Does functional redundancy affect ecological stability and resilience? A review and meta-analysis

CHRISTOPHER R. BIGGS, LAUREN A. YEAGER, DEREK G. BOLSER, CHRISTINA BONSELL, ANGELINA M. DICHIERA, ZHENXIN HOU, SPENCER R. KEYSER, ALEXIS J. KHURSIGARA, KAIJUN LU, ARLEY F. MUTH, BENJAMIN NEGRETE JR., AND BRAD E. ERISSMAN

Marine Science Institute, The University of Texas at Austin, 750 Channel View Drive, Port Aransas, Texas 78373 USA

Citation: Biggs, C. R., L. A. Yeager, D. G. Bolser, C. Bonsell, A. M. Dichiera, Z. Hou, S. R. Keyser, A. J. Khursigara, K. Lu, A. F. Muth, B. Negrete Jr., and B. E. Erisman. 2020. Does functional redundancy affect ecological stability and resilience? A review and meta-analysis. Ecosphere 11(7):e03184. 10.1002/ecs2.3184

Abstract. In light of rapid shifts in biodiversity associated with human impacts, there is an urgent need to understand how changing patterns in biodiversity impact ecosystem function. Functional redundancy is hypothesized to promote ecological resilience and stability, as ecosystem function of communities with more redundant species (those that perform similar functions) should be buffered against the loss of individual species. While functional redundancy is being increasingly quantified, few studies have linked differences in redundancy across communities to ecological outcomes. We conducted a review and meta-analysis to determine whether empirical evidence supports the asserted link between functional redundancy and ecosystem stability and resilience. We reviewed 423 research articles and assembled a data set of 32 studies from 15 articles across aquatic and terrestrial ecosystems. Overall, the mean correlation between functional redundancy and ecological stability/resilience was positive. The mean positive effect of functional redundancy was greater for studies in which redundancy was measured as species richness within functional groups (vs. metrics independent of species richness), but species richness itself was not correlated with effect size. The results of this meta-analysis indicate that functional redundancy may positively affect community stability and resilience to disturbance, but more empirical work is needed including more experimental studies, partitioning of richness and redundancy effects, and links to ecosystem functions.

Key words: biodiversity; community structure; disturbance; ecosystem function; functional diversity; global change; time series data.

Received 3 April 2020; accepted 27 April 2020; final version received 22 May 2020. Corresponding Editor: Debra P. C. Peters.

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† E-mail: cbiggs@utexas.edu

INTRODUCTION

Humans are drastically altering the composition of ecological communities globally (Dornelas et al. 2014, Elahi et al. 2015), which has cascading impacts on associated ecological functions and services (Cardinale et al. 2012). In particular, increasing rates of species extinctions associated with human impacts have caused intense interest in the implications of this biodiversity loss on ecological processes (Ceballos et al. 2015). The relationship between species richness and overall ecosystem function has been studied extensively (Loreau et al. 2001, Cardinale et al. 2006, van der Plas 2019); it is generally held that greater species richness leads to increases in
overall ecosystem function, such as biogeochemical activities, the transfer of energy, ecological services, and production of biomass, either through niche complementarity or sampling effects (Loreau and Hector 2001). The degree to which the loss of an individual species impacts overall ecosystem structure and function, however, depends on whether there are other species within the community that perform similar ecosystem functions, a property commonly referred to as functional redundancy (Walker 1992, Naeem 1998).

The functional redundancy of ecological communities is thought to primarily be important in enhancing the temporal stability of associated ecosystem function, as communities with more species performing similar functions would be buffered from losses of any given species (Naeem 1998, Petchey et al. 2007). For example, Fonseca and Ganade (2001) estimated that if species extinctions were random within South American plant communities, 75% of species could be removed before an entire functional group was lost. They suggest that communities with more species, a more even distribution of species across functional groups, and lower functional richness should be less likely to lose an entire functional group from a community based on stochastic processes alone. By extension, communities with more functionally redundant species may also be more resilient to loss in function following disturbance events. As natural ecosystems are being threatened by an increasing frequency of both anthropogenic (e.g., overexploitation, habitat removal) and environmental disturbances (e.g., fire, hurricanes), identifying which community properties promote resilience is useful in setting conservation or management targets (Elmqvist et al. 2003, Oliver et al. 2015). Higher functional redundancy therefore provides a form of insurance against stochastic population fluctuations or species loss, resulting in stability in community structure or ecosystem function.

Stability can be realized as either resistance to change or resilience in recovering from disturbance. However, the relationship between functional redundancy and stability has not been well established empirically. Studies have instead focused on how biodiversity influences production, resource use, and stability in response to disturbances. Biodiversity may affect resistance to disturbance (experiencing proportionally smaller changes in production), but not resilience (returning to pre-disturbance levels of function; Isbell et al. 2015). Greater biodiversity promotes ecosystem functions (van der Plas 2019) and stability. However, stability effects were only evident in multitrophic systems (Jiang and Pu 2009) but displayed similar effect sizes regardless of trophic group or between terrestrial and aquatic ecosystems (Cardinale et al. 2006). Overall, there have been mixed results with respect to diversity effects on stability (van der Plas 2019), inspiring the search for other factors, such as functional redundancy, that may more consistently correlate with stability or resilience in ecosystem function.

Thus, managing for or conserving high functional redundancy has been suggested to be a potentially important goal in enhancing ecological stability in the face of disturbance. This may be especially true when response traits (i.e., traits that determine a species response to environmental conditions) and effect traits (i.e., traits which mediate an ecological process or function) differ (Walker 1995, Oliver et al. 2015). In other words, if species within a functional group vary in their sensitivity to a given disturbance (possess variable response traits), functional groups with more species in them should be more resistant or resilient to changes in environmental conditions (Diaz and Cabido 2001).

Because of the hypothesized importance of functional redundancy in mediating ecological stability, functional redundancy has been increasingly measured and discussed within the literature. For instance, a literature search within the Institute of Scientific Information Web of Science database on 25 June 2019 revealed that the proportion of ecological studies that use the term “functional redundancy” has quadrupled over the last 15 yr (Fig. 1). Some biodiversity inventories even point to relatively low functional redundancy measured within natural ecological faunas as a signal that they may be innately vulnerable to disturbance (e.g., Petchey et al. 2007, Mouillot et al. 2014). In light of the increasing frequency by which functional redundancy is measured and discussed, a quantitative assessment of whether it does in fact enhance desirable ecological properties like stability and resilience is greatly needed.
Our overall objective was to evaluate whether empirical evidence supports the purported link between functional redundancy and ecological stability. First, we conducted a literature review to understand and summarize the number and types of studies that have examined this relationship. Next, we completed a meta-analysis to calculate the mean effect size across studies and quantify which factors were important in mediating the mean effect. We focused on relationships between functional redundancy, temporal stability (resistance), and resilience in ecological structure/function, rather than the total magnitude of ecological function, as this is the primary way by which redundancy is theorized to mediate ecosystem function. We also examined which ecological (e.g., trophic group of focal taxa, species richness of the community) and methodological factors (e.g., study duration, functional redundancy metric used) may mediate the overall effect size to inform future research on this topic.

METHODS

Literature search and data collection

We conducted a systematic literature search of all databases in the Institute of Scientific Information’s Web of Science on 22 February 2018 and 14 June 2019 to identify primary literature examining the effect of functional redundancy on stability or resilience of ecological communities and ecological function. Our search included the following 2 sets of search terms: (1) “functional redundancy” AND (disturbance OR stability OR resilience), and (2) terms for metrics that represent the inverse of functional redundancy: (“functional originality” OR “functional uniqueness” OR “functional vulnerability”) AND (resilience OR disturbance OR stability). We also added one article (McLean et al. 2019) that was too recently published to be included within the database during our search. After initial screening for relevance to ecology, all remaining articles were re-assessed for inclusion by two separate reviewers based on four criteria: (1) Functional redundancy was the independent variable (or could be treated as the independent variable with re-analysis); (2) two or more time points were measured (before and after a disturbance event, or multiple measurements from the same community through time); (3) sufficient data were reported to calculate effect size; and (4) the response variable was some measure of community structure or ecosystem function. In some cases, there were multiple assessments of links between functional redundancy and ecological responses within an individual article. For the purpose of the current paper, we termed each independent assessment a “study” in contrast to an “article” which is used to refer to each published unit.

Calculation of effect sizes

We used the Pearson correlation coefficient ($r$) as the standardized effect size measure to compare the association between functional redundancy and an ecological response variable within each study. We were interested in stability in these response variables temporally or following disturbance, so response variables were compared before and after a disturbance or at multiple time points. Ecological response variables included measures of community structure (e.g., total biomass, diversity) or ecosystem function (e.g., primary production, pollination). We used stability in the response through time (e.g., 1/coefficient of variation through time), changes in community state following disturbance, or
changes in ecosystem function (pollination, or primary production) following disturbance as the response variable (see Data S1 for the full list of response variables).

Pearson’s $r$ statistics were either extracted directly from the original study, calculated from correlation tests we performed on the raw data, or converted from other reported test statistics. Because the distribution of $r$-values becomes skewed when $r$ approaches ± 1, $r$-values were transformed into $z$ scores using Fisher’s $z$ transformation (Rosenberg et al. 2013). We also accounted for the positive bias associated with Fisher’s $z$ transformations by applying the correction recommended by Overton (1998; for details, see Appendix S1).

**Statistical analysis**

First, we calculated the mean effect size across all observations (based on $z$ scores with bias correction) to examine the overall association between functional redundancy and measures of ecological stability or resilience. Next, to account for non-independence of effect sizes taken from the same article, we conducted a maximum likelihood random-effects regression on bias-corrected, unweighted $z$ scores (lme4 in R; Bates et al. 2015, R Core Team 2018) with article ID treated as a random effect (random intercept). Modeled effect sizes and 95% confidence intervals (CIs) around our estimates (confint function in R; Nakagawa and Cuthill 2007) were back-transformed from Fisher’s $z$ to $r$ by taking the hyperbolic tangent of the estimate (Rosenberg et al. 2013). To examine whether the stability effects of functional redundancy were independent of species richness, we compared the correlation of maximum species richness to the effect size ($r$) for each study.

In addition to examining the overall mean effect, we also compared mean effect sizes across a priori designated subsets of observations. These comparisons among groups included (1) studies that examined variation in ecological variables over time without disturbance vs. those that examined the response following a disturbance; (2) studies in which the function redundancy metric was dependent on species richness (i.e., species richness within functional groups) vs. those in which the metric was statistically independent of species richness (e.g., Gini-Simpson coefficient–Rao’s $Q$); (3) studies in which the response variable measured community structure vs. those in which the response variable measured ecosystem function; (4) observations in which the functionally redundant taxa were producers vs. those in which the functionally redundant taxa were consumers; and (5) observations from aquatic systems vs. those from terrestrial systems. Similar random-effects models were calculated for each subset of the data set.

Due to the limited number of studies included in the meta-analysis, we took an exploratory approach to evaluate patterns in the study meta-data and associations with reported effect sizes. This approach included examining histograms of the number of studies conducted across different groupings of biome types and Pearson correlations between raw, mean effect sizes for a given article and continuous meta-data variables (e.g., study duration, species richness, number of traits).

**RESULTS**

**Literature database and study meta-data**

Our original literature search yielded 423 published articles (Appendix S2: Fig. S1). We excluded articles that were not relevant to the topic or did not link difference in functional redundancy to other measures of community stability or ecosystem function. We identified 32 replicate studies (i.e., quantitative assessments) across 15 published articles which met our set selection criteria and were retained for the quantitative meta-analysis (Auster and Link 2009, Pillar et al. 2013, Rice et al. 2013, Gerisch 2014, Brandl et al. 2016, Lipoma et al. 2016, Nash et al. 2016, Kaiser-Bunbury et al. 2017, Aune et al. 2018, Correia et al. 2018, da Costa Santana et al. 2018, Richardson et al. 2018, Sanders et al. 2018, Bruno et al. 2019, McLean et al. 2019, Data S1). These 15 articles included in the meta-analysis spanned five continents and diverse biomes across aquatic and terrestrial realms (Appendix S2: Fig. S2). Study duration ranged from 98 d to 39 yr, and richness of the species pool ranged from 11 to 274. All studies were conducted in the field, and only one article involved an experimental manipulation of functional redundancy. Five of the 15 articles examined
patterns in time series data, while the remaining 10 examined responses to natural and anthropogenic disturbances.

There was wide variation among articles in the methods used to assess functional redundancy as well as the traits considered (Data S1). The simplest metric included examining the number of species within designated functional groups, with more redundant communities having more species within a group on average. This metric is not independent of species richness, as estimated redundancy increases as more species are added to the community. Other metrics were statistically independent of species richness and relied largely on estimating the amount of functional diversity not explained by species diversity, including using newer metrics proposed by de Bello et al. (2007) and Ricotta et al. (2016; Data S1). Functional redundancy was related to a suite of community structure (e.g., stability in organismal abundance, biomass, and diversity through time) and ecosystem function (e.g., pollination, primary productivity) response metrics (Data S1).

**Meta-analysis of relationship between functional redundancy and ecological stability/resilience**

There was wide variation across studies in the relationship between functional redundancy and stability and resilience in ecological response that ranged from strong positive correlations (max $r = 0.85$) to strong negative correlations (min $r = -0.72$; Data S1). Overall, the mean effect (calculated from bias-corrected, back-transformed z scores) of functional redundancy on ecological stability and resilience was positive (mean $r = 0.18$, 95% CI = $-0.02$, 0.37). The mean effect when estimated with the random-effects model to account for study ID was similar (mean $r = 0.20$, 95% CI = 0.03, 0.38; Fig. 2).

The mean $r$ for studies using functional redundancy metrics dependent on species richness was also positive (mean $r = 0.40$, 95% CI = 0.10, 0.69), while that for studies using metrics statistically independent of species richness was lower with a 95% CI that overlapped zero (mean $r = 0.09$, 95% CI = $-0.11$, 0.30). However, the correlation between species richness and effect size was negative, but nonsignificant ($r = -0.15$, $P = 0.4$). In studies that examined a measure of community structure as the ecological response, functional redundancy had a more consistent, positive effect (mean $r = 0.24$, 95% CI = 0.03, 0.45) when compared to those in which a measure of ecosystem function was the response (mean $r = 0.10$, 95% CI = $-0.30$, 0.47), although the sample size for the former group was much larger ($n = 26$ vs. 6). The mean $r$ was positive, but with 95% CI intervals overlapping zero for all other subsets of the data (Fig. 2).

**Exploration of study characteristics and effect size relationships**

There was a positive but nonsignificant correlation between study duration and the mean effect size by article ($r = 0.44$, $P = 0.1$;
Appendix S2: Fig. S3). There was not a strong correlation between species richness of the focal community ($r = -0.32$, $P = 0.2$; Appendix S2: Fig. S4) nor the number of traits considered ($r = -0.05$, $P = 0.9$; Appendix S2: Fig. S5) and the mean effect size by article.

**DISCUSSION**

Through the meta-analysis of 32 functional redundancy–ecological resilience and stability relationships, we found an overall positive association between the two, supporting ecological theory related to effects of biodiversity on ecosystem function. Specifically, in our analysis, ecological communities with more functionally redundant species were more likely to display higher resilience following disturbance or greater stability in community structure or ecological function over time relative to those with fewer functionally redundant species. Though more research into the mechanism underlying this relationship is needed, it is possible that redundant species were able to compensate for disturbance-mediated or natural population fluctuations when functionally similar species declined. Notably, the number of published articles that have quantitatively evaluated this relationship was few (15 published articles, 32 studies), compared to the much more numerous set of studies on other forms of biodiversity–ecosystem function relationships (e.g., species richness magnitude of ecosystem function). Additionally, most studies included a measure of community structure as the response variable, although theory predicts functional redundancy should be important in predicting overall ecosystem function, not community structure per se (Walker 1992). That is, functional redundancy should be important in stabilizing overall ecosystem function in spite of fluctuations in community structure (e.g., loss of species). Nonetheless, these initial results support a growing focus on functional redundancy as a key component of biodiversity research and conservation.

Functional redundancy was measured using a range of metrics across studies ranging from simply counting species within functional groups to those that partition species diversity into functional richness and functional redundancy components. These approaches measure functional redundancy in fundamentally different ways and will vary in the response to both variations in community assembly filters and in effects on ecological processes. For example, by simply counting (or averaging) the number of species within a functional group, communities with more species would be quantified as more redundant, but it is unclear whether this is really a redundancy or richness effect. Other metrics that control for species richness would not necessarily increase redundancy as more species are added as the relative overlap in trait space is what is measured. Importantly, when we divided studies based on the type of metric used, the mean effect size was only different from zero for studies using functional redundancy metrics based on species richness. However, the correlation between species richness and the effect size was nonsignificant, indicating that the factors other than species richness were affecting the observed differences. The development of newer quantitative methods, like that proposed by Ricotta et al. (2016), that provide a standardized method for calculating functional redundancy that controls for species richness should help increase comparability of results across studies if adopted by more researchers. Additionally, just like any assessment of functional diversity, the functional redundancy measured will be sensitive to how functional traits or groups are defined, which and how many traits are considered, and the resolution of trait assessment (Petchey and Gaston 2006).

Two components of stability are the resistance to change and resilience in recovery from a disturbance (Donohue et al. 2016). There has been conflicting evidence on the effects of species richness with respect to resistance and resilience. In grassland communities, diversity had an effect in resistance to change, but was not a factor in the resilience or recovery of a system after disturbance (Isbell et al. 2015). Conversely, other studies have found the opposite relationship where diversity promotes recovery after a disturbance but does not result in resistance (van Ruijven and Berendse 2010). Further, a meta-analysis examining the relationship between biodiversity and ecosystem function found that biodiversity promotes biomass production, pollination, and temporal stability, but neutral or negative relationships were common regarding other
functions (e.g., decomposition, carbon sequestration; van der Plas 2019). We were not able to make a distinction between which aspect of stability the response variables in each study were capturing, but both aspects were likely included given the wide range of systems included, the differences in disturbance, and the range of study durations (98 d to 39 yr).

In addition to the dearth of studies empirically testing the functional redundancy–stability/resilience relationships, one of the most striking results of this systematic literature review was the wide variation in methods employed across studies, which likely limits our ability to detect patterns. Characteristics of experimental design may have a significant effect on studies of diversity–stability relationships, especially the spatial and temporal scale at which the experiments are conducted (Loreau et al. 2001, Campbell et al. 2011). Further, implicit differences in the structures and dynamics of marine and terrestrial systems may affect the stability and time scale at which those systems will vary and respond to disturbance (Steele 1985). Due to the low number of studies that independently tested stability effects of functional redundancy, there was a wide range of response variables marine and terrestrial ecosystems, further complicating comparisons, analysis, and possibly confounding results. Moreover, all the studies reviewed except one (Sanders et al. 2018) relied upon measuring natural variation in functional redundancy and variation in ecological responses through time. By relying on natural variation in functional redundancy alone, it is difficult to tease apart the effect of functional redundancy from potential confounding factors that may drive variation in community structure in the first place (e.g., environmental stress gradients or disturbance history). Experimental studies that manipulate functional redundancy (while controlling for functional richness) of communities in the field or within the laboratory and track ecological responses are greatly needed to more rigorously link the two.

By restricting our analyses to studies that used the term “functional redundancy” (or similar terms), we likely missed some studies that collected data suitable for evaluating the effects of functional redundancy but did not describe it as such. Furthermore, reviews of previous studies have found that there is a generally positive relationship between species richness and stability in ecosystem function (Loreau et al. 2001, Cardinale et al. 2006), with the proposed mechanisms being that richer communities may be more redundant and thus better able to buffer against loss or population fluctuations within individual species (Peterson et al. 1998). Revisiting some of this past research or future research that specifically partitions these diversity effects would help elucidate the overall importance of redundancy on ecosystem stability and resilience.

The conservation of biodiversity is often motivated by the positive link between biodiversity and the provisioning of ecosystem services provided to humans (Worm et al. 2006). In this context, it is often desirable to have ecosystem services that are not only high in magnitude, but also stable and generally resilient to disturbances (Kremen 2005). For example, fishers want large fisheries yields and yields that are predictable from year to year (Hilborn et al. 2003). Thus, the conservation of functional redundancy may be an important goal for managing stable and resilient ecosystem services (Neeam 1998, Cadotte et al. 2011). Since some services are tied to ecosystem function, while others are tied to the presence of certain species or species complexes, it is valuable to consider both community structure and ecosystem function when evaluating the impact of functional redundancy. While this systematic literature review and meta-analysis highlights the need for more empirical research to parse out the effect of functional redundancy on community stability and resilience across contexts, these initial findings support the growing interest in functional redundancy as a potentially important biodiversity target.

ACKNOWLEDGMENTS

We thank C. Tang for help with data collection. This analysis was conducted as part of a Meta-analysis in Ecology graduate course in the Marine Science Department at The University of Texas at Austin. Support for LY was also provided from NSF grant #OCE-1661683. LY and BE conceptualized and taught the course, while all authors developed the topic. AM organized the group code of conduct. CRB, KL, SK, AM, and BNJ organized the literature database. All authors reviewed the literature and collected data from original studies. BNJ, AJK, KL, AMD, ZH, CB, CRB, SK,
and LY calculated the effect sizes. CB curated the extracted effect size database. CRB, CB, DGB, AJK, SRK, and LY analyzed the data. AMD, ZH, BNJ, and LY produced the figures. LY wrote the first draft of the manuscript, all authors provide feedback on the text, and CRB revised the manuscript for publication.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3184/full

Appendix S1: Supplemental methods for the literature review and meta-analysis

Appendix S2: Supplementary figures: Meta-data for studies included in meta-analysis

Data S1: Meta-data and effect sizes for studies included in the meta-analysis