the terrestrial realm were non-additive ($z = -3.561$, $p = 0.0004$). Although most studies comprising the space-for-time subset were conducted in the terrestrial realm (164 vs. 41 replicates, respectively), the high level of replication overall validates the robustness of these results, particularly the patterns observed in terrestrial datasets.

Alongside increases in species richness through time, species evenness increased with years since restoration in both study designs (space-for-time, $t = 2.840$, $p = 0.0051$; longitudinal, $t = 3.105$, $p = 0.0028$; see Figures 4a, 4b, 6b and 6d). However, restoration treatment and realm (including random slopes for the effect of restoration across realms) were removed as factors from models predicting species evenness in both study designs. Thus, the way in which species evenness increased over time was consistent across restored and control sites in freshwater and terrestrial realms in space-for-time and longitudinal studies.

Overall, I found that over the course of the restoration programmes included in these datasets, sites increased through time both in terms of the number of species present (species richness)

and in the regularity of the distribution of individuals across these species (species evenness).

In general, these relationships through time held for positive control, restored and negative control sites. Aside from the effect of time, there were some increases in richness in restored sites relative to negative control sites, but these were not consistent across restoration

5 treatments, realms and study designs.

4) Does restoration increase functional diversity relative to negative controls, and does this effect change with time?

10 Echoing results found for species richness, I found a ubiquitous increase in functional richness and functional dispersion as time since restoration increased (space-for-time, FRic, $t = 5.142$, $p < 0.0001$; longitudinal, FRic, $t = 3.050$, $p = 0.0026$; space-for-time, FDis, $t = 2.076$, $p = 0.0411$; longitudinal, FDis, $t = 2.690$, $p = 0.0077$; see Table S19 in Appendix D and Figures 5c, 5d, 5e, 5f, 6a and 6c). However, there was no significant interaction between

15 restoration treatment and time since restoration began where this could be detected (longitudinal data: interaction term removed in model selection). Thus, the observed increases in functional richness and functional dispersion over time were observed all sites, including negative control sites. As with species richness, space-for-time data showed that freshwater sites increased in functional richness over time much more rapidly than terrestrial

20 sites (realm * time interaction: $t = -4.625$, $p = 0.0001$), although at project initiation there was no significant difference between realms (realm main effect: $t = -0.657$, $p = 0.5241$).

Model selection for functional richness in both longitudinal and space-for-time designs retained actively and passively restored as separate factor levels. In space-for-time studies,

25 actively restored freshwater sites were not significantly richer in species than freshwater

negative controls ($t = -0.937$, $p = 0.5224$), however, for terrestrial sites there was a significant positive interaction where the negative (but nonsignificant) main effects of active restoration and terrestrial realm on species richness were sub-additive (interaction: $t = 3.607$, $p = 0.0004$). Additionally, in the space-for-time design, actively restored sites increased more slowly over time in terms of functional richness compared with passively restored sites (interaction: $t = -2.338$, $p = 0.0212$).

The random effects for taxon and ecoregion were retained in the best-fitting model of functional richness in space-for-time sites, with individual taxon and ecoregion intercepts varying from 0.137 to 0.537 and 0.282 to 0.456 respectively. Random slopes for treatment across taxa and ecoregions were also retained, with plants and ants having particularly large differences between active and passive restoration, whereas fish and macroinvertebrates had smaller effects of restoration type. In terms of ecoregions, the largest differences between restoration types were in Indo-Malayan and Afrotropical sites and the smallest differences in the Nearctic and Neotropical sites. However, the replication of sites in these four realms were five, eight, two and 131, respectively, so any ecoregion-specific inferences should be made cautiously.

In longitudinal studies, there were no significant differences in functional richness between actively restored or passively restored sites when compared with negative control sites ($t = 0.804$, $p = 0.4251$; $t = 0.473$, $p = 0.6377$, respectively). Functional richness in longitudinal studies did not differ significantly between positive and negative freshwater control sites (comparison of control site fitted means: $t = -0.160$, $p = 0.8734$), though negative control sites were functionally richer than positive control sites when looking at terrestrial sites alone (fitted mean: $t = -2.413$, $p = 0.0186$). However, in comparing positive control with negative

control sites in freshwater and terrestrial realms, replication in the latter was very low (37 vs. 87 and 6 vs. 6 respectively), so caution must be taken when making inferences about realm-specific differences between control treatments.

- 5 In longitudinal studies, active and passive restoration were collapsed into a single factor level in model selection for functional dispersion. This model revealed that restored sites were significantly more functionally dispersed than negative control sites at project initiation (i.e. species in restored sites were on average significantly further away from the community trait centroid than species in negative control sites; $t = 2.507$, $p = 0.0151$; see Figure 6a).
- 10 Additionally, the increase in functional dispersion over time was much more rapid in negative control than positive control sites (interaction: $t = -2.620$, $p = 0.0107$). In space-for-time studies, there were no significant differences in the distance of species from the community average in trait space (i.e. functional dispersion) between realms or restoration treatments (realm and restoration treatment were removed in model selection).

15

- Following the lack of change in species evenness following restoration, in both study designs I found no significant differences in functional evenness between restored and negative control sites or as time since restoration increased (Figures 4c and d; restoration treatment and years since restoration were removed in model selection). In space-for-time data,
- 20 terrestrial sites tended to be more even in their distribution in trait space than freshwater sites, though strictly speaking this was not statistically significant ($t = 2.177$, $p = 0.0504$).

- Overall, space-for-time studies reported positive effects of restoration (i.e. years since restoration main effect) on functional richness and dispersion. In longitudinal data, restored
- 25 sites were more functionally dispersed than negative control sites at project initiation,

however all sites (positive control, restored and negative control) improved over time both in terms of functional richness and dispersion. Finally, across all sites in both study designs, functional evenness did not change with restoration or time since restoration.

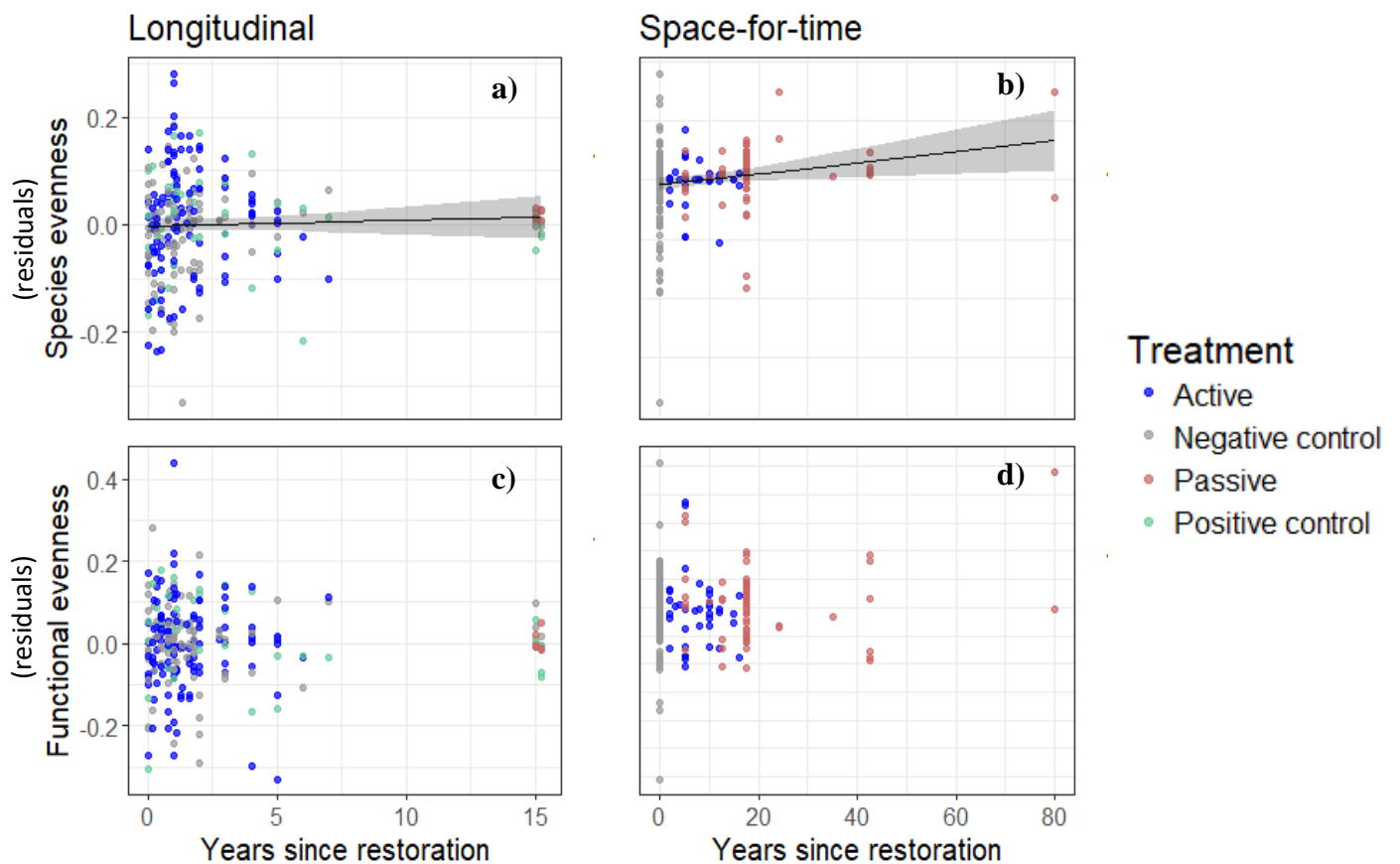


Figure 4. The relationship between species evenness (a and b) and functional evenness (c and d) with years since restoration. Data from longitudinal studies are shown in a and c; data from space-for-time studies are shown in b and d. Plotted values are the residuals having taken into account all random effects in each model (see Tables S18-19 in Appendix D). Predicted lines are shown, bounded by 95% confidence intervals, where significant relationships were found.

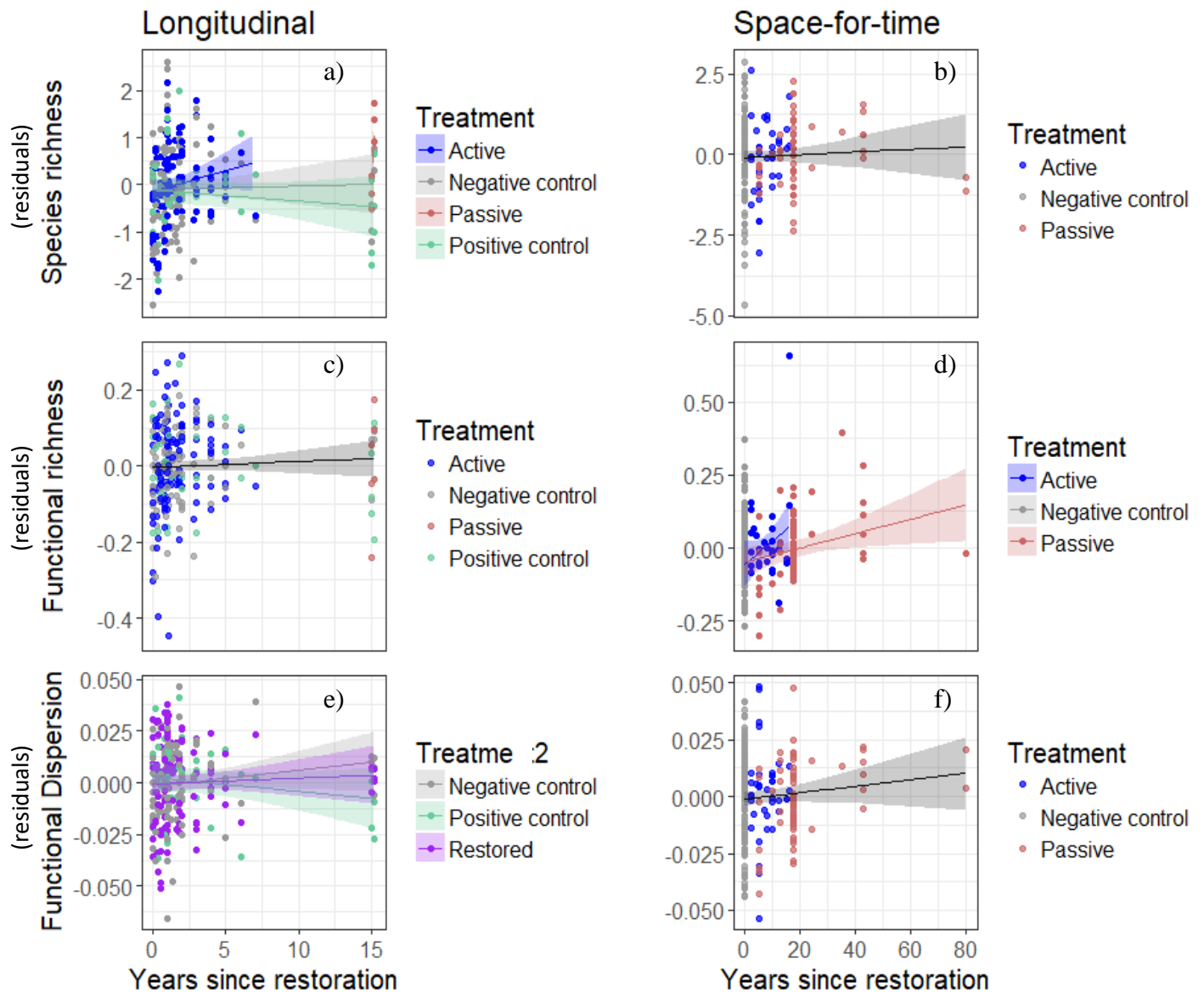


Figure 5. The relationship between species richness (a and b), functional richness (c and d) and functional dispersion (e and f) with years since restoration in longitudinal and space-for-time studies. Data from longitudinal studies are shown in a, c and e; data from space-for-time studies are shown in b, d and f. Plotted values are the residuals having taken into account all random effects in each model (see Tables S18-19 in Appendix D). Predicted lines are shown, bounded by 95% confidence intervals, where significant relationships were found, and separated by treatment in graphs depicting models where this factor was significant. The model selection for e, active and passive restoration were collapsed into one level in the factor for restoration treatment.

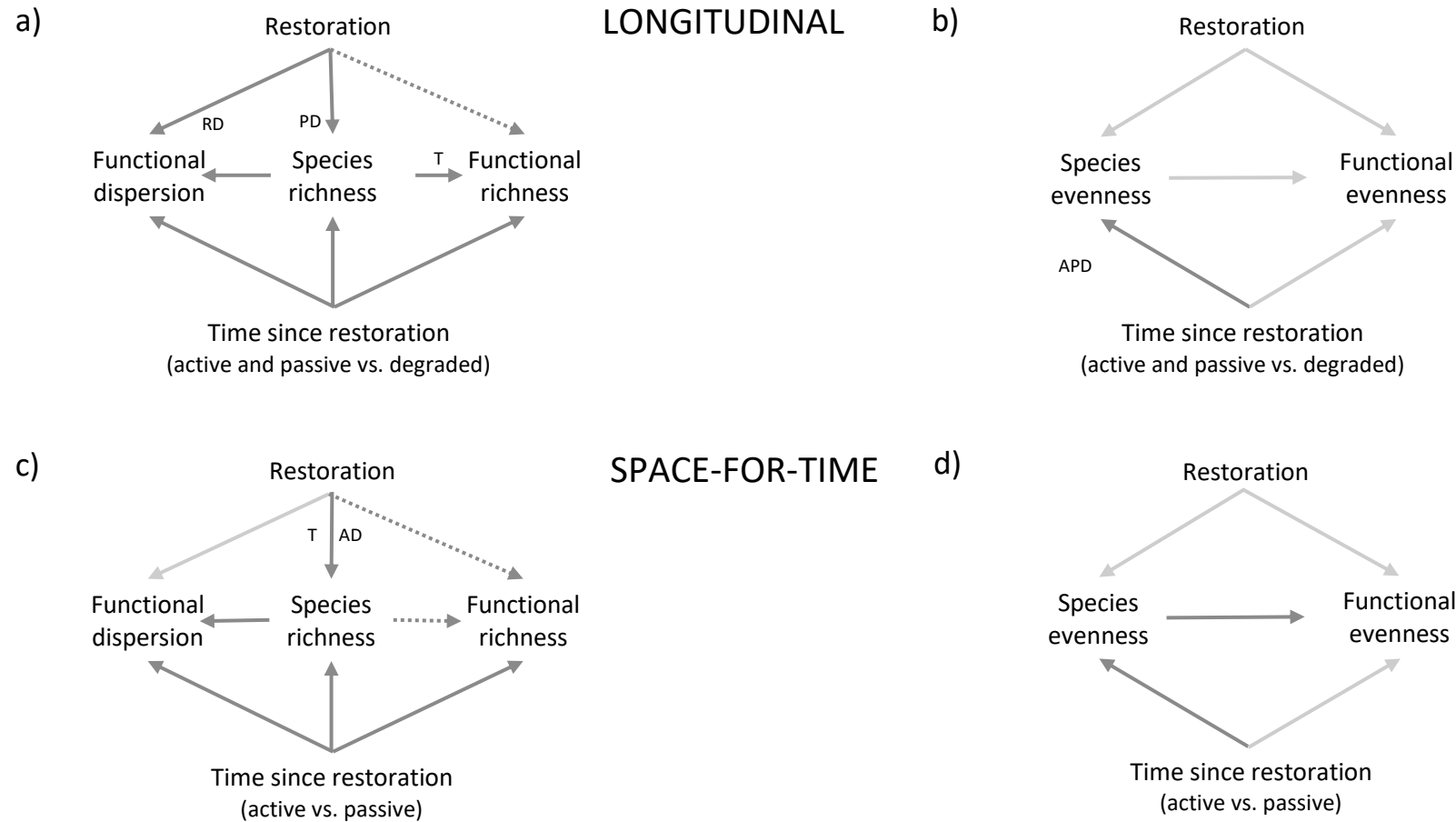


Figure 6. The relationships between species diversity and functional diversity measures, and the effects on both of restoration treatment and years since restoration. a) and b) present data from longitudinal studies; c) and d) present data from space-for-time studies. Dark grey solid arrows represent significant and positive relationships, dark grey dashed arrows represent non-significant relationships (where $p > 0.05$ but the variable was retained in model selection), and light grey arrows represent variables removed in model selection. In all cases, the effects of time and restoration were additive, not synergistic. Arrows depicting significant effects of restoration on diversity are coded by between which sites the restoration effects report a difference: AD = active vs. degraded; PD = passive vs. degraded; RD = restored (with active and passive collapsed into one factor level) vs. degraded. Where a 'T' is adjacent to an arrow, the relationship varied with taxon (taxon was retained as a random effect in model selection). In space-for-time studies, interpretation should focus on the time since restoration effect, rather than the main effect of restoration treatment (see main text). Although not shown, realm was also included as a predictor in model selection.

5) *Does the effect of restoration on functional diversity exceed that expected by chance given species richness?*

Across restored, positive control and negative control sites, the observed level of functional richness did not differ from what could be expected at random; restoration treatment was removed as a predictor of z-scores (deviation of observed functional diversity from random, given the number of species) during model selection for both longitudinal and space-for-time studies. In space-for-time studies there was a non-significant tendency for the z-scores of terrestrial sites to be lower than those of freshwater sites ($t = -2.747$, $p = 0.0909$), and in both terrestrial and freshwater realms, z-scores tended to be lower than the mean of the null distribution (coefficient estimates of -0.7868 and -0.2710 respectively; see Table S20 in Appendix D). However, neither estimate fell near either tail of their respective null distributions, thus the level of functional richness observed reflected what could be expected by chance alone, given species richness, and irrespective of restoration.

6) *Does the functional diversity of restored sites progress towards that of positive control sites over time, and is this change faster than in negative controls?*

Over time, both restored and negative control sites progressed towards positive control sites in trait space with respect to all functional diversity measures tested (relationship between time since restoration began and: functional richness, $t = -2.627$, $p = 0.0115$; functional evenness, $t = -2.390$, $p = 0.0181$; functional dispersion, $t = -3.216$, $p = 0.0016$; see Figures 7a, b and c and Table S21 in Appendix D). This progression was observed for sites in both freshwater and terrestrial realms and, in the cases of functional evenness and dispersion, was

consistent across ecoregions and taxonomic groups (both random effects were removed in model selection). In testing functional richness in this context, taxon and ecoregion were retained as random effects, as were random slopes for the effect of treatment across these. However, treatment was removed in model selection, so the retained random slopes cannot be
5 meaningfully interpreted.

In exploring whether sites approached the functional dispersion of positive controls, the best-fitting model retained actively and passively restored as distinct factor levels after model selection. Passively restored sites were significantly more distant than negative control sites
10 from positive control sites in terms of functional dispersion ($t = 5.492$, $p < 0.0001$), though actively restored sites were not significantly more distant than negative control sites from positive control sites ($t = 0.645$, $p = 0.5196$).

Taking the functional diversity of positive control sites as a yardstick for restoration, these
15 results suggest that actively restored, passively restored and negative control sites progress over time; sites progress in how much trait space they occupy, how functionally even communities are in trait space, and how dissimilar species are from their community average.

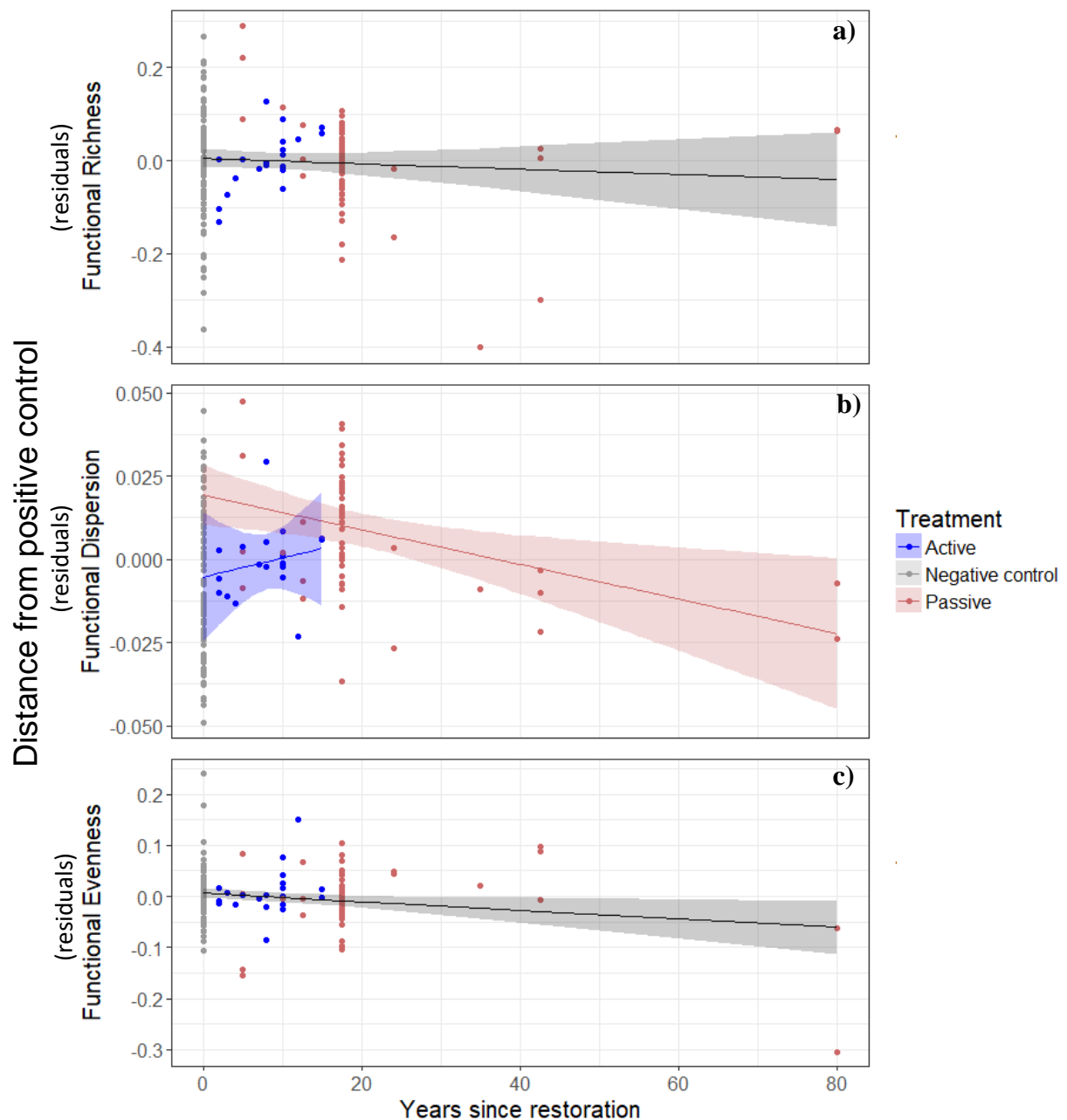


Figure 7. The distance of actively restored, passively restored and negative control sites from their respective positive control sites, with respect to functional richness (a), functional dispersion (b) and functional evenness (c) over time. Plotted values are the residuals having taken into account all random effects in each model (see Table S21 in Appendix D). Predicted lines are shown, bounded by 95% confidence intervals, where significant relationships were found, and separated by treatment in graphs depicting models where this factor was significant.

Discussion

To the best of my knowledge, this research provides the first comprehensive global assessment of the effectiveness of prior restoration projects in the recovery of functional diversity. This meta-analysis incorporated information from 576 sites of 30 restoration projects representing six unique taxonomic groups conducted across six ecoregions, and results are based on functional trait data calculated for 1,875 species. Overall, restoration appears to be effective in space-for-time studies, with restored sites improving across multiple diversity measures over time. However, the lack of systematic improvements over time in richness or functional diversity following restoration in longitudinal studies, beyond that observed in negative control sites, contradicts a key assumption of space-for-time substitution: that the negative control sites would remain constant. This contradiction suggests that the positive results found in space-for-time data may be an artefact of the inability of the study design to control for regional changes across all sites. Further explanations are detailed below.

Space-for-time data report positive effects of restoration on species and functional diversity, but caveats apply

Of all sites included in my analyses, over half (56%) came from studies where space-for-time substitution was implemented in their study design. This technique has been used widely in ecological monitoring, for example in measuring community responses to invasion (Thomaz et al. 2012) and climate change (Blois et al. 2013). In substituting space for time, the critical assumption is made that each site has an identical history in terms of its abiotic and biotic

components, such that sites differ only in age (Johnson and Miyanishi 2008), or in this case, time since restoration. Since the inception of this technique, concerns have continued to be raised about the appropriateness and validity of inferences about temporal changes in biodiversity and ecosystem processes based on chronosequence-based approximations of succession (Gleason 1927, Pickett 1989, Johnson and Miyanishi 2008).

In light of this, for the purposes of my meta-analysis there are several key points to keep in mind to avoid making erroneous inferences from space-for-time studies. Firstly, the main effect terms for actively and passively restored sites as predictors of diversity measures represent deviations from control at the intercept (i.e. when years since restoration = 0).

However, in this design all restored sites by definition have positive values for years since restoration, so the restoration-treatment intercepts have therefore been extrapolated beyond the scope of the data. Further, negative control sites – as a starting point in a recovery trajectory – are assumed to remain invariable over time (years since restoration was assigned as zero). If there was inherent variability in these sites over time, it was not possible to take this variability into account in models (Leps et al. 2016). This complicates the assignment of negative controls as a factor level for restoration treatment, because the state of negative control sites is supposed to represent the state of a site immediately prior to restoration. Given these inherent constraints of the design, in the interpretation of results I took diversity changes with time since restoration as a measure of the effects of restoration as a treatment, with the caveat that the temporal component of this variable can only apply to actively and passively restored sites.

In space-for-time studies, I found positive effects of restoration (i.e. significant main effects of years since restoration) on functional richness and functional dispersion, as well as on species richness, with the latter being also a significant predictor of the functional diversity metrics (see Figures 3b and d, 5b, d and f, and 6c). Restoration efforts also improved species evenness, but not functional evenness, and species evenness was not a significant predictor of functional evenness (Figures 3f, 4b and d, and 6d). Additionally, restoration positively affected sites in their progression towards positive control sites with respect to all functional diversity metrics. The positive intercept term of passively restored sites in terms of their distance from the functional dispersion of positive control sites (i.e. the functional dispersion of passively restored sites is lower than that of positive control sites), taken with the significant improvement over time, suggest that over time, sites with stressors removed will frequently improve unassisted, but that it is crucial that enough time be allowed for this process to unfold (Jones and Schmitz 2009). On average, passively restored sites in this meta-analysis would have taken 43.3 years to reach the functional dispersion of positive control sites. This slow recovery is supported by recent work, where Wallace et al. (2017) reported a critical threshold where conditions became suitable for spontaneous regeneration approximately 20 years after initial restoration planting. In contrast, a global review of 78 forest restoration assessments by Gatica-Saavedra et al. (2017) found that most investigators evaluated treatment effects for only 6 – 10 years after implementation, even though it has been highlighted that monitoring conditions in the later stages of restoration is just as important, because short-term data may be a poor predictor of succession trajectories and ecosystem responses in the long-term (Cortina et al. 2011). Of all data included in my meta-analysis where sites were sampled repeatedly through time (i.e. longitudinal data), studies on average measured restoration for 2.8 years after project initiation.

Longitudinal data did not exhibit improvements in restored sites beyond changes exhibited by negative control sites

In addressing longitudinal data, the caveats necessary in interpreting space-for-time data do not apply, as all sites (restored, negative control and positive control treatments) were sampled through time. Longitudinal data showed an almost unanimous improvement in diversity measures over time, such that for active and passive restoration treatments, as well as negative controls, sites became more diverse in terms of species richness, species evenness, functional richness and functional dispersion. Time elapsed since restoration began has been found to be a key driver of restoration success in previous work, including a recent meta-analysis of 221 study landscapes (Crouzeilles et al. 2016). Here, biodiversity was quantified as the abundance, richness, diversity and similarity of species, without any reference to functional diversity. Additionally, my model selection retained the interaction between years since restoration and restoration treatment (with active and passive levels collapsed) in predicting functional dispersion in longitudinal data, though this interaction was not significant. This indicates that negative control sites improved through time, but at a rate that did not differ significantly from that of restored sites. This suggests that temporal invariability of negative control sites (as assumed in space-for-time substitution) is a false assumption, and that the positive effect of restoration on various measures of diversity in space-for-time designs may have been an artefact of this assumption.

Beyond the effect of time, the only observed difference between restored and negative control sites in my analyses was in terms of functional dispersion at the time of project initiation (i.e. when years since restoration = 0). Therefore, it appears that restoration does not

systematically improve richness or functional diversity in the studies that were best able to detect an effect (i.e. longitudinal studies). The lack of significant difference between restored and negative control sites over time is surprising and perhaps counterintuitive: my hypothesised positive relationship aligned with previous assessments of restoration success rates in terms of biodiversity (Benayas et al. 2009). Both Kail et al. (2015) and Curran et al. (2014) reported increases in richness attributed to restoration, though in the former, site age was the most important factor and in the latter the authors stressed the substantial uncertainty and time lags associated with this result. Furthermore, neither of these meta-analyses distinguished space-for-time from longitudinal designs, and the influence of space-for-time studies might have underpinned their conclusions.

Of the recently published studies where functional diversity was measured directly following restoration, irrespective of whether they found a positive effect of restoration on species diversity (Tullos et al. 2009, Díaz-García et al. 2017), functional diversity (Modiba et al. 2017, Derhé et al. in press), both (Qin et al. 2016, Rocha-Ortega et al. 2018) or neither (Audino et al. 2014, González-Tokman et al. 2018), all studies either 1) lacked negative controls with which to compare all restored sites, 2) only compared positive and negative controls with restored sites of unspecified age at one point in time or 3) used space-for-time substitution in their study design. The only study calculating functional diversity following restoration that was measured through time (i.e. longitudinal data) found initial increases in functional diversity beyond levels of negative controls, but these were followed by sustained decreases in functional diversity over the remainder of the project (D'Astous et al. 2013). These findings contextualise my results, whereby the positive results detected may in fact be an artefact of unsuitable study design, and the studies that were best able to detect a

difference (i.e. replicated longitudinal data) did not find sustained benefits of restoration for functional diversity.

Other factors may impede restoration gains

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Based on the above findings, it appears that factors unaccounted for by restoration studies are playing a crucial role in determining the functional diversity levels measured across all sites.

That is, the lack of improvements in restored sites beyond those seen in unmanipulated control sites over time (in longitudinal studies) may be due to regional effects overshadowing

10 any localised efforts. There are many non-mutually-exclusive factors that have been shown to influence patterns of diversity. These include spatial composition of patches (Bovo et al. in press), quality of the regional species pool (Sundermann et al. 2011), connectivity (Winking et al. 2014), and species' perception of and response to the surrounding landscape (Dias et al. 2016), as well as other catchment- or landscape-scale processes (Leps et al. 2016). Beyond
15 this, it may be necessary to reinstate natural disturbance regimes (Fuhlendorf et al. 2009).

Recognition of legacies of past land-use may also be required, where abiotic-biotic feedbacks may foil restoration efforts, such that prior degradation of a site determines the community trajectory (Suding 2011). Beyond these factors, the specific techniques employed in restoration (beyond the coarse classification of 'active' vs. 'passive') are pivotal in

20 determining outcomes. For example, increasing habitat heterogeneity is widely employed in freshwater restoration, and in many of the freshwater studies in my meta-analysis, this was achieved via re-meandering or addition of physical structures (see Appendix A). However, Palmer et al. (2010) found that heterogeneity was relatively unimportant in determining biodiversity outcomes, and in fact only a third of studies they analysed found a positive

relationship between heterogeneity and biodiversity. Therefore, in order to yield successful restoration outcomes, it is important to consider the abiotic and biotic context of the study site, at the local as well as regional scale, and the availability of biodiversity (Tschamntke et al. 2012).

5

In general, active restoration measures were no better than passive restoration

As restoration techniques are being scrutinised for their effectiveness (or lack thereof) in meeting restoration targets, a key trend emerging from recent literature is the emphasis on
10 passive restoration (i.e. natural regeneration) as the potential best way forward in terms of restoration, with particular evidence from tropical forest systems (Crouzeilles et al. 2017, Meli et al. 2017, Jones et al. 2018). Crouzeilles et al. (2017) conducted a meta-analysis of 133 studies and demonstrated that restoration success (in terms of biodiversity) was up to 56% higher in naturally regenerated than actively restored systems, and Meli et al. (2017) in
15 166 studies of actively and passively restoring forests showed that cessation of land use alone was generally enough to enable forest recovery. Not only did the longitudinal studies I analysed report species richness as best improved by passive restoration, I found a benefit also for functional richness, which increased more rapidly through time in passively restored than in actively restored sites in space-for-time studies. Although more technical measures
20 may be necessary in cases of highly stressed or highly productive environments (Prach and Hobbs 2008), in general passive measures are advocated in the restoration of degraded sites, and have been proven to be more cost-effective than active restoration (Birch et al. 2010). This cost-effectiveness is not a reflection of a resounding failure of active restoration, but more reflects the ability of natural regeneration (i.e. passive restoration) to yield similar

benefits, without incurring the costs (both labour and capital) necessary for active restoration. These indications notwithstanding, the results I found that support passive restoration should be interpreted with caution, due to low number of passively restored sites in longitudinal data and previously explained caveats associated with space-for-time data. Nevertheless, the unexpected lack of evidence for passive restoration being outperformed by active restoration in the studies I addressed supports the emphasis of passive restoration as an avenue with potential for success.

Species-based measures may be sufficient proxies for functional diversity

In those individual studies where richness did improve considerably with restoration, this would likely improve functional diversity also, because the two were generally positively related across all studies and designs. Further, the reported levels of functional richness were not significantly different from what could be expected if communities of species were assembled at random. In fact, across all studies, only 7.8% of sites (longitudinal and space-for-time together) fell outside the bounds of 95% of the null distribution, which would indicate that their functional diversity differed from random expectation. Of these 41 sites falling outside the 95% bounds, in most cases (75%) functional diversity was higher than random. Thus, not only was species richness in general an acceptable proxy for measuring changes in functional richness (Petchey and Gaston 2002), but knowing the level of species richness in most cases successfully predicted the functional richness of a site, irrespective of realm or treatment. Further, I did not find any strong evidence that trait occupancy was limited by habitat filtering (Keddy 1992, Mouillot et al. 2007), but in a minority of sites there was significant trait expansion beyond random, which could be caused by niche

differentiation to reduce competition (MacArthur and Levins 1967, Kraft et al. 2008). These sites were scattered randomly across the dataset, without any obvious pattern in terms of study design, taxonomic group, restoration treatment or realm. As a caveat to this interpretation, it is also possible that habitat filtering could have occurred equally across all sites (including controls), because my null model only drew species that were sampled in any of the sites within a study, rather than from the entire regional species pool.

Contrary to findings for functional richness and functional dispersion, functional evenness was only found to increase with species evenness in space-for-time, but not in longitudinal studies, and did not increase with restoration treatment or time since restoration. Lower functional evenness may correspond to the underutilisation of niches, and suggests lower response diversity (Schriever et al. 2015), where in general a greater diversity in traits represents stronger effects on ecosystem functioning (Díaz and Cabido 2001). Interestingly, previous work has also found a negative relationship between functional evenness and ecosystem functioning, where ecosystem functioning was higher when functional evenness was low (Gagic et al. 2015). This would suggest that for some ecosystem functions, the presence of a few dominant species may be enough to provide the functional diversity necessary to deliver that function (e.g. primary production; Loreau et al. 2001) though this dominance may come at a cost of reduced persistence of other species in the community (Rohr et al. 2016). However, the positive but saturating relationships of functional richness and functional dispersion with species richness align with the current biodiversity-ecosystem functioning literature (Hooper et al. 2005), wherein functioning saturates at high diversity, but functionally diverse communities provide redundancy that promotes resilience. In the context of restoration, this suggests that the contribution of additional species to the functional diversity and resilience of a previously degraded area will likely depend on the

size and traits of the existing species pool (i.e. where the site is in relation to the level of richness at which functional diversity saturates).

Further caveats

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In studies of functional diversity, results are influenced by the number and type of functional traits included in analyses (Petchey and Gaston 2006, Cadotte et al. 2011). Although I took steps to standardise the acquisition and use of trait data, given the estimation and aggregation that was conducted out of necessity, it is important to acknowledge the caveats to my chosen
10 approach. Firstly, species can adopt different life-history strategies throughout their life cycle (e.g. macroinvertebrates; Prather et al. 2008); without data on the age or life stage of the species extracted from my 30 datasets, it may be possible that the trait data I assigned to species are not representative of the exact functional role of a given species at the time of sampling. The way in which functional traits are measured in the field is also important
15 (Lavorel et al. 2008), however, as I compiled these data from published literature and databases, I could not control for any consequences of trait measurement. Nevertheless, these caveats would only influence my findings if there were a systematic difference in life stage representation or use of methods across sites of different restoration treatments or ages. As a further caveat, Verberk et al. (2013) highlighted that a species' success in an environment is
20 controlled by many interacting traits, such that the adaptive value of any particular trait may differ across species. As I have calculated functional diversity metrics based on multiple traits from different trait classes, this is less of a concern than if my results were based on metrics quantified from single traits alone. Finally, Roscher et al. (in press) highlighted the importance of considering the origins of trait data, having demonstrated that plants can adjust

their traits based on the surrounding community, such that the functional diversity of a full community differs from the sum of each species therein if grown in monoculture. It is important, therefore, to consider the potential within-species trait variation that was not accounted for in my analyses.

5

In the null models I constructed, sets of species were drawn at random for each level of species richness (see ‘Model structure’ in Methods). However, in real conditions as a site increases in species richness, the set of species contained is constrained by the species formerly present, such that the differences between samples of the same site over time are non-random. In light of this temporal autocorrelation, the results of my null models of longitudinal data should be interpreted with caution. In space-for-time data, however, each site has in fact had the potential for a distinct community trajectory (i.e. older sites are not direct descendants of younger sites), so the results of the null models are more applicable.

15 Despite the strengths of meta-analyses in synthesising research, there are also limitations to the meta-analytic approach that need to be considered. Gurevitch and Hedges (1999) identified four significant limitations: incomplete data reporting, potential for non-independence among effect-size estimates, publication bias, and research bias. By utilising raw species data from the published studies, and conducting primary analysis on these rather than effect sizes, I removed any potential for non-independence among effect-size estimates. I minimised publication bias by utilising the papers contained within two recently published meta-analyses (i.e. following their selection criteria), rather than conducting my own searches for publications on functional diversity per se. Both Kail et al. (2015) and Curran et al. (2014) had different focal response variables than I (i.e. neither quantified functional diversity); this

removed the possibility of my selected literature being an artefact of my research question. However, both meta-analyses I used as sources quantified metrics of species diversity after restoration, so the potential for bias should be kept in mind when making inferences from the results of Question 3 which addressed species diversity.

5

Implications for future restoration practice

As restoration often focuses on the maintenance of biodiversity and ecosystem functioning, and how these progress through time, there is much to be learned from restoration about the assembly of communities (Wainwright et al. 2018). Four key concepts in community assembly were outlined in Mayfield et al. (2010): 1) species pool, 2) environmental filters, 3) competitive exclusion and 4) functional redundancy. I found that, in the majority of sites, functional richness was no different than what could be expected by chance alone given species richness, which suggests that environmental filters were not constraining the recovery of diversity following restoration, and there was relatively little evidence of competition for niche space. The saturating relationships of functional richness and dispersion with increasing species richness demonstrate a pattern of functional redundancy, and this was true across restored and control sites. Finally, without contextual data for each study included in this meta-analysis, it was not possible to assess the extent to which the surrounding species pool was contributing to the diversity of restored sites. However, the lack of difference between restored sites and unmanipulated negative controls through time in longitudinal studies suggests that the contribution of regional processes may be substantial, both in determining which species and which traits are present in a community.

A widely advocated goal of restoration is to yield ecosystems that have adaptive capacity in light of future environmental change (Suding 2011). In this context, promoting resilience is beneficial, and the saturating increase in functional richness with species richness observed in my longitudinal studies implies a level of functional redundancy (i.e. a resilience against

5 perturbation). However, resilience can be as much or even greater in systems with low diversity compared with high diversity systems (Suding et al. 2004); in fact, in the context of coral reefs it has been argued that degradation increases resilience to climate change, as the species still present despite the degraded conditions may be more able to tolerate further perturbations (Côté and Darling 2010). In surveying riparian vegetation after restoration,

10 Bauer et al. (in press) reported the presence of a ‘restoration threshold,’ such that plant communities were resilient to and buffered from restoration efforts. This negative resilience requires a greater change in environmental conditions than the pathway of degradation it previously followed in order to yield gains for biodiversity and functioning (Suding and Hobbs 2009). This has important implications in the context of restoration, as negative

15 resilience could play a role in hindering the improvements in biodiversity that were hypothesised, and therefore should be considered in the creation and assessment of restoration project goals.

In assigning and promoting restoration goals, it is important to acknowledge that the

20 importance of restoration extends beyond a purely ecological context; in fact, it is often the socio-economic landscape of restoration that determines the distribution of resources toward restoration (Stanford et al. 2018). It is important to ensure that restored efforts are distributed according to ecological need, whilst as much as possible acknowledging the potential for disparity in the distribution of restoration benefits within society. In this way, there may be a

25 need to reconcile multiple conflicting goals, for example within the ecosystem services

framework (Bullock et al. 2011). Conflicting goals are likely to lead to challenges in agreeing on the criteria upon which judgement of success should be based (Palmer et al. 2005), which could hinder the ability to obtain mutually beneficial outcomes from restoration.

5 Beyond the assignment of goals for restoration, it is pivotal that post-implementation monitoring be conducted in such a way that the data collected are sufficient to detect whether current efforts will meet assigned goals, and if necessary, make changes to ensure that criteria are met. The observed changes in negative control sites along with restored sites over time support the need for long-term monitoring, and suggest that prematurely assessing the
10 effectiveness of restoration may lead to conclusions unrepresentative of site conditions to come. This has implications for applications such as biodiversity offsetting (Curran et al. 2014), where the destruction of biodiversity in one area is justified by the restoration of an ‘ecologically equivalent’ area. With particular reference to the positive effects of restoration I found, which may in essence be artefacts of the space-for-time study design, insufficient data
15 of offset restoration outcomes may result in net losses of biodiversity, particularly if the uncertainty of outcomes (i.e. the likelihood of success) fails to be incorporated into decision-making (Moilanen et al. 2009). Further, for the restoration offset to achieve no net loss of biodiversity, it needs to replace not only the number of species, but the interactions and ecosystem functions lost in development (Walker et al. 2009). Although the gains in species
20 richness with restoration in individual studies I analysed were likely to be associated with improvements in functional diversity, quantifying the recovery of specific ecological interactions and functions is more intensive and challenging than simply measuring species richness, reiterating that the data collected must be sufficient to track and assess the recovery (or lack thereof) of project targets.

Where it was possible to quantify how positive control sites compared with negative control sites, no differences were found. This suggests that there are other characteristics of these distinct ecosystems – factors that determine their pristineness or degradedness – that aren't being captured by the quantification of species and functional diversity alone. This supports a multi-faceted approach to the monitoring and ongoing management of restoring ecosystems, including assessment of abiotic conditions beyond strictly biotic measures alone (Rubin et al. 2017). It may also be necessary to explore trajectories of functional composition following restoration, as diversity may remain constant despite a shift to a new functional state (Boersma et al. 2016).

There is an urgent need for scientists and practitioners alike to understand how and if restoration efforts can reinstate biodiversity, including functional diversity, and to apply this knowledge to efficiently and effectively allocate resources to promote actual realised gains.

By extending previous work that addressed richness-based measures alone, I showed that restoration efforts were generally ineffective in improving functional diversity beyond levels observed in unmanipulated degraded sites. This result stresses the indispensability of including negative controls in ongoing monitoring to correctly partition the consequences of restoration efforts from unassisted temporal changes.

Beyond this, further research should be directed to improving data quality for less developed regions, as it was for these areas that trait data were most difficult to obtain. This finding echoes the recently highlighted misalignment between regions where investigations into

restoration take place compared with the areas where such investigations should be prioritised, given observed rates of change (Gatica-Saavedra et al. 2017).

To some extent, “restoration will always be a gamble” (Suding 2011). The inability of
5 restoration to improve functional diversity beyond that of degraded negative control sites
supports recent conclusions that restoration alone should not be considered a substitute for
conservation (Jones et al. 2018). However, improvements in functional diversity across all
sites through time offer hope that restoration efforts need not be complicated or expensive;
rather, the most effective restoration strategy in many cases may simply be to remove
10 stressors such as agriculture and let ecosystems repair themselves (Jones et al. 2018). The
lower cost of this approach may even allow a greater area to be restored for a given
availability of resources. Thus, although restoration alone may not succeed in fully meeting
conservation targets, by harnessing restoration as one of multiple complementary
management tools, scientists and practitioners together could successfully stymie biodiversity
15 loss and ensure that restored ecosystems are resilient to future global change.

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- 40

Appendix A. Study details

In Appendix A, details are reported for each of the 30 original datasets incorporated in my meta-analysis, arranged by taxonomic group. For each taxonomic group, supplementary

5 tables report the proportion of species for which trait data were estimated (and where necessary, aggregated) at a higher taxonomic level than species were reported in original publications. A species is reported as having its trait data estimated if one or more traits (of up to 95 traits) for that species were estimated using data from a higher taxonomic level.

Therefore, the reported proportion of trait data estimated does not typically apply to every

10 trait, so the total proportion of all trait data estimated is less than this reported value (i.e. it is the reported value multiplied by the proportion of traits for which these values were

estimated). In Tables S1 and S4 (for ant and macroinvertebrate studies, respectively), the

‘number of taxa retained’ refers to the number of taxa retained in the species list without

undergoing aggregation, because those taxa were unique in their traits (i.e. the values of each

15 of those taxa across all their traits were non-identical to any other taxa in that dataset).

Ants

Trait data for the three datasets examining the effect of restoration on ant communities (all

20 from the meta-analysis of Curran et al. 2014) were acquired primarily from Silvestre et al.

(2003). Where gaps remained (individual trait by species combinations), these were filled

first from Hölldobler and Wilson (1990), and thereafter from a range of existing published

literature (outlined per study below) and AntWeb (available from <https://www.antweb.org>).

Where necessary, body size was estimated from scaled specimen photos supplied on AntWiki

(available from <http://www.antwiki.org>). Where traits for multiple taxa were estimated at a common higher taxonomic level than that reported in the original study, taxa were aggregated into one group to be included in analyses (see ‘Data extraction and collection – trait data’ in Methods).

5

Table S1. Summary of taxa lists in ant studies and the proportion of trait data estimated (and aggregated) at higher taxonomic levels than originally reported.

Study	Initial number of taxa	Number of taxa retained	Number of taxa aggregated	Number of unique groups of aggregated taxa	Final number of taxa
Bihn et al. (2008)	40	40	0	NA	40
Gove et al. (2005)	41	27	14	7	34
Roth et al. (1994)	37	24	12	5	29

Bihn et al. (2008)

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Bihn et al. (2008) compared the richness and composition of ant assemblages in the Atlantic forest in southern Brazil. Twenty-seven sites were established along a chronosequence (5, 12.5 and 42.5 years after abandonment) of forest and these compared to pasture sites as negative controls. Sites were blocked by soil type (Cambisol and Gleysol) and samples collected from litter and soil. At four of the 27 sites, only litter samples were collected; for consistency, I included only the 23 sites where taxa lists were derived from samples of species occupying soil and litter.

15

An alternative to this would have been to include all 27 sites but use samples collected in soil only (i.e. exclude the 23 litter samples). However, exploring this option revealed that of the four sites that would have remained, two would be excluded from analyses because species richness was too low to calculate functional diversity (i.e. less than four). My chosen

20

approach therefore maximised both the quality and quantity of data kept for this study whilst adhering to my inclusion criteria.

Most trait data were filled by Silvestre et al. (2003), and the gaps that remained were filled using data from Smith and Wing (1954), Brown Jr and Kempf (1969), Krombein et al. (1979), Fowler (1985), Ito (1991), Galvis and Fernández (2009), Moffett (2010), Ward and Fisher (2016) and AntWeb (available at <https://www.antweb.org>).

Gove et al. (2005)

This study was undertaken in the central coastal plain of Veracruz, Mexico, and the diversity of ant communities quantified for three each of passively restoring, primary forest (positive control) and pasture (negative control) sites. Restoring sites had been previously cleared for agriculture or grazing and subsequently abandoned. Sampling occurred in November 2001 and March 2002, 15 and 15.25 years after restoration. Data were supplied for both pitfall traps and arboreal samples, but as arboreal samples were not available for all treatments (i.e. not possible for pasture) I used only the data from pitfall traps. In addition to these nine sites, communities were also sampled on remnant trees within pasture sites. Sites can only be included as negative controls if it can be assumed that the characteristics of those sites reflect the characteristics of restored sites had they not been restored. Without data disclosing whether the vegetation in restored sites is ‘remnant’ or not (i.e. whether it was present before abandonment), I cannot say with confidence that the ant communities of isolated remnant trees reflect those of the restored sites if they were still being used for agriculture, therefore they were not included in analyses.

Missing body sizes were estimated from scale specimen photos on AntWiki (available from <http://www.antwiki.org>), and other gaps filled from Philpott et al. (2008). Some ant species were common to multiple datasets, so gaps in trait data for Gove et al. (2005) were filled from sources mentioned for Bihn et al. (2008) and Roth et al. (1994).

5

Roth et al. (1994)

Roth et al. studied the diversity of ant communities in two restoring sites (24 years after abandonment of cacao plantation practices), four productive cacao sites (negative controls) and three sites in primary forests (positive controls) in the Sarapiquí Valley of Costa Rica. Data were also reported for two productive banana plantations, but these were not deemed suitable negative controls for the two abandoned cacao sites so were excluded from my analyses.

15 Silvestre et al. (2003) was supplemented with trait data from Wilson (1959), Brown (1963), Ward (1988), Beckers et al. (1989), Fowler and Delabie (1995), Collingwood et al. (1997), McGlynn et al. (2004), Heinze and Delabie (2005), Wetterer (2009).

Birds

20

For both Aerts et al. (2008) and O'Dea and Whittaker (2007), data for the habitat and dispersal trait classes were acquired from BirdLife International Data Zone (BirdLife International 2017). As the sites in both studies were terrestrial-based, marine habitat subcategories were classified broadly as coastal or intertidal, but all terrestrial and freshwater

habitats in the narrower categories outlined in this source (see <http://datazone.birdlife.org/species/spchabalt>), apart from the nine artificial aquatic landscapes, which were also collapsed into one variable. All habitat traits were coded by importance as ‘suitable’, ‘major’, ‘marginal’ or ‘not suitable’ and were thus included as

5 categorical variables in functional diversity calculations.

Where ecozones or ecosystems were not stated explicitly for a given species on the BirdLife International factsheet, the ecosystem was inferred from the level 1 and 2 habitats occupied (e.g. if permanent freshwater marshes and ponds were deemed as ‘suitable’ habitats for a

10 given species, the ‘freshwater’ ecosystem was deemed suitable, and ecozones (e.g. Afrotropical, Palearctic, Nearctic) were determined by the map provided on the BirdLife International factsheet if not stated explicitly.

Table S2. Summary of taxa lists in bird studies and the proportion of trait data estimated at higher taxonomic levels than originally reported.

Study	Number of taxa with trait data from correct taxonomic level	Number of taxa with trait data estimated	Total number of taxa
Aerts et al. (2008)	145	25	170
O’Dea and Whittaker (2007)	177	34	201

Aerts et al. (2008)

This study compared avian communities in forest fragments, grazing exclosures (10-year-old

20 forest restoration areas without wood extraction and grazing livestock) and adjacent grazing lands in northern Ethiopia. Aerts et al. measured 277 one-hour species counts across 47 sites, although for the purposes of my work only 18 sites’ species data were used (five passively

restored sites, three degraded control sites and ten positive control sites), as the remainder did not meet my previously outlined selection criteria.

As sampling effort (i.e. the number of timed species counts) was uneven across the 18 sites

5 relevant for my work (range, 10-29; median, 15.50), it was necessary to take further steps to minimise any possible biases this unevenness may cause in the calculation of diversity metrics (Gotelli and Colwell 2001). To do this, for each site I randomly sampled 10 counts (the minimum number of counts across the 18 sites) and took the sum of these counts for each species to determine their abundance. This step was repeated 1000 times per site, and
10 for each repetition I calculated functional diversity metrics following the steps outlined in the ‘Functional diversity calculations’ section of the main text. I then took a median value of all diversity measures (functional richness, evenness and dispersion as well as species richness) from the 1000 repetitions for each site. Aggregating the simulated data after calculating functional diversity ensures that all simulated data are scaled in the same space. From here, I
15 then used these data alongside the remainder of my functional diversity data to test my research questions.

Trait data for body dimensions, diet, phenology, and reproduction were extracted from

Brown et al. (1982) and habitat, migration and range trait data from BirdLife International
20 (2017). Where bill length was not provided in Brown et al. (1982), values were estimated from scaled drawings in the *Handbooks of the Birds of the World* (Del Hoyo et al. 1992). The majority of data were extracted from these sources, but the missing values were filled by a range of published literature (von Henglin 1871, Dresser 1881, Salvadori 1891, Harrison
1975, Del Hoyo et al. 1992, Pol 2001, Stevenson and Fanshawe 2004, Ash and Atkins 2010,
25 Fry and Fry 2010, Harris 2010).

O'Dea and Whittaker (2007)

O'Dea and Whittaker (2007) examined the richness and diversity of bird communities in
5 threatened forest habitats of the tropical Andes, northern Ecuador. They used data from a
point count survey of 300 counts at 150 sites (41 passively restored sites, 60 degraded
negative control sites and 49 positive control sites), 75 in each of the Maquipucuna and Santa
Lucia Reserves and adjacent lands. The 41 restoring sites were 15- to 20-year-old stands
regenerating from abandoned agricultural lands. Trait data were extracted from Brown et al.
10 (1982) and habitat, migration and range data from BirdLife International (2017). The
majority of data were extracted from these sources, but the missing values (particularly for
weights and clutch size) were filled by a range of existing published literature as well as the
Handbook of the Birds of the World website (Sclater 1879, Skutch 1985, Hilty and Brown
1986, Greeney 1999, 2005, Greeney et al. 2005, Greeney and Gelis 2008, Jetz et al. 2008,
15 Greeney et al. 2009, Dyrce and Greeney 2010, Greeney et al. 2010a, Greeney et al. 2010b).

For two species, *Geothlypis semiflava* and *Psarocolius angustifrons*, the relevant Handbook
of the Birds of the World specified the lower altitudinal limit as 'lowland' but did not specify
this in metres. Because many other species found at these sites had values for their lower
20 altitudinal limit down to 0 m, I assumed lowlands as 0 m and recorded it accordingly.

Fish

Trait data for studies measuring the response of fish communities to restoration (all from Kail
25 et al. 2015) were acquired from region-specific sources: data for the five studies from the

United States (Edwards et al. 1984, Moerke and Lamberti 2003, Shields et al. 2006, Schwartz and Herricks 2007, Baldigo and Warren 2008) were extracted from the FishTraits database www.fishtraits.info (Frimpong and Angermeier 2009); data for the three European studies (Langler and Smith 2001, Wolter 2010, Lüderitz et al. 2011) primarily from Schmidt-Kloiber and Hering (2015) and data for the one Australasian study (Bond and Lake 2005) from Sternberg et al. (2014) and Froese and Pauly (2012).

Table S3. Summary of taxa lists in fish studies and the proportion of trait data estimated at higher taxonomic levels than originally reported.

Study	Number of taxa with trait data from correct taxonomic level	Number of taxa with trait data estimated	Total number of taxa
Baldigo and Warren (2008)	18	1	19
Bond and Lake (2005)	6	0	6
Edwards et al. (1984)	43	0	43
Langler and Smith (2001)	10	0	10
Lüderitz et al. (2011)	39	0	39
Moerke and Lamberti (2003)	15	1	16
Schwartz and Herricks (2007)	12	0	12
Shields et al. (2006)	31	1	32
Wolter (2010)	25	0	25

Baldigo and Warren (2008)

Baldigo and Warren (2008) compared fish population densities in three study streams of the Catskill Mountains (New York, United States) following the implementation of several natural channel design (NCD) restoration demonstration projects. Restored, negative control and positive control reaches in each study stream were repeatedly sampled up to six years after restoration.

Bond and Lake (2005)

This study examined the response of fish populations to wood addition to two streams in south-eastern Australia that have been impacted by a large build-up of sediment from human-induced erosion. Manipulated sites had either one or four timber structures added, and these were compared with negative control sites four, six and 12 months after restoration. Trait data for native species (four) were acquired from Sternberg et al. (2014) and for invasive species (two) from Froese and Pauly (2012).

Edwards et al. (1984)

Edwards et al. studied the mitigating effects of artificial riffles and pools on fish communities in the Olentangy River at Columbus, Ohio, United States. Sampling occurred five, six and seven years after habitat manipulation in a natural control site, a mitigated channelised site (where riffles and pools were created) and an unmitigated channelised site.

Langler and Smith (2001)

In this study, the effectiveness of habitat restoration measures (creation of bays and grading of banks) on fish assemblages was examined in the Huntspill River in Somerset, England. Communities sampled in four manipulated sections (two each of one and two years since restoration) were compared with four control sections in the river.

The species list reported in this study included a hybrid (*Rutilus rutilus* × *Abrama brama*), and my trait source did not report trait data for any hybrids. Of the 22 binary traits acquired from Schmidt-Kloiber and Hering (2015) (see Table S14 in Appendix B), 17 values were common to both *Rutilus rutilus* and *Abrama brama* species. If either of the two species had a

‘1’ recorded for any of the remaining binary traits, I recorded a ‘1’ for the hybrid recorded in this study.

Lüderitz et al. (2011)

5

This study measured the success of structural improvements in improving biodiversity in the Main and Rodach rivers in Northern Bavaria, Germany, as compared with a positive control and negative control reach per river.

10 Information on the habitat guild and spawning guild of each species was provided in the original publication, so these data were used and supplemented with data from Schmidt-Kloiber and Hering (2015) for functional analyses. Spawning guild was categorised as: lithophilic, litho-pelagophilic, marin, ostracophilic, phythophilic, phytho-lithophilic, psammophilic or speleophilic, and habitat guild as rheophil, stagnophil or indifferent. Other
15 gaps were filled from Leonardos et al. (2008), Konečná and Reichard (2011), Sigsgaard et al. (2015).

Moerke and Lamberti (2003)

20 This study evaluated the responses of fish communities to restoration efforts (creation of new meanders) in two channelised streams (Juday Creek and Potato Creek) in northwestern Indiana. Fish communities in both streams were sampled three times in the 34 months following, in positive and negative control reaches as well as restored reaches. Species

richness was reported as common, rare or absent, rather than as qualitative numeric data, so data were converted to presence-absence data for my analyses to avoid ambiguity. Therefore, this dataset was excluded from tests of species evenness.

5 *Schwartz and Herricks (2007)*

Schwartz and Herricks evaluated the effect of pool-riffle naturalisation structures on the fish community in a 620 m reach of the North Branch of the Chicago River in Northbrook, Illinois, United States. Communities were surveyed two and 13 months after modification,
10 and restored sites compared against positive and negative control sites.

Shields et al. (2006)

Shields et al. evaluated the effects of large wood addition for habitat rehabilitation on fish
15 communities in Little Topashaw Creek, Mississippi, United States. Sampling occurred at the time of manipulation and four years later, in the restored reach as well as in reaches upstream and downstream of the site. The few species by trait combinations not available in the FishTraits database were filled from Lindquist and Page (1984) and NatureServe (2013).

20 *Wolter (2010)*

This study assessed the recovery of fish communities in two restoration projects, in the Müggelspre and Spree rivers in Berlin, Germany. Restored sites were compared with

negative control sites in both Müggelspree and Spree rivers, one and two years after restoration, respectively.

Information on the flow preference and spawning preference of each species was provided in the original publication, so these data were used and supplemented with data from Schmidt-Kloiber and Hering (2015) for functional analyses. Spawning preference was categorised as: ariadnophilic, lithophilic, ostracophilic, phythophilic, phytho-lithophilic, pelagophilic or psammophilic, and flow preference as rheophilic, limnophilic or eurotopic.

Although Wolter (2010) collected multiple samples through time for some sites, all but one sampling occasion occurred before restoration commenced. As explained in ‘Data extraction and collection – species data’ in my Methods chapter, I excluded all pre-restoration sampling data. Therefore, this study was treated as space-for-time rather than longitudinal for the purposes of my analyses.

Macroinvertebrates

As it was not possible to acquire complete region-specific trait data for this taxon, trait data for the 11 datasets examining the effect of restoration on freshwater macroinvertebrate communities (all from the meta-analysis of Kail et al. 2015) were acquired from Bis and Usseglio-Polatera (2004). In this source, each taxon was assigned a score describing its affinity for each trait category; a score of 0 indicated ‘no affinity’ and 5 indicated ‘high affinity.’

Table S4. Summary of taxa lists in macroinvertebrate studies and the proportion of trait data estimated (and aggregated) at higher taxonomic levels than originally reported.

Study	Initial number of taxa	Number of taxa retained	Number of taxa aggregated	Number of unique groups of aggregated taxa	Final number of taxa
Ebrahimnezihad and Harper (1997)	104	40	64	15	55
Gørtz (1998)	87	43	44	8	51
Lorenz et al. (2009)	140	76	64	25	101
Lüderitz et al. (2011)	155	83	72	19	102
Nakano and Nakamura (2006)	48	31	17	6	37
Pedersen et al. (2007)	134	78	56	21	99
Pretty and Dobson (2004)	105	65	40	14	79
Purcell et al. (2002)	34	30	4	2	32
Testa et al. (2011)	149	73	76	22	95
Walther and Whiles (2008)	92	57	35	13	70

5

Ebrahimnezihad and Harper (1997)

This study compared the diversity of macroinvertebrate communities in three artificially constructed riffles, three original channelised stretches and a natural control riffle in

- 10 Northampshire, United Kingdom. Samples were collected 12, 15, 19 and 21 months after riffle construction.

Gørtz (1998)

- 15 This study compared the macroinvertebrate fauna of three restored and two reference sections of the River Esrom in Zealand, Denmark, collecting kick samples four and five years after physical habitat manipulation was conducted (using gravel, boulders and stream

concentrators). In addition to kick samples collected from all five sites, rock samples were collected for all but one; for consistency, species lists were compiled from kick sample data only.

5 *Lorenz et al. (2009)*

Lorenz et al. assessed the effectiveness of re-meandering restoration projects in two German lowland rivers, the Schwalm and the Gartroper Mühlenbach, with sampling taking place 10 and two years after project initiation, respectively. Macroinvertebrate communities in both
10 rivers were compared with the communities in straightened (i.e. not re-meandered) sites in both rivers.

Lüderitz et al. (2011)

15 This study measured the success of structural improvements in improving biodiversity in the Main and Rodach rivers in Northern Bavaria, Germany, as compared with a negative control reach per river.

Nakano and Nakamura (2006)

20

Sampling for this study was conducted in a channelised segment of the Shibetsu River in Eastern Hokkaido Island, Northern Japan. Sampling of macroinvertebrate communities occurred three and nine months after restoration, with a channelised site used as the negative

control against which to compare two restored sites: one where meanders had been reconstructed and the other where groynes had been installed. A groyne is an in-stream structure projecting from a bank into the stream to manipulate the current, intended to enhance transportation and protect banks.

5

Pedersen et al. (2007)

This study evaluated the short-term effects of the restoration of the Skjern River (Denmark), which entailed re-meandering, creation of riffles and substantial alterations to morphological cross-sectional profiles. Four reaches (three restored and one negative control) were sampled
10 in 2000 and 2003 and the macroinvertebrate communities compared therein.

Pretty and Dobson (2004)

15 This study investigated the response of aquatic invertebrates to log additions (to increase detritus retention) in streams in Kielder Forest (Northumberland, United Kingdom). Sampling took place three, six, nine, 13, 16 and 19 months after manipulation, and the macroinvertebrates of restored sites were compared with unmanipulated negative controls in each stream.

20

Purcell et al. (2002)

Purcell et al. assessed a small urban stream restoration project in Baxter Creek, El Cerrito (California, United States). This project involved opening a previously culverted channel, planting riparian vegetation, and adding in-stream step-pool sequences and sinuosity. The restored site and negative control site in Baxter Creek were compared to the nearby
5 Strawberry Creek, deemed to have the ‘best attainable conditions’ for this site.

Testa et al. (2011)

This study examined the aquatic macroinvertebrate community response to the addition of
10 large wood to Little Topashaw Creek, a fourth-order stream in north-central Mississippi, United States. Two restored sub-reaches were compared with one upstream positive control sub-reach and to two downstream negative control sub-reaches. Samples were collected nine, 12 and 21 months after restoration.

15 *Walther and Whiles (2008)*

Walther and Whiles sampled macroinvertebrate communities in response to constructed riffles (rock weirs) in the Cache River, Illinois, United States. Three newly constructed rock weirs were compared with two unrestored negative control sites and to two old rock weirs
20 (treated as positive controls), and samples collected three, six, nine and 12 months after restoration. Samples were collected from the stream bed and from snags (fallen trees in the river), but only the stream bed samples were included, as these were deemed to be more directly comparable across sites.

Plants

For the four datasets that evaluated the recovery of plant communities following restoration, in both terrestrial (Kardol et al. 2005, Piqueray et al. 2011) and freshwater (Clarke and Wharton 2000, Lüderitz et al. 2011) realms, trait data were acquired from the TRY database (Kattge et al. 2011). Due to the sheer volume of trait data in the TRY database, as well as discrepancies in information between the databases contained therein, I acquired data for each trait class from a single database within TRY for all studies. These are as follows: trait data for body dimensions, dispersal and phenology trait classes were acquired from the LEDA traitbase (Kleyer et al. 2008), data for feeding and reproduction trait classes from the ecological flora database (Fitter and Peat 1994) and data for the habitat preferences trait class from (Hill et al. 2004).

Table S5. Summary of taxa lists in plant studies and the proportion of trait data estimated at higher taxonomic levels than originally reported.

Study	Number of taxa with trait data from correct taxonomic level	Number of taxa with trait data estimated	Total number of taxa
Clarke and Wharton (2000)	97	3	100
Kardol et al. (2005)	127	8	135
Lüderitz et al. (2011)	11	0	11
Piqueray et al. (2011)	191	13	204

Clarke and Wharton (2000)

Clarke and Wharton (2000) investigated macrophyte communities following habitat enhancement (bank re-profiling and planting) on the River Torne, north Nottinghamshire and

Lincolnshire, United Kingdom. Marginal and riparian vegetation were sampled in ten each of enhanced and conventionally-engineered reaches, five years after restoration.

Of the species surveyed in this study, 93.5% were vascular plants, and the remainder (seven
5 of 107 species) were non-vascular plants (algae or mosses). Although well-documented
relationships exist between vascular and non-vascular plants and how they respond to
environmental change (Cornelissen et al. 2001), they contribute differently to the functioning
of ecosystems (Díaz and Cabido 2001, Rice et al. 2008); for this reason I included only
vascular plants in my analyses of this study. The seven taxa excluded were *Amblystegium*
10 *fluvatile*, *Amblystegium riparium*, *Cladophora glomerata* agg., *Enteromorpha*, *Plagiomnium*
undulatum, *Rhychostegium ripariodes* and *Sphagnum* spp.

Kardol et al. (2005)

15 Kardol et al. studied plant community development on a chronosequence of 26 ex-arable sites
(ranging from 1 to 34 years since cultivation abandonment) in the Netherlands. These sites
were compared against three agricultural fields (negative controls) and three semi-natural
sites (positive controls).

20 As the three negative control sites were monocultures (wheat or maize), species richness was
too low for functional diversity to be calculated for these sites. Without negative controls to
compare with, I could not include the restored (i.e. ex-arable) sites in analyses of the effect of
restoration on species and functional diversity. I included the species diversity and functional
diversity data of restored (26) and positive control (three) sites in testing for the relationship

between species diversity and functional diversity, as restoration was not considered in these models.

Lüderitz et al. (2011)

5

This study measured the success of structural improvements in improving biodiversity in the Main and Rodach rivers in Northern Bavaria, Germany, as compared with a negative control reach per river.

10 *Piqueray et al. (2011)*

This study compared vascular plant communities in 12 grasslands restored from forest stands (half from pine stands and half from oak coppices) to eight reference grasslands (positive controls) and eight pre-restoration forest stands (negative controls) in the Viroin Valley and the Lesse and Lomme Valleys in the Belgian region of Wallonia. The 12 restored sites were
15 equally distributed across three age classes: 2-4 years, 5-8 years and 10-15 years. Data were reported as presence-absence rather than abundance, so this study was not included when testing for species evenness.

20 *Reptiles*

For the final two studies included in my meta-analysis, I could not find a primary published source that could provide sufficient trait data for the majority of species sampled. This may

be due in part to the studies having been conducted in areas less documented (Dominican Republic and rural northern India). Therefore, trait data were acquired mainly from online sources, with information standardised within traits and within taxonomic groups as much as possible.

5

Table S6. Summary of taxa lists in reptile studies and the proportion of trait data estimated (and aggregated) at higher taxonomic levels than originally reported.

Study	Number of taxa with trait data from correct taxonomic level	Number of taxa with trait data estimated	Total number of taxa
Glor et al. (2001)	3	9	12
Pawar et al. (2004)	9	7	16

10 *Glor et al. (2001)*

This study surveyed the diversity of lizard fauna (using glue traps) in two active cacao sites (negative controls), two restored sites (previously active cacao plantations abandoned 80 years prior) and two forest sites (positive controls) in Los Haitises National Park and the surrounding region in the

15 Dominican Republic.

Sampling also occurred in oil palm plantations (three sites), home gardens (12 sites), *mogote* hilltops (four sites) and pasture sites (one active and three abandoned). Although the active pasture site could act as a negative control for the three abandoned (i.e. passively restored) pasture sites, species

20 richness was too low to calculate functional diversity in the active site and it was therefore excluded from analyses. Without a pre-abandonment negative control for comparison, the three abandoned pasture sites were also excluded to adhere to this selection criterion, as were the home garden sites.

Active oil palm plantations and *mogote* hilltops were too different from abandoned cacao sites to be

used as additional negative and positive control sites, respectively, so I did not include these in my analyses.

The traits for *Anolis* sp. were taken to be the mean (or mode, in the cases of categorical variables) of all species within that genus. Species-specific sources of trait data are reported in Table S7.

Pawar et al. (2004)

Pawar et al. (2004) studied the recovery of lizard communities in Mizoram, Northeast India. Five previously-cultivated restoring sites were sampled (five to 35 years after abandonment) and compared with three mature forest (positive control) sites and two negative control sites. Data were also collected for two teak plantation sites, but these were deemed unfit to include as controls for the restoring sites, because they did not represent the state that the restored sites would have been in had no restoration actions been taken. This study also surveyed amphibian communities, but because my selection criteria necessitated having multiple datasets of a given taxa for study inclusion, only data from reptile communities were included in my analyses. Data were reported as presence-absence rather than abundance, so this study was not included in models including species evenness or functional evenness.

The traits for *Mabuya* sp. were taken to be the mean (or mode if trait was categorical) value of *Mabuya macularia* and *Mabuya multifasciata*, and for *Ptyctolaemus gularis* the mean (or mode if trait was categorical) value of all species in the same family (Agamidae): *Draco maculatus*, *Calotes versicolor* and *Calotes emma*. Species-specific sources of trait data are reported in Table S8.

Table S7. Sources of trait data for each species in Glor et al. (2001).

Species	Vertical foraging stratum (Habitat)	Diet (Diet)	Diel (Phenology)	Maximum adult body size (Body Dimensions)	Number of offspring/eggs per clutch (Reproduction)
<i>Anolis baleatus</i>	http://eol.org/pages/795854/details	http://eol.org/pages/795854/details	http://www.anoleannals.org/2013/06/27/fill-in-the-blank-obscure-anole-life-history-traits/#comments	http://www.iucngisd.org/gisd/species.php?sc=1681	http://www.anoleannals.org/tag/reproduction/
<i>Anolis chlorocyanus</i>	http://myfwc.com/wildlifehabitats/nonnatives/reptiles/hispaniolan-green-anole/	http://explorer.natureserve.org/servlet/NatureServe?searchName=Anolis+chlorocyanus	http://www.anoleannals.org/2013/06/27/fill-in-the-blank-obscure-anole-life-history-traits/#comments	http://www.iucngisd.org/gisd/species.php?sc=1681	http://www.anoleannals.org/tag/reproduction/
<i>Anolis cybotes</i>	http://eol.org/pages/795854/details	http://eol.org/pages/795854/details	http://www.anoleannals.org/2013/06/27/fill-in-the-blank-obscure-anole-life-history-traits/#comments	http://www.iucngisd.org/gisd/species.php?sc=1681	http://www.anoleannals.org/tag/reproduction/
<i>Anolis distichus</i>	https://en.wikipedia.org/wiki/Anolis_distichus	http://www.iucngisd.org/gisd/species.php?sc=1681	http://www.anoleannals.org/2013/06/27/fill-in-the-blank-obscure-anole-life-history-traits/#comments	http://www.iucngisd.org/gisd/species.php?sc=1681	http://www.anoleannals.org/tag/reproduction/
<i>Anolis semilineatus</i>	http://www.iucnredlist.org/details/178321/0	http://eol.org/pages/795854/details	http://www.anoleannals.org/2013/06/27/fill-in-the-blank-obscure-anole-life-history-traits/#comments	http://www.iucngisd.org/gisd/species.php?sc=1681	http://www.anoleannals.org/tag/reproduction/
<i>Anolis</i> sp.	Sources for <i>A. baleatus</i> , <i>A. chlorocyanus</i> , <i>A. cybotes</i> , <i>A. distichus</i> and <i>A. semilineatus</i>	Sources for <i>A. baleatus</i> , <i>A. chlorocyanus</i> , <i>A. cybotes</i> , <i>A. distichus</i> and <i>A. semilineatus</i>	Sources for <i>A. baleatus</i> , <i>A. chlorocyanus</i> , <i>A. cybotes</i> , <i>A. distichus</i> and <i>A. semilineatus</i>	Sources for <i>A. baleatus</i> , <i>A. chlorocyanus</i> , <i>A. cybotes</i> , <i>A. distichus</i> and <i>A. semilineatus</i>	Sources for <i>A. baleatus</i> , <i>A. chlorocyanus</i> , <i>A. cybotes</i> , <i>A. distichus</i> and <i>A. semilineatus</i>
<i>Antillophis parvifrons</i>	http://www.iucnredlist.org/details/190582/0	http://www.iucnredlist.org/details/190582/0	http://naturewatch.org.nz/observations/116011	http://naturewatch.org.nz/observations/7469707	Sajdak and Henderson (1982)
<i>Celestus</i> sp.	http://www.iucnredlist.org/details/203037/0	https://en.wikipedia.org/wiki/Celestus_warreni	http://www.iucnredlist.org/details/63698/0	Thomas and Hedges (1989)	Vitt and Caldwell (2013)
<i>Epicrates striatus</i>	Brooks and McLennan (2012)	Henderson et al. (1987)	Knapp and Owens (2004)	Henderson et al. (1987)	Hamlett (2012)
<i>Sphaerodactylus difficilis</i>	http://www.dwarfgeckos.com/sphaerodactylus/s_diff/sphaerodactylus_difficilis.php	http://www.dwarfgeckos.com/sphaerodactylus/s_diff/sphaerodactylus_difficilis.php	http://www.supremegecko.com/sphaerodactylus-difficilis	Powell and Henderson (2008)	http://www.cyberlizard.org.uk/geckos_sphaero.htm
<i>Sphaerodactylus samenensis</i>	http://www.iucnredlist.org/details/75605882/0	http://www.iucnredlist.org/details/75605367/0	http://www.supremegecko.com/sphaerodactylus-difficilis	Powell and Henderson (2008)	http://www.cyberlizard.org.uk/geckos_sphaero.htm

<i>Tropidophis haitianis</i>	http://www.reptilesmagazine.com/Snakes/Snake-Care/Keeping-Dwarf-Boas-of-the-Caribbean/	http://snakesarelong.blogspot.co.nz/2015/01/dwarf-boas.html	http://snakesarelong.blogspot.co.nz/2015/01/dwarf-boas.html	http://www.reptilesmagazine.com/Snakes/Snake-Care/Keeping-Dwarf-Boas-of-the-Caribbean/	Iverson (1986)
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Table S8. Sources of trait data for each species in Pawar et al. (2004).

Species	Vertical foraging stratum (Habitat)	Diet (Diet)	Diel (Phenology)	Snout to vent length (Body Dimensions)	Number of offspring/eggs per clutch (Reproduction)
<i>Calotes emma</i>	https://en.wikipedia.org/wiki/Calotes_emma	https://en.wikipedia.org/wiki/Calotes_emma	https://en.wikipedia.org/wiki/Calotes_emma	https://en.wikipedia.org/wiki/Calotes_emma	https://en.wikipedia.org/wiki/Calotes_emma
<i>Calotes versicolor</i>	http://www.ecologyasia.com/verts/lizards/changeable_lizard.htm	https://en.wikipedia.org/wiki/Oriental_garden_lizard	http://www.wildsingapore.com/wildfacts/vertebrates/reptilia/versicolor.htm	https://en.wikipedia.org/wiki/Oriental_garden_lizard	https://en.wikipedia.org/wiki/Oriental_garden_lizard
<i>Cosymbotus platyurus</i>	https://www.gbif.org/species/5816059	http://www.ecologyasia.com/verts/lizards/flat-tailed_gecko.htm	http://www.ecologyasia.com/verts/lizards/flat-tailed_gecko.htm	https://en.wikipedia.org/wiki/Flat-tailed_house_gecko	http://eol.org/pages/1056420/overview
<i>Draco maculatus</i>	http://www.iucnredlist.org/details/170396/0	http://www.ecologyasia.com/verts/lizards/spotted_gliding_lizard.htm	http://animaldiversity.org/accounts/Draco_volans/	https://en.wikipedia.org/wiki/Draco_maculatus	http://animaldiversity.org/accounts/Draco_volans/
<i>Gekko gekko</i>	https://en.wikipedia.org/wiki/Tokay_gecko	https://en.wikipedia.org/wiki/Tokay_gecko	https://en.wikipedia.org/wiki/Tokay_gecko	Norval et al. (2011)	http://eol.org/pages/794412/overview
<i>Hemidactylus garnoti</i>	http://www.californiaherps.com/lizards/pages/h.garnoti.html	https://srelherp.uga.edu/lizards/hemgar.htm	https://srelherp.uga.edu/lizards/hemgar.htm	https://en.wikipedia.org/wiki/Indo-Pacific_gecko	http://www.californiaherps.com/lizards/pages/h.garnoti.html
<i>Mabuya macularia</i>	http://www.ecologyasia.com/verts/lizards/speckled_forest_skink.htm	https://en.wikipedia.org/wiki/Eutropis_macularia	http://www.ecologyasia.com/verts/lizards.htm	https://en.wikipedia.org/wiki/Eutropis_macularia	http://www.wildsingapore.com/wildfacts/vertebrates/reptilia/multifasciata.htm
<i>Mabuya multifasciata</i>	http://www.wildsingapore.com/wildfacts/vertebrates/reptilia/multifasciata.htm	http://www.ecologyasia.com/verts/lizards/many-lined_sun_skink.htm	http://www.wildsingapore.com/wildfacts/vertebrates/reptilia/multifasciata.htm	http://www.ecologyasia.com/verts/lizards/many-lined_sun_skink.htm	http://www.wildsingapore.com/wildfacts/vertebrates/reptilia/multifasciata.htm
<i>Mabuya</i> sp.	Sources for <i>Mabuya macularia</i> and <i>Mabuya multifasciata</i>	Sources for <i>Mabuya macularia</i> and <i>Mabuya multifasciata</i>	Sources for <i>Mabuya macularia</i> and <i>Mabuya multifasciata</i>	Sources for <i>Mabuya macularia</i> and <i>Mabuya multifasciata</i>	Sources for <i>Mabuya macularia</i> and <i>Mabuya multifasciata</i>
<i>Ptychozoon lionotum</i>	http://www.iucnredlist.org/details/177831/0	http://www.geckosunlimited.com/community/gecko-care-sheets/30602-flying-geckos-	http://www.iucnredlist.org/details/177831/0	http://www.ecologyasia.com/verts/lizards/smooth-backed_gliding_gecko.htm	http://www.geckosunlimited.com/community/gecko-care-sheets/30602-flying-geckos-

		personal-care-sheet-ptychozoon-species.html			personal-care-sheet-ptychozoon-species.html
<i>Ptyctolaemus gularis</i>	Sources for <i>Draco maculatus</i> , <i>Calotes versicolor</i> and <i>Calotes emma</i> .	Sources for <i>Draco maculatus</i> , <i>Calotes versicolor</i> and <i>Calotes emma</i> .	Sources for <i>Draco maculatus</i> , <i>Calotes versicolor</i> and <i>Calotes emma</i> .	Sources for <i>Draco maculatus</i> , <i>Calotes versicolor</i> and <i>Calotes emma</i> .	Sources for <i>Draco maculatus</i> , <i>Calotes versicolor</i> and <i>Calotes emma</i> .
<i>Sphenomorphus courcyanum</i>	Zhu et al. (2015)	https://www.biosch.hku.hk/ecology/hkreptiles/lizard/Sphe nomorphus_indicus.html	https://www.biosch.hku.hk/ecology/hkreptiles/lizard/Sphe nomorphus_indicus.html	https://en.wikipedia.org/wiki/Sphe nomorphus_indicus	Huang (2010)
<i>Sphenomorphus indicus</i>	Zhu et al. (2015)	https://www.biosch.hku.hk/ecology/hkreptiles/lizard/Sphe nomorphus_indicus.html	https://www.biosch.hku.hk/ecology/hkreptiles/lizard/Sphe nomorphus_indicus.html	https://en.wikipedia.org/wiki/Sphe nomorphus_indicus	Huang (2010)
<i>Sphenomorphus maculatum</i>	https://www.thainationalparks.com/species/sphenomorphus-maculatus	https://www.thainationalparks.com/species/sphenomorphus-maculatus	https://www.thainationalparks.com/species/sphenomorphus-maculatus	https://www.thainationalparks.com/species/sphenomorphus-maculatus	Huang (2010)
<i>Takydromus sexlineatus</i>	https://en.wikipedia.org/wiki/Takydromus_sexlineatus	https://en.wikipedia.org/wiki/Takydromus_sexlineatus	https://en.wikipedia.org/wiki/Takydromus_sexlineatus	https://en.wikipedia.org/wiki/Takydromus_sexlineatus	Telford (1969)
<i>Tropidophorus assamensis</i>	https://en.wikipedia.org/wiki/Tropidophorus_assamensis	https://en.wikipedia.org/wiki/Tropidophorus_grayi	https://www.biosch.hku.hk/ecology/hkreptiles/lizard/Tropidophorus_sinicus.html	Das et al. (2009)	https://en.wikipedia.org/wiki/Tropidophorus_grayi

Appendix B. Species traits by taxa

Table S9. Traits collected for all macroinvertebrate taxa for the calculation of functional diversity metrics.

Class	Trait type	Trait	Type	Units	Taxon	Primary Data Source	Study
body dimensions	maximal potential size	≤ 0.25 cm	bounded discrete		macroinvertebrates	Bis and Usseglio-Polatera (2004)	all
body dimensions	maximal potential size	0.25 - 0.5 cm	bounded discrete		macroinvertebrates	Bis and Usseglio-Polatera (2004)	all
body dimensions	maximal potential size	0.5 - 1 cm	bounded discrete		macroinvertebrates	Bis and Usseglio-Polatera (2004)	all
body dimensions	maximal potential size	1 - 2 cm	bounded discrete		macroinvertebrates	Bis and Usseglio-Polatera (2004)	all
body dimensions	maximal potential size	2 - 4 cm	bounded discrete		macroinvertebrates	Bis and Usseglio-Polatera (2004)	all
body dimensions	maximal potential size	4 - 8 cm	bounded discrete		macroinvertebrates	Bis and Usseglio-Polatera (2004)	all
body dimensions	maximal potential size	> 8 cm	bounded discrete		macroinvertebrates	Bis and Usseglio-Polatera (2004)	all
diet	feeding habits	absorber	bounded discrete		macroinvertebrates	Bis and Usseglio-Polatera (2004)	all
diet	feeding habits	deposit feeder	bounded discrete		macroinvertebrates	Bis and Usseglio-Polatera (2004)	all
diet	feeding habits	shredder	bounded discrete		macroinvertebrates	Bis and Usseglio-Polatera (2004)	all
diet	feeding habits	scraper	bounded discrete		macroinvertebrates	Bis and Usseglio-Polatera (2004)	all
diet	feeding habits	filter feeder	bounded discrete		macroinvertebrates	Bis and Usseglio-Polatera (2004)	all
diet	feeding habits	piercer (plants or animals)	bounded discrete		macroinvertebrates	Bis and Usseglio-Polatera (2004)	all
diet	feeding habits	predator (carver/engulfer/swallower)	bounded discrete		macroinvertebrates	Bis and Usseglio-Polatera (2004)	all
diet	feeding habits	parasite	bounded discrete		macroinvertebrates	Bis and Usseglio-Polatera (2004)	all
dispersal	locomotion and substrate relation	flier	bounded discrete		macroinvertebrates	Bis and Usseglio-Polatera (2004)	all
dispersal	locomotion and substrate relation	surface swimmer	bounded discrete		macroinvertebrates	Bis and Usseglio-Polatera (2004)	all
dispersal	locomotion and substrate relation	full water swimmer	bounded discrete		macroinvertebrates	Bis and Usseglio-Polatera (2004)	all
dispersal	locomotion and substrate relation	crawler	bounded discrete		macroinvertebrates	Bis and Usseglio-Polatera (2004)	all
dispersal	locomotion and substrate relation	burrower (epibenthic)	bounded discrete		macroinvertebrates	Bis and Usseglio-Polatera (2004)	all
dispersal	locomotion and substrate relation	interstitial (endobenthic)	bounded discrete		macroinvertebrates	Bis and Usseglio-Polatera (2004)	all
dispersal	locomotion and substrate relation	temporary attached	bounded discrete		macroinvertebrates	Bis and Usseglio-Polatera (2004)	all
dispersal	locomotion and substrate relation	permanently attached	bounded discrete		macroinvertebrates	Bis and Usseglio-Polatera (2004)	all
habitat	transversal distribution	river channel	bounded discrete		macroinvertebrates	Bis and Usseglio-Polatera (2004)	all
habitat	transversal distribution	banks, connected side-arms	bounded discrete		macroinvertebrates	Bis and Usseglio-Polatera (2004)	all
habitat	transversal distribution	ponds, pools, disconnected side-arms	bounded discrete		macroinvertebrates	Bis and Usseglio-Polatera (2004)	all
habitat	transversal distribution	marshes, peat bogs	bounded discrete		macroinvertebrates	Bis and Usseglio-Polatera (2004)	all
habitat	transversal distribution	temporary waters	bounded discrete		macroinvertebrates	Bis and Usseglio-Polatera (2004)	all
habitat	transversal distribution	lakes	bounded discrete		macroinvertebrates	Bis and Usseglio-Polatera (2004)	all
habitat	transversal distribution	groundwaters	bounded discrete		macroinvertebrates	Bis and Usseglio-Polatera (2004)	all
phenology	life cycle duration	≤ 1 year	bounded discrete		macroinvertebrates	Bis and Usseglio-Polatera (2004)	all
phenology	life cycle duration	> 1 year	bounded discrete		macroinvertebrates	Bis and Usseglio-Polatera (2004)	all
reproduction	potential number of reproductive cycles per year	< 1	bounded discrete		macroinvertebrates	Bis and Usseglio-Polatera (2004)	all
reproduction	potential number of reproductive cycles per year	1	bounded discrete		macroinvertebrates	Bis and Usseglio-Polatera (2004)	all
reproduction	potential number of reproductive cycles per year	> 1	bounded discrete		macroinvertebrates	Bis and Usseglio-Polatera (2004)	all

Table S10. Traits collected for all plant taxa for the calculation of functional diversity metrics.

Class	Trait type	Trait	Type	Taxon	Data Source	Primary Data Source	Study
body dimensions	shoot growth form	floating leaves attached to the substrate	binary	plants	Kattge et al. (2011)	Kleyer et al. (2008)	Clarke, Lüderitz
body dimensions	shoot growth form	free floating plants	binary	plants	Kattge et al. (2011)	Kleyer et al. (2008)	Clarke, Lüderitz
body dimensions	shoot growth form	submerged attached to the substrate	binary	plants	Kattge et al. (2011)	Kleyer et al. (2008)	Clarke, Lüderitz
body dimensions	shoot growth form	lianas and climbers	binary	plants	Kattge et al. (2011)	Kleyer et al. (2008)	Clarke, Kardol, Piqueray
body dimensions	shoot growth form	emergent attached to the substrate	binary	plants	Kattge et al. (2011)	Kleyer et al. (2008)	Clarke, Kardol, Lüderitz
body dimensions	shoot growth form	stem ascending to prostrate	binary	plants	Kattge et al. (2011)	Kleyer et al. (2008)	Clarke, Kardol, Lüderitz, Piqueray
body dimensions	shoot growth form	stem erect	binary	plants	Kattge et al. (2011)	Kleyer et al. (2008)	Clarke, Kardol, Lüderitz, Piqueray
body dimensions	shoot growth form	stem prostrate	binary	plants	Kattge et al. (2011)	Kleyer et al. (2008)	Clarke, Kardol, Lüderitz, Piqueray
diet	nutrition	kills insects but not carnivorous	binary	plants	Kattge et al. (2011)	Fitter and Peat (1994)	Kardol, Piqueray
diet	nutrition	parasitic	binary	plants	Kattge et al. (2011)	Fitter and Peat (1994)	Piqueray
diet	nutrition	hemi-parasitic	binary	plants	Kattge et al. (2011)	Fitter and Peat (1994)	Piqueray
diet	nutrition	does not kill insects	binary	plants	Kattge et al. (2011)	Fitter and Peat (1994)	Piqueray
diet	nutrition	autotrophic	binary	plants	Kattge et al. (2011)	Fitter and Peat (1994)	Clarke, Kardol, Lüderitz, Piqueray
dispersal	dispersal agent	blastochor	binary	plants	Kattge et al. (2011)	Kleyer et al. (2008)	Clarke, Kardol, Piqueray
dispersal	dispersal agent	boleochor	binary	plants	Kattge et al. (2011)	Kleyer et al. (2008)	Clarke, Kardol, Piqueray
dispersal	dispersal agent	ethelochor	binary	plants	Kattge et al. (2011)	Kleyer et al. (2008)	Clarke, Kardol, Piqueray
dispersal	dispersal agent	herpochor	binary	plants	Kattge et al. (2011)	Kleyer et al. (2008)	Clarke, Kardol, Piqueray
dispersal	dispersal agent	multi seeded generative dispersule	binary	plants	Kattge et al. (2011)	Kleyer et al. (2008)	Clarke, Kardol, Piqueray
dispersal	dispersal agent	ombrochor	binary	plants	Kattge et al. (2011)	Kleyer et al. (2008)	Clarke, Kardol, Piqueray
dispersal	dispersal agent	speirochor	binary	plants	Kattge et al. (2011)	Kleyer et al. (2008)	Clarke, Kardol, Piqueray
dispersal	dispersal agent	bythisochor	binary	plants	Kattge et al. (2011)	Kleyer et al. (2008)	Piqueray
dispersal	dispersal agent	zoochor	binary	plants	Kattge et al. (2011)	Kleyer et al. (2008)	Clarke, Kardol
dispersal	dispersal agent	agochor	binary	plants	Kattge et al. (2011)	Kleyer et al. (2008)	Clarke, Kardol, Lüderitz, Piqueray
dispersal	dispersal agent	autochor	binary	plants	Kattge et al. (2011)	Kleyer et al. (2008)	Clarke, Kardol, Lüderitz, Piqueray
dispersal	dispersal agent	ballochor	binary	plants	Kattge et al. (2011)	Kleyer et al. (2008)	Clarke, Kardol, Lüderitz, Piqueray
dispersal	dispersal agent	chamaeochor	binary	plants	Kattge et al. (2011)	Kleyer et al. (2008)	Clarke, Kardol, Lüderitz, Piqueray
dispersal	dispersal agent	dysochor	binary	plants	Kattge et al. (2011)	Kleyer et al. (2008)	Clarke, Kardol, Lüderitz, Piqueray
dispersal	dispersal agent	endozoochor	binary	plants	Kattge et al. (2011)	Kleyer et al. (2008)	Clarke, Kardol, Lüderitz, Piqueray
dispersal	dispersal agent	epizoochor	binary	plants	Kattge et al. (2011)	Kleyer et al. (2008)	Clarke, Kardol, Lüderitz, Piqueray
dispersal	dispersal agent	generative dispersule	binary	plants	Kattge et al. (2011)	Kleyer et al. (2008)	Clarke, Kardol, Lüderitz, Piqueray
dispersal	dispersal agent	germinule	binary	plants	Kattge et al. (2011)	Kleyer et al. (2008)	Clarke, Kardol, Lüderitz, Piqueray
dispersal	dispersal agent	hemerochor	binary	plants	Kattge et al. (2011)	Kleyer et al. (2008)	Clarke, Kardol, Lüderitz, Piqueray
dispersal	dispersal agent	meteorochor	binary	plants	Kattge et al. (2011)	Kleyer et al. (2008)	Clarke, Kardol, Lüderitz, Piqueray
dispersal	dispersal agent	nautochor	binary	plants	Kattge et al. (2011)	Kleyer et al. (2008)	Clarke, Kardol, Lüderitz, Piqueray
dispersal	dispersal agent	one seeded generative dispersule	binary	plants	Kattge et al. (2011)	Kleyer et al. (2008)	Clarke, Kardol, Lüderitz, Piqueray
dispersal	dispersal agent	other	binary	plants	Kattge et al. (2011)	Kleyer et al. (2008)	Clarke, Kardol, Lüderitz, Piqueray
habitat	species environmental indicator value according to Ellenberg	moisture	bounded discrete	plants	Kattge et al. (2011)	Hill et al. (2004)	Clarke, Kardol, Lüderitz, Piqueray
phenology	plant lifespan	annuals	binary	plants	Kattge et al. (2011)	Kleyer et al. (2008)	Clarke, Kardol, Lüderitz, Piqueray
phenology	plant lifespan	perennials	binary	plants	Kattge et al. (2011)	Kleyer et al. (2008)	Clarke, Kardol, Lüderitz, Piqueray
reproduction	pollen vector	insect	binary	plants	Kattge et al. (2011)	Fitter and Peat (1994)	Clarke, Kardol, Lüderitz, Piqueray
reproduction	pollen vector	self-fertilised	binary	plants	Kattge et al. (2011)	Fitter and Peat (1994)	Clarke, Kardol, Lüderitz, Piqueray
reproduction	pollen vector	wind	binary	plants	Kattge et al. (2011)	Fitter and Peat (1994)	Clarke, Kardol, Lüderitz, Piqueray

Table S11. Traits collected for all ant taxa for the calculation of functional diversity metrics.

Class	Trait type	Trait	Type	Taxon	Primary Data Source	Study
body dimensions	body size	< 1 mm	binary	ants	Silvestre et al. (2003)	all
body dimensions	body size	1 - 2 mm	binary	ants	Silvestre et al. (2003)	all
body dimensions	body size	2 - 3 mm	binary	ants	Silvestre et al. (2003)	all
body dimensions	body size	> 3 mm	binary	ants	Silvestre et al. (2003)	all
body dimensions	body size	large polymorph	binary	ants	Silvestre et al. (2003)	all
diet	feeding strategy	cultivates fungus from fresh leaves	binary	ants	Silvestre et al. (2003)	all
diet	feeding strategy	cultivates fungus from decomposing organic matter	binary	ants	Silvestre et al. (2003)	all
diet	feeding strategy	generalist predator	binary	ants	Silvestre et al. (2003)	all
diet	feeding strategy	specialist predator	binary	ants	Silvestre et al. (2003)	all
diet	feeding strategy	omnivore/detritivore	binary	ants	Silvestre et al. (2003)	all
dispersal	recruitment	solitary	binary	ants	Silvestre et al. (2003)	all
dispersal	recruitment	tandem running	binary	ants	Silvestre et al. (2003)	all
dispersal	recruitment	mass recruitment	binary	ants	Silvestre et al. (2003)	all
dispersal	recruitment	legionary	binary	ants	Silvestre et al. (2003)	all
dispersal	recruitment	trophic collects plant exudates	binary	ants	Silvestre et al. (2003)	all
habitat	foraging substrate	vegetation	binary	ants	Silvestre et al. (2003)	all
habitat	foraging substrate	aboveground	binary	ants	Silvestre et al. (2003)	all
habitat	foraging substrate	belowground	binary	ants	Silvestre et al. (2003)	all
reproduction	estimated population size of mature colony	< 100	binary	ants	Silvestre et al. (2003)	all
reproduction	estimated population size of mature colony	100 - 1000	binary	ants	Silvestre et al. (2003)	all
reproduction	estimated population size of mature colony	1000 - 10000	binary	ants	Silvestre et al. (2003)	all
reproduction	estimated population size of mature colony	> 10000	binary	ants	Silvestre et al. (2003)	all

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Table S12. Traits collected for all reptile taxa for the calculation of functional diversity metrics.

Class	Trait type	Trait	Type	Units	Taxon	Primary Data Source	Study
body dimensions	length	maximum adult body size	continuous	mm	reptiles	see Appendix A	Glor
body dimensions	length	snout to vent length	continuous	mm	reptiles	see Appendix A	Pawar
diet	diet	arthropods	binary		reptiles	see Appendix A	Glor, Pawar
diet	diet	vertebrates	binary		reptiles	see Appendix A	Glor, Pawar
habitat	vertical foraging stratum	fossorial	binary		reptiles	see Appendix A	Glor
habitat	vertical foraging stratum	terrestrial	binary		reptiles	see Appendix A	Glor, Pawar
habitat	vertical foraging stratum	aquatic	binary		reptiles	see Appendix A	Glor, Pawar
habitat	vertical foraging stratum	arboreal	binary		reptiles	see Appendix A	Glor, Pawar
phenology	diel	diurnal	binary		reptiles	see Appendix A	Glor, Pawar
phenology	diel	nocturnal	binary		reptiles	see Appendix A	Glor, Pawar
reproduction	litter size	minimum number of offspring/eggs per clutch	continuous		reptiles	see Appendix A	Glor, Pawar
reproduction	litter size	maximum number of offspring/eggs per clutch	continuous		reptiles	see Appendix A	Glor, Pawar

Table S13. Traits collected for all bird taxa for the calculation of functional diversity metrics.

Class	Trait type	Trait	Type	Unit	Taxon	Primary Data Source	Study
body dimensions	length	wing length - male	continuous	mm	birds	Brown et al. (1982)	Aerts
body dimensions	length	wing length - female	continuous	mm	birds	Brown et al. (1982)	Aerts
body dimensions	length	tail length - male	continuous	mm	birds	Brown et al. (1982)	Aerts
body dimensions	length	tail length - female	continuous	mm	birds	Brown et al. (1982)	Aerts
body dimensions	length	bill length	continuous	mm	birds	Brown et al. (1982)	Aerts
body dimensions	length	tarsus length - male	continuous	mm	birds	Brown et al. (1982)	Aerts
body dimensions	length	tarsus length - female	continuous	mm	birds	Brown et al. (1982)	Aerts
body dimensions	weight	weight - male	continuous	g	birds	Brown et al. (1982)	Aerts
body dimensions	weight	weight - female	continuous	g	birds	Brown et al. (1982)	Aerts
body dimensions	length	total length - male	continuous	mm	birds	Del Hoyo et al. (1992)	O'Dea
body dimensions	length	total length - female	continuous	mm	birds	del Hoyo et al. (1992)	O'Dea
body dimensions	weight	weight - male	continuous	g	birds	del Hoyo et al. (1992)	O'Dea
body dimensions	weight	weight - female	continuous	g	birds	del Hoyo et al. (1992)	O'Dea
diet	diet	fruit	binary		birds	Brown et al. (1982)	Aerts
diet	diet	nectar	binary		birds	Brown et al. (1982)	Aerts
diet	diet	other plant material	binary		birds	Brown et al. (1982)	Aerts
diet	diet	invertebrates	binary		birds	Brown et al. (1982)	Aerts
diet	diet	reptiles and amphibians	binary		birds	Brown et al. (1982)	Aerts
diet	diet	fish	binary		birds	Brown et al. (1982)	Aerts
diet	diet	birds	binary		birds	Brown et al. (1982)	Aerts
diet	diet	mammal	binary		birds	Brown et al. (1982)	Aerts
diet	diet	algae	binary		birds	Brown et al. (1982)	Aerts
diet	diet	carion	binary		birds	Brown et al. (1982)	Aerts
diet	diet	fruit	binary		birds	del Hoyo et al. (1992)	O'Dea
diet	diet	nectar	binary		birds	del Hoyo et al. (1992)	O'Dea
diet	diet	other plant material	binary		birds	del Hoyo et al. (1992)	O'Dea
diet	diet	invertebrates	binary		birds	del Hoyo et al. (1992)	O'Dea
diet	diet	reptiles and amphibians	binary		birds	del Hoyo et al. (1992)	O'Dea
diet	diet	fish	binary		birds	del Hoyo et al. (1992)	O'Dea
diet	diet	birds and birds eggs	binary		birds	del Hoyo et al. (1992)	O'Dea
diet	diet	mammal	binary		birds	del Hoyo et al. (1992)	O'Dea
diet	diet	algae	binary		birds	del Hoyo et al. (1992)	O'Dea
diet	diet	carion	binary		birds	del Hoyo et al. (1992)	O'Dea
dispersal	migration	nomadic	binary		birds	BirdLife International (2017)	O'Dea
dispersal	migration	non-migratory	binary		birds	BirdLife International (2017)	all
dispersal	migration	migratory	binary		birds	BirdLife International (2017)	all
dispersal	migration	altitudinal migrant	binary		birds	BirdLife International (2017)	all
habitat	ecozone	afrotropical	binary		birds	BirdLife International (2017)	all
habitat	ecozone	palaearctic	binary		birds	BirdLife International (2017)	all
habitat	ecozone	indomalayan	binary		birds	BirdLife International (2017)	all
habitat	ecozone	oceanic	binary		birds	BirdLife International (2017)	all
habitat	ecozone	nearctic	binary		birds	BirdLife International (2017)	all
habitat	ecozone	neotropical	binary		birds	BirdLife International (2017)	all
habitat	ecozone	antarctic	binary		birds	BirdLife International (2017)	all
habitat	ecosystem	freshwater	binary		birds	BirdLife International (2017)	all

habitat	ecosystem	marine	binary		birds	BirdLife International (2017)	all
habitat	ecosystem	terrestrial	binary		birds	BirdLife International (2017)	all
habitat	habitat	artificial landscapes (aquatic)	categorical	4 levels	birds	BirdLife International (2017)	all
habitat	habitat	arable land	categorical	4 levels	birds	BirdLife International (2017)	all
habitat	habitat	pastureland	categorical	4 levels	birds	BirdLife International (2017)	all
habitat	habitat	plantations	categorical	4 levels	birds	BirdLife International (2017)	all
habitat	habitat	rural gardens	categorical	4 levels	birds	BirdLife International (2017)	all
habitat	habitat	subtropical/tropical heavily degraded former forest	categorical	4 levels	birds	BirdLife International (2017)	all
habitat	habitat	urban areas	categorical	4 levels	birds	BirdLife International (2017)	all
habitat	habitat	hot desert	categorical	4 levels	birds	BirdLife International (2017)	all
habitat	habitat	temperate desert	categorical	4 levels	birds	BirdLife International (2017)	all
habitat	habitat	subtropical/tropical dry forest	categorical	4 levels	birds	BirdLife International (2017)	all
habitat	habitat	subtropical/tropical lowland moist forest	categorical	4 levels	birds	BirdLife International (2017)	all
habitat	habitat	subtropical/tropical montane moist forest	categorical	4 levels	birds	BirdLife International (2017)	all
habitat	habitat	temperate forest	categorical	4 levels	birds	BirdLife International (2017)	all
habitat	habitat	subtropical/tropical swamp forest	categorical	4 levels	birds	BirdLife International (2017)	all
habitat	habitat	subtropical/tropical mangrove	categorical	4 levels	birds	BirdLife International (2017)	all
habitat	habitat	boreal forest	categorical	4 levels	birds	BirdLife International (2017)	all
habitat	habitat	subarctic forest	categorical	4 levels	birds	BirdLife International (2017)	Aerts
habitat	habitat	subtropical/tropical (lowland) dry grassland	categorical	4 levels	birds	BirdLife International (2017)	all
habitat	habitat	subtropical/tropical high-altitude grassland	categorical	4 levels	birds	BirdLife International (2017)	all
habitat	habitat	subtropical/tropical (lowland) seasonally wet/flooded grassland	categorical	4 levels	birds	BirdLife International (2017)	all
habitat	habitat	temperate grassland	categorical	4 levels	birds	BirdLife International (2017)	all
habitat	habitat	tundra	categorical	4 levels	birds	BirdLife International (2017)	Aerts
habitat	habitat	rocky areas	categorical	4 levels	birds	BirdLife International (2017)	all
habitat	habitat	dry savanna	categorical	4 levels	birds	BirdLife International (2017)	all
habitat	habitat	moist savanna	categorical	4 levels	birds	BirdLife International (2017)	all
habitat	habitat	subtropical/tropical (lowland) dry shrubland	categorical	4 levels	birds	BirdLife International (2017)	all
habitat	habitat	subtropical/tropical high altitude shrubland	categorical	4 levels	birds	BirdLife International (2017)	all
habitat	habitat	temperate shrubland	categorical	4 levels	birds	BirdLife International (2017)	all
habitat	habitat	Mediterranean-type shrubland	categorical	4 levels	birds	BirdLife International (2017)	Aerts
habitat	habitat	boreal shrubland	categorical	4 levels	birds	BirdLife International (2017)	Aerts
habitat	habitat	subarctic shrubland	categorical	4 levels	birds	BirdLife International (2017)	Aerts
habitat	habitat	subtropical/tropical (lowland) moist shrubland	categorical	4 levels	birds	BirdLife International (2017)	all
habitat	habitat	caves	categorical	4 levels	birds	BirdLife International (2017)	Aerts
habitat	habitat	bogs, marshes, swamps, fens, peatlands	categorical	4 levels	birds	BirdLife International (2017)	all
habitat	habitat	freshwater lakes (>8 ha) – permanent	categorical	4 levels	birds	BirdLife International (2017)	all
habitat	habitat	freshwater marshes/pools (under 8ha) - permanent	categorical	4 levels	birds	BirdLife International (2017)	Aerts
habitat	habitat	rivers, streams, creeks – permanent	categorical	4 levels	birds	BirdLife International (2017)	all
habitat	habitat	freshwater lakes (>8 ha) - seasonal/intermittent	categorical	4 levels	birds	BirdLife International (2017)	Aerts
habitat	habitat	freshwater marshes/pools (under 8ha) - seasonal/intermittent	categorical	4 levels	birds	BirdLife International (2017)	Aerts
habitat	habitat	rivers, streams, creeks -seasonal/intermittent/irregular	categorical	4 levels	birds	BirdLife International (2017)	Aerts
habitat	habitat	saline, brackish or alkaline lakes and flats - seasonal/intermittent	categorical	4 levels	birds	BirdLife International (2017)	Aerts
habitat	habitat	shrub dominated wetlands	categorical	4 levels	birds	BirdLife International (2017)	Aerts
habitat	habitat	alpine wetlands	categorical	4 levels	birds	BirdLife International (2017)	Aerts
habitat	habitat	freshwater springs	categorical	4 levels	birds	BirdLife International (2017)	Aerts
habitat	habitat	intertidal	categorical	4 levels	birds	BirdLife International (2017)	all
habitat	habitat	coastal	categorical	4 levels	birds	BirdLife International (2017)	all
habitat	altitudinal limit	upper limit	continuous	m	birds	del Hoyo et al. (1992)	O'Dea
habitat	altitudinal limit	lower limit	continuous	m	birds	del Hoyo et al. (1992)	O'Dea
phenology	breeding season	January	binary		birds	Brown et al. (1982)	Aerts

phenology	breeding season	February	binary		birds	Brown et al. (1982)	Aerts
phenology	breeding season	March	binary		birds	Brown et al. (1982)	Aerts
phenology	breeding season	April	binary		birds	Brown et al. (1982)	Aerts
phenology	breeding season	May	binary		birds	Brown et al. (1982)	Aerts
phenology	breeding season	June	binary		birds	Brown et al. (1982)	Aerts
phenology	breeding season	July	binary		birds	Brown et al. (1982)	Aerts
phenology	breeding season	August	binary		birds	Brown et al. (1982)	Aerts
phenology	breeding season	September	binary		birds	Brown et al. (1982)	Aerts
phenology	breeding season	October	binary		birds	Brown et al. (1982)	Aerts
phenology	breeding season	November	binary		birds	Brown et al. (1982)	Aerts
phenology	breeding season	December	binary		birds	Brown et al. (1982)	Aerts
phenology	breeding season	January	binary		birds	del Hoyo et al. (1992)	O'Dea
phenology	breeding season	February	binary		birds	del Hoyo et al. (1992)	O'Dea
phenology	breeding season	March	binary		birds	del Hoyo et al. (1992)	O'Dea
phenology	breeding season	April	binary		birds	del Hoyo et al. (1992)	O'Dea
phenology	breeding season	May	binary		birds	del Hoyo et al. (1992)	O'Dea
phenology	breeding season	June	binary		birds	del Hoyo et al. (1992)	O'Dea
phenology	breeding season	July	binary		birds	del Hoyo et al. (1992)	O'Dea
phenology	breeding season	August	binary		birds	del Hoyo et al. (1992)	O'Dea
phenology	breeding season	September	binary		birds	del Hoyo et al. (1992)	O'Dea
phenology	breeding season	October	binary		birds	del Hoyo et al. (1992)	O'Dea
phenology	breeding season	November	binary		birds	del Hoyo et al. (1992)	O'Dea
phenology	breeding season	December	binary		birds	del Hoyo et al. (1992)	O'Dea
reproduction	breeding behaviour	colonial	binary		birds	Brown et al. (1982)	Aerts
reproduction	breeding behaviour	solitary	binary		birds	Brown et al. (1982)	Aerts
reproduction	egg dimensions	length	continuous	mm	birds	Brown et al. (1982)	Aerts
reproduction	egg dimensions	width	continuous	mm	birds	Brown et al. (1982)	Aerts
reproduction	nesting	clutch size	continuous		birds	Brown et al. (1982)	Aerts
reproduction	nesting	clutch size	continuous		birds	del Hoyo et al. (1992)	O'Dea

Table S14. Traits collected for all fish taxa for the calculation of functional diversity metrics.

Class	Trait type	Trait	Type	Units	Taxon	Region	Primary Data Source	Study
body dimensions	length	maximum total length	continuous	cm	fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
diet	diet	nonfeeder	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
diet	diet	benthic feeder	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
diet	diet	surface or water column feeder	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
diet	diet	algae or phytoplankton, including filamentous algae	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
diet	diet	any part of macrophytes and vascular plants	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
diet	diet	detritus or unidentifiable vegetative matter	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
diet	diet	aquatic and terrestrial invertebrates and larval fishes	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
diet	diet	larger fishes, crayfishes, crabs, frogs, etc	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
diet	diet	for parasitic lampreys that feed mainly on blood	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
diet	diet	eggs of fishes, frogs, etc	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
diet	diet	other diet components	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
dispersal	migration	potamodromous or anadromous	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
habitat	substrate	pelagophils	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
habitat	substrate	polyphils	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
habitat	substrate	lithophils (rock-gravel)	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
habitat	substrate	lithophils (gravel-sand)	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
habitat	substrate	lithophils (silt-mud)	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
habitat	substrate	phytophils	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
habitat	substrate	psammophils	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
habitat	substrate	speleophils (rock cavity/roof)	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
habitat	substrate	speleophils (bottom burrows or natural holes)	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
habitat	substrate	speleophils (cavity generalist)	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
habitat	substrate	substrate indifferent	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
habitat	substrate	lithopelagophils	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
habitat	substrate	ariadnophils	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
habitat	substrate	phytolithophils	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
habitat	habitat preference	euryhaline	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
habitat	habitat preference	muck substrate	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
habitat	habitat preference	clay or silt substrate	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
habitat	habitat preference	sand substrate	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
habitat	habitat preference	gravel substrate	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
habitat	habitat preference	cobble or pebble substrate	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
habitat	habitat preference	boulder substrate	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
habitat	habitat preference	bedrock substrate	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
habitat	habitat preference	aquatic vegetation	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
habitat	habitat preference	organic debris or detrital substrate	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
habitat	habitat preference	large woody debris	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
habitat	habitat preference	pelagic	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
habitat	habitat preference	lotic and lentic systems but more often in lotic	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
habitat	habitat preference	lotic and lentic systems but more often in lentic	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
habitat	habitat preference	medium to large river	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
habitat	habitat preference	stream to small river	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
habitat	habitat preference	creek	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
habitat	habitat preference	spring or subterranean water	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
habitat	habitat preference	lentic systems	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
habitat	habitat preference	lowland elevation	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz
habitat	habitat preference	upland elevation	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz

habitat	habitat preference	mountainous physiography	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz
habitat	habitat preference	slow current	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
habitat	habitat preference	moderate current	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
habitat	habitat preference	fast current	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
phenology	spawning season	proportion of January	bounded continuous		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
phenology	spawning season	proportion of February	bounded continuous		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
phenology	spawning season	proportion of March	bounded continuous		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
phenology	spawning season	proportion of April	bounded continuous		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
phenology	spawning season	proportion of May	bounded continuous		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
phenology	spawning season	proportion of June	bounded continuous		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
phenology	spawning season	proportion of July	bounded continuous		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
phenology	spawning season	proportion of August	bounded continuous		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
phenology	spawning season	proportion of September	bounded continuous		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
phenology	spawning season	proportion of October	bounded continuous		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
phenology	spawning season	proportion of November	bounded continuous		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
phenology	spawning season	proportion of December	bounded continuous		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
phenology	spawning season	approximate length of spawning season	bounded continuous		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
reproduction	longevity	age at maturity - female	continuous	years	fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
reproduction	longevity	longevity	continuous	years	fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
reproduction	spawning preference	fecundity	continuous		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
reproduction	spawning preference	serial or batch spawner	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz
reproduction	spawning preference	nonguarders	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
reproduction	spawning preference	guarders	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
reproduction	spawning preference	open substratum spawners	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
reproduction	spawning preference	brood hiders	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
reproduction	spawning preference	substratum choosers	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
reproduction	spawning preference	nest spawners	binary		fish	United States	Frimpong and Angermeier (2009)	Baldigo, Edwards, Moerke, Schwartz, Shields
body dimensions	length at maturation	maximum total body length	continuous	cm	fish	Australia	Sternberg et al. (2014)	Bond
diet	diet	benthic invertebrates	binary		fish	Australia	Sternberg et al. (2014)	Bond
diet	diet	algae	binary		fish	Australia	Sternberg et al. (2014)	Bond
diet	diet	plants	binary		fish	Australia	Sternberg et al. (2014)	Bond
diet	diet	fish	binary		fish	Australia	Sternberg et al. (2014)	Bond
diet	diet	detritus	binary		fish	Australia	Sternberg et al. (2014)	Bond
diet	diet	mollusca	binary		fish	Australia	Sternberg et al. (2014)	Bond
diet	diet	crustacea	binary		fish	Australia	Sternberg et al. (2014)	Bond
dispersal	migration	potamodromous or anadromous	binary		fish	Australia	Sternberg et al. (2014)	Bond
habitat	spawning substrate	organic substrate (plants/wood)	binary		fish	Australia	Sternberg et al. (2014)	Bond
habitat	spawning substrate	mineral substrate (gravel/rocks)	binary		fish	Australia	Sternberg et al. (2014)	Bond
phenology	longevity	maximum potential life span	continuous	years	fish	Australia	Sternberg et al. (2014)	Bond
reproduction	reproductive guild	nonguarders	binary		fish	Australia	Sternberg et al. (2014)	Bond
reproduction	reproductive guild	guarders	binary		fish	Australia	Sternberg et al. (2014)	Bond
reproduction	reproductive guild	open substratum spawners	binary		fish	Australia	Sternberg et al. (2014)	Bond
reproduction	reproductive guild	brood hiders	binary		fish	Australia	Sternberg et al. (2014)	Bond
reproduction	reproductive guild	substratum choosers	binary		fish	Australia	Sternberg et al. (2014)	Bond
reproduction	reproductive guild	nest spawners	binary		fish	Australia	Sternberg et al. (2014)	Bond
body dimensions	maximum body length	< 20 cm	binary		fish	Europe	Schmidt-Kloiber and Hering (2015)	Langler, Lüderitz, Wolter
body dimensions	maximum body length	20 to 39 cm	binary		fish	Europe	Schmidt-Kloiber and Hering (2015)	Langler, Lüderitz, Wolter
body dimensions	maximum body length	> 39 cm	binary		fish	Europe	Schmidt-Kloiber and Hering (2015)	Langler, Lüderitz, Wolter
diet	diet	invertivorous	binary		fish	Europe	Schmidt-Kloiber and Hering (2015)	Langler, Lüderitz, Wolter
diet	diet	piscivorous	binary		fish	Europe	Schmidt-Kloiber and Hering (2015)	Langler, Lüderitz, Wolter
diet	diet	phytophagous	binary		fish	Europe	Schmidt-Kloiber and Hering (2015)	Langler, Lüderitz, Wolter

diet	diet	omnivorous	binary		fish	Europe	Schmidt-Kloiber and Hering (2015)	Langler, Lüderitz, Wolter
diet	diet	carnivorous	binary		fish	Europe	Schmidt-Kloiber and Hering (2015)	Langler, Lüderitz, Wolter
diet	diet	other	binary		fish	Europe	Schmidt-Kloiber and Hering (2015)	Langler, Lüderitz, Wolter
dispersal	migration	diadromous	binary		fish	Europe	Schmidt-Kloiber and Hering (2015)	Langler, Lüderitz, Wolter
dispersal	migration	potamodromous	binary		fish	Europe	Schmidt-Kloiber and Hering (2015)	Langler, Lüderitz, Wolter
dispersal	migration	no migration	binary		fish	Europe	Schmidt-Kloiber and Hering (2015)	Langler, Lüderitz, Wolter
dispersal	migration	oceanodromous	binary		fish	Europe	Schmidt-Kloiber and Hering (2015)	Langler, Lüderitz, Wolter
habitat	habitat	pelagic	binary		fish	Europe	Schmidt-Kloiber and Hering (2015)	Langler, Lüderitz, Wolter
habitat	habitat	benthopelagic	binary		fish	Europe	Schmidt-Kloiber and Hering (2015)	Langler, Lüderitz, Wolter
habitat	habitat	demersal	binary		fish	Europe	Schmidt-Kloiber and Hering (2015)	Langler, Lüderitz, Wolter
habitat	habitat guild	habitat guild	categorical	3 levels	fish	Europe	Lüderitz et al (2011)	Lüderitz
habitat	flow preference	flow preference	categorical	3 levels	fish	Europe	Wolter (2010)	Wolter
phenology	life span	< 8 years	binary		fish	Europe	Schmidt-Kloiber and Hering (2015)	Langler, Lüderitz, Wolter
phenology	life span	8 to 15 years	binary		fish	Europe	Schmidt-Kloiber and Hering (2015)	Langler, Lüderitz, Wolter
phenology	life span	> 15 years	binary		fish	Europe	Schmidt-Kloiber and Hering (2015)	Langler, Lüderitz, Wolter
reproduction	fecundity (no. oocytes)	< 55000	binary		fish	Europe	Schmidt-Kloiber and Hering (2015)	Langler, Lüderitz, Wolter
reproduction	fecundity (no. oocytes)	55000 to 60000	binary		fish	Europe	Schmidt-Kloiber and Hering (2015)	Langler, Lüderitz, Wolter
reproduction	fecundity (no. oocytes)	> 60000	binary		fish	Europe	Schmidt-Kloiber and Hering (2015)	Langler, Lüderitz, Wolter
reproduction	spawning guild	spawning guild	categorical	8 levels	fish	Europe	Lüderitz et al (2011)	Lüderitz
reproduction	spawning preference	spawning preference	categorical	7 levels	fish	Europe	Wolter (2010)	Wolter

Appendix C. Excluded studies

For a study to be included in my meta-analysis, it needed to meet the following criteria: (1) restoration activities (either passive or active) were intentionally implemented and measured in the study, as opposed to simply comparing between habitat types, (2) at least one unmanipulated (i.e. degraded) control site was included, against which to compare restored sites, (3) data were sufficiently replicated (i.e. a dataset was excluded if they sampled only two sites: one unmanipulated control site and one restored site), (4) accumulated species lists included at least three different taxonomic families, so as to ensure meaningful variation in functional diversity, (5) species presence or abundance data were provided for all individual sites across all sampling occurrences and (6) focal taxa appeared in at least two datasets (to enable across-taxa comparisons). Below, ‘Curran’ refers to Curran et al. (2014) and ‘Kail’ to Kail et al. (2015).

Table S15. Studies excluded from my meta-analysis (149), including details of focal taxonomic group(s), location of study and reason for exclusion.

Source	Citation	Taxon	Country	Reason for exclusion
Curran	Barlow et al. (2007a)	Birds	Brazil	(1) Not restoration
Curran	Barlow et al. (2007b)	Butterflies	Brazil	(1) Not restoration
Curran	Blake and Loiselle (2001)	Birds	Costa Rica	(1) Not restoration
Curran	Bobo et al. (2006)	Butterflies	Cameroon	(1) Not restoration
Curran	Bowman et al. (1990)	Birds, butterflies and reptiles	Papua New Guinea	(1) Not restoration
Curran	Bragagnolo et al. (2007)	Harvestmen	Brazil	(1) Not restoration
Curran	Castro-Luna et al. (2007)	Bats	Mexico	(1) Not restoration
Curran	Chapman and Chapman (1997)	Plants	Uganda	(1) Not restoration
Curran	Chung et al. (2000)	Beetles	Malaysia	(1) Not restoration
Curran	de Souza et al. (2008)	Amphibians	Brazil	(1) Not restoration
Curran	Dranzoa (1998)	Birds	Uganda	(1) Not restoration
Curran	Eggleton et al. (1997)	Termites	Malaysia	(1) Not restoration
Curran	Eilu and Obua (2005)	Plants	Uganda	(1) Not restoration

Curran	Estrada et al. (1994)	Non-volant small mammals	Mexico	(1) Not restoration
Curran	Faria (2006)	Bats	Brazil	(1) Not restoration
Curran	Fermon et al. (2005)	Butterflies	Indonesia	(1) Not restoration
Curran	Fimbel (1994)	Large mammals	Sierra Leone	(1) Not restoration
Curran	Gardner et al. (2007)	Reptiles and amphibians	Brazil	(1) Not restoration
Curran	Gardner et al. (2008)	Beetles	Brazil	(1) Not restoration
Curran	Gillison et al. (2003)	Termites	Indonesia	(1) Not restoration
Curran	Grove (2002)	Saproxylis beetles	Australia	(1) Not restoration
Curran	Hawes et al. (2009)	Moths	Brazil	(1) Not restoration
Curran	Klein (1989)	Beetles	Brazil	(1) Not restoration
Curran	Lambert (1992)	Birds	Malaysia	(1) Not restoration
Curran	Law and Chidel (2001)	Bats	Australia	(1) Not restoration
Curran	Li et al. (2011)	Epiphytes	China	(1) Not restoration
Curran	Lieberman (1986)	Reptiles and amphibians	Costa Rica	(1) Not restoration
Curran	Luja et al. (2008)	Reptiles	Mexico	(1) Not restoration
Curran	Marsden (1998)	Birds	Indonesia	(1) Not restoration
Curran	Medellin and Equihua (1998)	Non-volant small mammals	Mexico	(1) Not restoration
Curran	Moola and Vasseur (2004)	Plants	Canada	(1) Not restoration
Curran	Nakagawa et al. (2006)	Non-volant small mammals	Malaysia	(1) Not restoration
Curran	Owiunji and Plumptre (1998)	Birds	Uganda	(1) Not restoration
Curran	Parry et al. (2007)	Large mammals and birds	Brazil	(1) Not restoration
Curran	Peh et al. (2005)	Birds	Malaysia	(1) Not restoration
Curran	Powers et al. (2009)	Plants	Costa Rica	(1) Not restoration
Curran	Purata (1986)	Plants	Mexico	(1) Not restoration
Curran	Quintero and Roslin (2005)	Beetles	Brazil	(1) Not restoration
Curran	Raman (2001)	Birds	India	(1) Not restoration
Curran	Renner et al. (2006)	Birds	Guatemala	(1) Not restoration

Curran	Sáfián et al. (2011)	Butterflies	Ghana	(1) Not restoration
Curran	Schonberg et al. (2004)	Ants	Costa Rica	(1) Not restoration
Curran	Selmants and Knight (2003)	Plants	United States	(1) Not restoration
Curran	Shahabuddin and Tschardtke (2005)	Beetles	Indonesia	(1) Not restoration
Curran	Sodhi et al. (2005)	Birds	Indonesia	(1) Not restoration
Curran	Vallan (2002)	Amphibians	Madagascar	(1) Not restoration
Curran	Vasconcelos (1999)	Ants	Brazil	(1) Not restoration
Curran	Waltert et al. (2005)	Butterflies	Indonesia	(1) Not restoration
Curran	Willett (2001)	Spiders	United States	(1) Not restoration
Curran	Wu et al. (1996)	Non-volant small mammals	China	(1) Not restoration
Curran	Abbott et al. (2003)	Cockroaches, grasshoppers, crickets and spiders	Australia	(2) No negative control
Curran	Aidar et al. (2001)	Plants	Brazil	(2) No negative control
Curran	Andersen and Nelson (1999)	Non-volant small mammals	United States	(2) No negative control
Curran	Andersen (1993)	Ants	Australia	(2) No negative control
Curran	Andrade and Rubio-Torgler (1994)	Birds	Colombia	(2) No negative control
Curran	Aravena et al. (2002)	Plants	Chile	(2) No negative control
Curran	Bowen et al. (2009)	Birds	Australia	(2) No negative control
Curran	Buckney and Morrison (1992)	Plants	Australia	(2) No negative control
Curran	Costa et al. (2010)	Ants	Brazil	(2) No negative control
Curran	Ernst and Rödel (2005)	Amphibians	Ivory Coast	(2) No negative control
Curran	Fang and Peng (1997)	Plants	China	(2) No negative control
Curran	Farwig et al. (2008)	Birds	Kenya	(2) No negative control
Curran	Floren et al. (2001)	Ants	Malaysia	(2) No negative control
Curran	Fukushima et al. (2008)	Plants	Thailand	(2) No negative control
Curran	Grau et al. (1997)	Plants	Argentina	(2) No negative control
Curran	Heinen (1992)	Reptiles and amphibians	Costa Rica	(2) No negative control

Curran	Hingston and Grove (2010)	Birds	Australia	(2) No negative control
Curran	Hopp et al. (2010)	Beetles	Brazil	(2) No negative control
Curran	House et al. (2006)	Ants	Australia	(2) No negative control
Curran	Ishida et al. (2005)	Plants	Japan	(2) No negative control
Curran	Kennard (2002)	Plants	Bolivia	(2) No negative control
Curran	Kindscher and Tieszen (1998)	Plants	United States	(2) No negative control
Curran	Kritzinger and Van Aarde (1998)	Birds	South Africa	(2) No negative control
Curran	Liebsch et al. (2007)	Plants	Brazil	(2) No negative control
Curran	Liebsch et al. (2008) and contained studies	Plants	Brazil	(2) No negative control
Curran	Majer (1992)	Ants	Brazil	(2) No negative control
Curran	Marin-Spiotta et al. (2007)	Plants	Puerto Rico	(2) No negative control
Curran	Michael et al. (2011)	Reptiles	Australia	(2) No negative control
Curran	Palladini et al. (2007)	Ants	United States	(2) No negative control
Curran	Parrotta and Knowles (2001)	Plants	Brazil	(2) No negative control
Curran	Pascarella et al. (2000)	Plants	Puerto Rico	(2) No negative control
Curran	Patten (1997)	Non-volant small mammals	United States	(2) No negative control
Curran	Sarmiento et al. (2003)	Plants	Venezuela	(2) No negative control
Curran	Silva et al. (2007)	Ants	Brazil	(2) No negative control
Curran	Stark et al. (2006)	Plants	Canada	(2) No negative control
Curran	Stenbacka et al. (2010)	Beetles	Sweden	(2) No negative control
Curran	Veddeler et al. (2005)	Butterflies	Indonesia	(2) No negative control
Kail	Baatrup-Pedersen et al. (2000)	Plants	Denmark	(2) No negative control
Kail	Bradford et al. (2011)	Fish	Canada	(2) No negative control
Kail	Brooks et al. (2002)	Macroinvertebrates	United States	(2) No negative control
Kail	Carline and Walsh (2007)	Macroinvertebrates	United States	(2) No negative control
Kail	Chin et al. (2010)	Macroinvertebrates	United States	(2) No negative control
Kail	Chovanec et al. (2002)	Amphibians, dragonflies, fish	Austria	(2) No negative control

Kail	Cowx and Van Zyll de Jong (2004)	Fish	Canada/United Kingdom	(2) No negative control
Kail	Hohausova and Jurajda (2005)	Fish	Czech Republic	(2) No negative control
Kail	Layzer and Scott (2006)	Mussels and fish	United States	(2) No negative control
Kail	Marks et al. (2010)	Fish	United States	(2) No negative control
Kail	Muehlbauer et al. (2009)	Macroinvertebrates	United States	(2) No negative control
Kail	Negishi and Richardson (2003)	Macroinvertebrates	Canada	(2) No negative control
Kail	Quinn and Kwak (2000)	Fish	United States	(2) No negative control
Kail	Shields et al. (1993)	Fish	United States	(2) No negative control
Kail	Yu et al. (2010)	Macroinvertebrates	China	(2) No negative control
Kail	Albertson et al. (2011)	Macroinvertebrates	United States	(3) Only two sites
Kail	Brooks et al. (2006)	Fish	Australia	(3) Only two sites
Kail	Friberg et al. (1994)	Macroinvertebrates	Denmark	(3) Only two sites
Kail	Henry et al. (1995)	Macroinvertebrates and fish	France/Switzerland	(3) Only two sites
Kail	Jungwirth et al. (1993)	Macroinvertebrates and fish	Austria	(3) Only two sites
Kail	Sarriquet et al. (2007)	Macroinvertebrates	France	(3) Only two sites
Kail	Shields et al. (1998)	Fish	United States	(3) Only two sites
Kail	Spänhoff et al. (2006)	Macroinvertebrates	Germany	(3) Only two sites
Curran	Nicolas et al. (2009)	Non-volant small mammals	Guinea	(4) < 3 taxonomic families
Curran	Sorensen and Fedigan (2000)	Large mammals	Costa Rica	(4) < 3 taxonomic families
Kail	Avery (1996)	Fish	United States	(4) < 3 taxonomic families
Kail	Fjellheim et al. (2003)	Fish	Norway	(4) < 3 taxonomic families
Kail	House (1996)	Fish	United States	(4) < 3 taxonomic families
Kail	Jones and Tonn (2004)	Fish	Canada	(4) < 3 taxonomic families

Kail	Kelly and Bracken (1998)	Fish	Ireland	(4) < 3 taxonomic families
Kail	Lehane et al. (2002)	Fish	Ireland	(4) < 3 taxonomic families
Kail	Merz et al. (2004)	Fish	United States	(4) < 3 taxonomic families
Kail	Muhar et al. (2007)	Fish	Austria	(4) < 3 taxonomic families
Kail	Newbury and Gaboury (1993)	Fish	Canada	(4) < 3 taxonomic families
Kail	Palm et al. (2010)	Fish	Sweden	(4) < 3 taxonomic families
Kail	Pedersen et al. (2009)	Fish	Denmark	(4) < 3 taxonomic families
Kail	Sabaton et al. (2008)	Fish	France	(4) < 3 taxonomic families
Kail	Saunders and Smith (1962)	Fish	Canada	(4) < 3 taxonomic families
Kail	Scruton et al. (1998)	Fish	Canada	(4) < 3 taxonomic families
Kail	Shetter et al. (1949)	Fish	United States	(4) < 3 taxonomic families
Kail	Solazzi et al. (2000)	Fish	United States	(4) < 3 taxonomic families
Kail	van Zyll De Jong et al. (1997)	Fish	Canada	(4) < 3 taxonomic families
Kail	Zika and Peter (2002)	Fish	Liechtenstein	(4) < 3 taxonomic families
Curran	Chambers et al. (1994)	Plants	United States	(5) Species data insufficient or absent
Curran	Gollan et al. (2011)	Beetles	Australia	(5) Species data insufficient or absent
Curran	Johns (1991)	Birds	Brazil	(5) Species data insufficient or absent
Curran	Kanowski et al. (2006) [1]	Reptiles	Australia	(5) Species data insufficient or absent

Curran	Kanowski et al. (2006) [2]	Reptiles	Australia	(5) Species data insufficient or absent
Curran	MacGregor-Fors et al. (2010)	Birds	Mexico	(5) Species data insufficient or absent
Curran	McLachlan and Knispel (2005)	Plants	Canada	(5) Species data insufficient or absent
Curran	Medellín et al. (2000)	Bats	Mexico	(5) Species data insufficient or absent
Curran	Wijesinghe and Brooke (2005)	Non-volant small mammals and birds	Sri Lanka	(5) Species data insufficient or absent
Kail	Gerhard and Reich (2000)	Macroinvertebrates	Germany	(5) Species data insufficient or absent
Kail	Haapala et al. (2003)	Macroinvertebrates	Finland	(5) Species data insufficient or absent
Kail	Howson et al. (2009)	Fish	Australia	(5) Species data insufficient or absent
Kail	Merz et al. (2005)	Macroinvertebrates	United States	(5) Species data insufficient or absent
Kail	Moerke et al. (2004)	Macroinvertebrates and fish	United States	(5) Species data insufficient or absent
Kail	Monahan and Caffrey (1996)	Macroinvertebrates	Ireland	(5) Species data insufficient or absent
Kail	Rosi-Marshall et al. (2006)	Macroinvertebrates and fish	United States	(5) Species data insufficient or absent
Kail	Shin et al. (2011)	Macroinvertebrates	South Korea	(5) Species data insufficient or absent
Curran	Andersen et al. (2001)	Grasshoppers	Australia	(6) Lone study of taxa
Kail	Passy and Blanchet (2007)	Algae	United States	(6) Lone study of taxa

Appendix D. Model output by focal question

The questions to which each output table responds matches those outlined in the Introduction, Methods and Results. Explanations for the abbreviations used throughout the following six

5 tables are as follows: Design, LON = longitudinal, SFT = space-for-time; Response, FRic = functional richness, FEve = functional evenness, FDis = functional dispersion, nbsp = species richness, lognbsp = log-transformed species richness, sp.Eve = species evenness, FRic.dist.from.pos = functional richness (distance from positive control, see ‘Model structure’ in Methods), FEve.dist.from.pos = functional evenness (distance from positive
10 control), FDis.dist.from.pos = functional dispersion (distance from positive control); Std. Error = standard error; # obs = number of observations. The number of observations of each random factor level are also presented in the following tables. Additionally, treatment is a categorical variable with active, passive, pos_control (= positive control) and neg_control (= negative control) as levels. Treatment2 is a categorical variable with active and passive
15 collapsed into one level (‘restored’), thus treatment2 has three levels: pos_control, restored and neg_control. Realm is a categorical variable with terrestrial and freshwater as levels. Years_since_restoration is a continuous variable reporting time since project initiation in years. In all models neg_control was taken as the baseline level (i.e. intercept condition) for both treatment and treatment2 variables, and freshwater was taken as the baseline level for
20 the factor realm.

In my models, background factors not accounted for by fixed effects were captured by random effects; in modelling longitudinal data, taxon was retained in model selection only in predicting species richness with restoration, and as a random effect it explained 50% of

model variance. In space-for-time data, 56% of variance was explained by the random effect for taxon in predicting functional richness with species richness, 28% explained by the random slope of active restoration treatment across different taxonomic groups in predicting species richness with restoration, 49% and 41% explained by the random slope for passive restoration treatment across different taxonomic groups and different ecoregion respectively in predicting functional richness with restoration, and finally in predicting FRic.dist.from.pos with restoration, taxon and ecoregion random effects explained 21% and 19% of variance, with a further 25% and 27% explained by random slopes of treatment (with active and passive levels collapsed) across different taxonomic groups and ecoregions respectively.

Table S16. Summary of coefficient estimates of models tested in Question 1) Does functional diversity increase with species diversity?

Design	Response	Fixed effect	Estimate	Std. Error	t-value	p-value	Random effect	# obs	site:(block:study)	block:study	study
LON	FRic	(intercept)	-0.68749	0.10657	-6.451	< 0.0001	–	257	90	26	15
		lognbsp	0.47392	0.02193	21.613	< 0.0001					
SFT	FRic	(intercept)	-0.15325	0.09588	-1.598	0.1738	(nbsp taxon) +	320	–	29	15
		nbsp	0.04583	0.01901	2.410	0.0591	(nbsp ecoregion)				
LON	FEve	(intercept)	0.57480	0.08159	7.045	0.0263	(sp.Eve taxon) +	245	86	25	14
		realmterrestrial	0.18733	0.24467	0.766	0.4710	(sp.Eve ecoregion)				
SFT	FEve	(Intercept)	0.65271	0.09545	6.838	< 0.0001	–	284	–	20	13
		sp.Eve	-0.20976	0.10885	-1.927	0.0572					
		realmterrestrial	-0.16517	0.12705	-1.300	0.2059					
		sp.Eve:	0.38148	0.12451	3.064	0.0027					
		realmterrestrial									
LON	FDis	(Intercept)	0.11820	0.01948	6.070	< 0.0001	–	257	90	26	15
		lognbsp	0.01444	0.00600	2.408	0.0169					
SFT	FDis	(Intercept)	0.08680	0.01614	5.377	< 0.0001	–	320	–	29	15
		lognbsp	0.02380	0.00384	6.197	< 0.0001					

Table S17. Summary of coefficient estimates of models tested in Question 2) Does the observed relationship between species and functional diversity differ from what would be expected by chance alone?

Design	Response	Fixed effect	Estimate	Std. Error	t-value	p-value	Random effect	# obs	site:(block:study)	block:study	study
LON	Z score	(intercept)	-0.14490	0.21810	-0.665	0.5170	–	244	87	23	15
		realmterrestrial	-0.36670	0.90720	-0.404	0.6910					
SFT	Z score	(intercept)	0.40090	0.42080	0.953	0.3860	(nbsp taxon)	279	–	25	13
		realmterrestrial	-1.09900	0.29560	-3.718	0.0003					

5 **Table S18. Summary of coefficient estimates of models tested in Question 3) Does restoration increase species diversity relative to negative controls, and does this increase with time? Where species richness was the response variable, generalised linear mixed-effects models were run and hence z-values reported; where species evenness was the response variable, linear mixed-effects models were run, so t-values reported. A term for individual-level fixed effects (1|newvar) was included in the space-for-time model of richness to correct for overdispersion.**

Design	Response	Fixed effect	Estimate	Std. Error	t- or z-value	p-value	Random effect	# obs	site:(block:study)	block:study	study
LON	nbsp	(Intercept)	2.48536	0.36095	6.886	< 0.0001	(1 taxon)	257	90	26	15
		realmterrestrial	-21.6704	8.31125	-2.607	0.0091					
		years_since_restoration	0.08108	0.01901	4.265	< 0.0001					
		treatmentactive	0.03690	0.04474	0.825	0.4095					
		treatmentpassive	0.31610	0.15215	2.078	0.0378					
		treatmentpos_control	-0.04296	0.06638	-0.647	0.5175					
		realmterrestrial:	1.34487	0.54668	2.460	0.0139					
		years_since_restoration									
SFT	nbsp	(Intercept)	3.00613	0.26464	11.359	< 0.0001	(treatment taxon) + (1 newvar)	205	–	27	14
		realmterrestrial	-0.43011	0.35348	-1.217	0.2237					
		treatmentactive	-0.30529	0.25055	-1.218	0.2231					
		treatmentpassive	0.08050	0.14181	0.568	0.5703					
		years_since_restoration	0.07356	0.02025	3.632	0.0003					
		realmterrestrial:	1.26873	0.18922	6.705	< 0.0001					
		treatmentactive									
		realmterrestrial:	-0.07105	0.01995	-3.561	0.0004					

		years_since_restoration								
		treatmentactive:	-0.01598	0.01197	-1.335	0.1820				
		years_since_restoration								
LON	sp.Eve	(Intercept)	0.56944	0.03800	14.984	< 0.0001	245	86	25	14
		years_since_restoration	0.01832	0.00590	3.105	0.0028				
SFT	sp.Eve	(Intercept)	0.70140	0.05051	13.890	< 0.0001	180	–	18	12
		years_since_restoration	0.00131	0.00046	2.840	0.0051				

Table S19. Summary of coefficient estimates of models tested in Question 4) Does restoration increase functional diversity relative to negative controls, and does this effect change with time?

Design	Response	Fixed effect	Estimate	Std. Error	t-value	p-value	Random effect	# obs	site:(block:study)	block:study	study
LON	FRic	(Intercept)	0.46998	0.05117	9.185	< 0.0001		257	90	26	15
		realInterrestrial	-0.19533	0.25945	-0.753	0.4561					
		treatmentactive	0.02545	0.03167	0.804	0.4251					
		treatmentpassive	0.04995	0.10559	0.473	0.6377					
		treatmentpos_control	-0.00782	0.04879	-0.160	0.8734					
		years_since_restoration	0.02728	0.00894	3.050	0.0026					
		realInterrestrial:	-0.24697	0.11632	-2.123	0.0378					
		treatmentpos_control									
SFT	FRic	(Intercept)	0.36261	0.11806	3.072	0.0175	(treatment taxon) + (treatment ecoregion)	205	–	27	14
		realInterrestrial	-0.08276	0.12601	-0.657	0.5241					
		treatmentactive	-0.09080	0.09695	-0.937	0.5224					
		treatmentpassive	0.28637	0.51583	0.555	0.6130					
		years_since_restoration	0.05555	0.01080	5.142	< 0.0001					
		realInterrestrial:	0.35657	0.09887	3.607	0.0004					
		treatmentactive									
		realInterrestrial:	-0.04948	0.01070	-4.625	< 0.0001					
		years_since_restoration									

		treatmentactive:	-0.01793	0.00767	-2.338	0.0212					
		years_since_restoration									
LON	FEve	(Intercept)	0.57738	0.04684	12.328	< 0.0001	257	90	26	15	
		realInterrestrial	0.20269	0.18480	1.097	0.2920					
SFT	FEve	(Intercept)	0.52209	0.06453	8.090	< 0.0001	205	–	27	14	
		realInterrestrial	0.19763	0.09077	2.177	0.0504					
LON	FDis	(Intercept)	0.13787	0.01257	10.967	< 0.0001	257	90	26	15	
		treatment2pos_control	0.00975	0.01023	0.953	0.3452					
		treatment2restored	0.01687	0.00673	2.507	0.0151					
		years_since_restoration	0.00449	0.00167	2.690	0.0077					
		treatment2pos_control:	-0.00387	0.00148	-2.620	0.0107					
		years_since_restoration									
		treatment2restored:	-0.00136	0.00136	-1.004	0.3184					
		years_since_restoration									
SFT	FDis	(Intercept)	0.16510	0.01239	13.329	< 0.0001	(treatment2	205	–	27	14
		years_since_restoration	0.00039	0.00019	2.076	0.0411	taxon)				

Table S20. Summary of coefficient estimates of models tested in Question 5) Does the effect of restoration on functional diversity exceed that expected by chance given species richness?

Design	Response	Fixed effect	Estimate	Std. Error	t-value	p-value	Random effect	# obs	site:(block:study)	block:study	study
LON	Z score	(intercept)	-0.14490	0.21810	-0.665	0.5170	—	244	87	23	15
		realmterrestrial	-0.36670	0.90720	-0.404	0.6910					
SFT	Z score	(intercept)	-0.27100	0.48110	-0.563	0.5938	(1 taxon)	200	—	25	13
		realmterrestrial	-0.78680	0.28650	-2.747	0.0909					

Table S21. Summary of coefficient estimates of models tested in Question 6) Does the functional diversity of restored sites progress towards that of positive control sites over time, and is this change faster than in negative controls?

Design	Response	Fixed effect	Estimate	Std. Error	t-value	p-value	Random effect	# obs	site:(block:study)	block:study	study
SFT	FRic.dist. from.pos	(Intercept)	0.14797	0.06655	2.223	0.0478	(treatment2 taxon) + (treatment2 ecoregion	160	–	18	9
		years_since_restoration	-0.00432	0.00164	-2.627	0.0115					
SFT	FEve.dist. from.pos	(Intercept)	0.00705	0.00926	0.762	0.4667		160	–	18	9
		years_since_restoration	-0.00091	0.00038	-2.390	0.0181					
SFT	FDis.dist. from.pos	(Intercept)	-0.01168	0.01175	-0.995	0.3511		160	–	18	9
		treatmentactive	0.00441	0.00683	0.645	0.5196					
		treatmentpassive	0.03158	0.00575	5.492	< 0.0001					
		years_since_restoration	-0.00073	0.00023	-3.216	0.0016					