

1 **Multiple Processes Generate Productivity-Diversity**
2 **Relationships in Experimental Wood-Fall**
3 **Communities**

4
5 **Running title:** Productivity and diversity of wood falls

6
7 Craig R. McClain *Department of Biology, Duke University, Box 90338, Durham, NC 27708 USA*

8 craig.mcclain@duke.edu 919-668-4590

9
10 James P. Barry *Monterey Bay Aquarium Research Institute, 7700 Sandholdt Rd., Moss Landing, CA*

11 *95039 USA* barry@mbari.org

12
13 Douglas Eernisse *Department of Biological Science, California State University, Fullerton, CA 92834*

14 *USA* deernisse@exchange.fullerton.edu

15
16 Tammy Horton *Ocean Biogeochemistry and Ecosystems, National Oceanography Centre, University of*

17 *Southampton Waterfront Campus,, European Way, Southampton SO14 3ZH, UK*

18 tammy.horton@noc.ac.uk

19

1 Jenna Judge *Department of Integrative Biology, University of California, Berkeley, 3040 Valley Life*
2 *Sciences Building, Berkeley, CA 94720 USA jennajudge@berkeley.edu*

3

4 Keiichi Kakui *Department of Natural History Sciences, Faculty of Science, Hokkaido University,*
5 *Sapporo 0600810, Japan k_kakui@mail.goo.ne.jp*

6

7 Chris Mah *Department of Invertebrate Zoology, Smithsonian Institution, National Museum of Natural*
8 *History, 10th and Constitution Ave, NW, Washington, DC 20560 USA brisinga@gmail.com*

9

10 Anders Warén *Department of Invertebrate Zoology, Swedish Museum of Natural History, Box 50007, SE-*
11 *10405 Stockholm, Sweden anders.waren@nrm.se*

1 **Abstract**

2 Energy availability has long been recognized as a predictor of community structure, and
3 changes in both terrestrial and marine productivity under climate change necessitate a deeper
4 understanding of this relationship. The productivity-diversity relationship (PDR) is well explored
5 in both empirical and theoretical work in ecology, but numerous questions remain. Here, we test
6 four different theories for PDRs (More-Individuals Hypothesis, Resource-Ratio Theory, More
7 Specialization Theory, and the Connectivity-Diversity Hypothesis) with experimental deep-sea
8 wood falls. We manipulated productivity by altering wood-fall sizes and measured responses
9 after 5 and 7 years. In November 2006, 36 *Acacia* sp. logs were deployed at 3203m in the
10 Northeast Pacific Ocean (Station Deadwood: 36.154098° N, 122.40852° W). Overall, we found a
11 significant increase in diversity with increased wood-fall size for these communities. Increases
12 in diversity with wood-fall size occurred because of the addition of rare species and increases of
13 overall abundance, although individual species responses varied. We also found that limited
14 dispersal helped maintain the positive PDR relationship. Our experiment suggests that multiple
15 interacting mechanisms influence PDRs.

16 **Keywords:** diversity, productivity, energy, deep sea, resource availability, connectivity

17

1 Introduction

2 Energy availability is historically recognized as a predictor of community structure
3 (Wallace 1878) and changes in terrestrial and marine productivity under climate change
4 necessitate a deeper understanding of this relationship. Recent research indicates that oceanic
5 production, as indexed by phytoplankton standing stock, declined at a rate of $\approx 1\%$ of the global
6 median per year (Boyce et al. 2010). Regional-scale changes were more heterogeneous, with the
7 equatorial Pacific productivity declining by $\approx 50\%$ over the last decade and polar regions
8 increasing by a comparable magnitude (Behrenfeld et al. 2006). Clearly, a more complete
9 understanding of energetics will enable greater understanding and predictive power for the
10 consequences of current and forthcoming climate change.

11 How productivity determines biological diversity in an area, the productivity-diversity
12 relationship (PDR), is well explored in ecology (Rosenzweig and Abramsky 1993, Chase and
13 Ryberg 2004) but numerous questions remain including the relationships very existence, shape,
14 and scale dependence (Waide et al. 1999, Mittelbach et al. 2001, Chase and Leibold 2002,
15 Cusens et al. 2012). Ecologists have proposed a variety of hypotheses to explain PDRs. These
16 individual hypotheses predict positive, negative (or at least the negative part of the concave
17 down unimodal PDR), and unimodal PDRs (Rosenzweig and Abramsky 1993, Waide et al.
18 1999). Here we examine four major mechanisms for PDRs 1) More-Individuals Hypothesis, 2)
19 Resource-Ratio Hypothesis, 3) Niche Position Hypothesis, and 4) Connectivity Hypothesis
20 (Table 1), while recognizing that other potential mechanisms may exist requiring further
21 examination, e.g. the one more trophic level hypothesis (Post 2002) and the competitive
22 exclusion model to predict negative PDRs (Rosenzweig and Abramsky 1993).

1 Wright (1983) and Wright et al. (1993) proposed that a positive linear PDR emerges
2 because productivity influences population size (the More-Individuals Hypothesis of (Srivastava
3 and Lawton 1998)). Low productivity reduces population sizes and increases risk of stochastic
4 extinction (Wright et al. 1993, Srivastava and Lawton 1998). As productivity and population
5 sizes increase, Allee effects are reduced and local coexistence increases (Wright et al. 1993,
6 Srivastava and Lawton 1998). This theory predicts a monotonically increasing PDR and a
7 positive relationship between energy and abundance as well as between abundance and diversity.

8 Tilman (1982) proposed the Resource Ratio Theory to predict the concave down,
9 unimodal PDR. With high levels of one resource (e.g. productivity) another resource will be
10 limiting. No single species can be competitively dominant at all resource ratios, i.e. species have
11 trade-offs in the capture or utilization efficiency for different resources. When resources are
12 balanced, e.g. intermediate productivities, species adapted to both ends of the spectrum, can
13 coexist because neither is competitively superior.

14 The More Specialization Theory (Schoener 1976, DeAngelis 1994) or Niche Position
15 Hypothesis (Evans et al. 1999, Evans et al. 2005) predicts a positive linear PDR. A minimum
16 amount of resource is needed to support specialist species. At low productivity some resources
17 are too rare to support these species. At high productivities, specialization is allowable and
18 prevents competitive exclusion (Schoener 1976, DeAngelis 1994). Increased energy may also
19 increase the amount of preferred resource, and species may decrease their consumption of less
20 optimal resources. This would reduce niche breadth in high energy areas and allow for greater
21 coexistence, e.g. Niche Width Hypothesis (Evans et al. 1999).

1 Lastly, Chase and Ryberg (2004), based on work in freshwater ponds, proposed PDRs are
2 scale dependent and reliant upon connectivity among sites. When connectivity is weak, positive
3 linear PDRs emerge with strong compositional differences among sites. As connectivity
4 strengthens, low productivity-low diversity sites acquire species from high productivity-high
5 diversity sites. This effect minimizes compositional differences and weakens the PDR
6 relationship.

7 Empirical research offers mixed support for each of these theories. Linear positive
8 relationships for some taxa across natural energy gradients support the Species-Energy Theory
9 (Kaspari et al. 2000, Hurlbert 2004, Evans et al. 2006, Mönkkönen et al. 2006). Yet, tests for
10 More Individuals Hypothesis in experimental systems are mixed (Srivastava and Lawton 1998,
11 Hurlbert 2006, Yee and Juliano 2007, McGlynn et al. 2010). The relationship between density
12 and species richness is mostly supported (Kaspari et al. 2000, Hurlbert 2004, Evans et al. 2006,
13 Hurlbert 2006, Mönkkönen et al. 2006, McGlynn et al. 2010) but often more complex than the
14 simple mechanism of the More-Individuals Hypothesis and influence by factors such as
15 disturbance, variability in productivity, and area (Hurlbert 2004, Evans et al. 2006, Mönkkönen
16 et al. 2006, Yee and Juliano 2007, McGlynn et al. 2010). The Resource-Ratio Theory is met
17 with support in terrestrial plants, marine phytoplankton, and aquatic phytoplankton (Tilman and
18 Wedin 1991, McKane et al. 2002, Venterink et al. 2008). In contrast, experimental nutrient
19 enrichment of microbial fungal assemblages lead to increases not decreases of diversity, even
20 while species composition changed (Kerekes et al. 2013). Many studies on animal communities
21 also report concave down, unimodal PDRs but it remains unclear if these patterns are attributable
22 to species tradeoffs with resource limitation or alternative mechanisms (Abramsky and

1 Rosenzweig 1984). Tests of the Niche Position Hypothesis are rare but provide support. In ants
2 and lake fish, specialist species only occur at higher productivity levels (Kaspari 2001, Mason et
3 al. 2008). In contrast, British breeding avifauna, despite exhibiting a positive species-energy
4 relationship, show no evidence of increased numbers of specialists at higher energy levels (Evans
5 et al. 2005). Yet at global scales, increased richness is associated with increased specialization
6 for birds (Belmaker et al. 2012).

7 Studying the effects of energy on community structure is often difficult because
8 determinants of available energy in natural systems are diverse and often unidentifiable (Arim et
9 al. 2007). However, microcosm experiments conducted for terrestrial and freshwater systems
10 (Srivastava and Lawton 1998, Hurlbert 2006, Chase 2010) have yielded substantial insights into
11 energetic community assembly. Here, we examine productivity-diversity relationships in
12 experimental deep-sea wood falls. Wood is transported to the oceans via rivers, and after drifting
13 and becoming saturated with water, eventually sinks to the ocean floor. On the deep-sea floor,
14 wood falls develop largely endemic and highly diverse communities consisting of wood and
15 sulfide obligates, and predators upon them (Voight 2007, McClain and Barry 2014). Wood-fall
16 communities in the deep sea are an ideal system for testing hypotheses about community
17 assembly and energetic theory for four reasons. With deep-sea wood falls we can precisely
18 control the total amount of energy available to the community, i.e. the size of the wood fall.
19 Second, deep-sea wood falls host an almost completely endemic and diverse fauna covering a
20 broad taxonomic composition, e.g. bivalves, gastropods, polyplacophorans, polychaetes, tanaids,
21 limnoriid isopods, amphipods, galatheids, ophiuroids, asteroids. The endemicity of wood falls
22 reflects an energetic link to wood falls because specific nutritional requirement for wood

1 (xylophagy), a requirement for sulfur produced at the wood fall, or predator specificity for a
2 wood-fall endemic species. Species located on wood falls are not typically hard substrate
3 specialists found on rocky habitats nearby (McClain et al. 2009, McClain et al. 2010). Third,
4 wood falls provide discrete habitat boundaries for the community that allow for the easy
5 quantification of abundance and diversity. This discrete community is also easily collected,
6 allowing the entire community to be sampled and quantified (Voight 2007, McClain and Barry
7 2014). In addition, wood falls in the deep sea, especially at the depths investigated here, are also
8 energetically isolated from the surrounding deep sea. Wood falls represent orders of magnitude
9 greater carbon delivery than that of the surrounding sediment. These wood-endemic species
10 receive little to no nutrition from the rain of organic debris upon which other deep-sea benthic
11 animals rely. Prior work has shown that wood falls exhibit varying communities over time
12 (McClain and Barry 2014). Moreover, at initial stages recruitment may primarily occur from a
13 regional pool. As wood-fall communities become mature with self-sustaining populations,
14 connectivity between nearby experimental wood falls may increase allowing specifically for
15 testing for the Connectivity Hypothesis (Chase and Ryberg 2004).

16 Ecological experiments are rare in the deep ocean due to the logistical and financial
17 constraints of repeated sampling and manipulation kilometers below the ocean surface. Despite
18 these difficulties, deep-sea experimental ecology has significantly increased our understanding of
19 this environment and contributed overall to our understanding of ecological processes at
20 energetic extremes (Snelgrove et al. 1992, Voight 2007). Using experimental deep-sea wood
21 falls, we specifically test four hypotheses about mechanisms underlying PDRs (Table 1) relating
22 differences in energy availability to diversity and community assembly. We quantified wood-

1 fall communities at two time intervals, 5 years and 7 years, to examine how productivity-
2 diversity relationships change with time.

3 **Methods**

4 **Sampling and collection**

5 In November 2006, 36 *Acacia* sp. logs were deployed at 3203 m in the Northeast Pacific
6 Ocean (Station Deadwood: 36.154098° N, 122.40852° W). The *Acacia* logs ranged in size from
7 0.6 to 20.6 kg and correspond to different level of energy available to the invertebrate
8 communities assembling on wood falls. Each log was sewn into a synthetic fiber mesh bag (5
9 mm mesh, large mesh size ensured larval settlement was not hindered). Mesh bags allowed for
10 collection at the end of the experiment of highly degraded wood falls (Voight 2007). Wood falls
11 were dispersed over a ~160m² area with ~5 meters between wood falls in 4 rows 10 m apart from
12 one another. Eighteen *Acacia* logs were collected in October 2011 (Set 1, 5 years). The
13 additional 18 *Acacia* logs were collected in October 2013 (Set 2, 7 years).

14 Logs were deployed and collected with the Monterey Bay Aquarium Research Institute's
15 Remotely Operated Vehicle (ROV) *Doc Ricketts* aboard the RV *Western Flyer*. Logs were
16 placed into 300 µm mesh bags with sealable closing lids during ROV retrieval, ensuring no loss
17 of individuals and/or cross contamination among different samples. All specimens were picked
18 from wood, preserved in either 95% ethanol or formalin. All of the taxa were identified to the
19 species level except *Actinaria* spp. Species names were assigned to all taxa were possible. For
20 each wood fall, we recorded the initial weight (kg), location, and surface area (m²). Additionally,

1 the experimental site was observed annually and HD video taken of each wood fall. Species and
2 wood-fall data are available at <https://datadryad.org/>

3 **Analyses**

4 Complete R scripts for the analyses are available at <https://datadryad.org/>. Linear fit
5 models were conducted with the R Package (2011) using the *lm* function. Multivariate analyses
6 were conducted in the R utilizing the *vegan* package (Oksanen et al. 2013).

7 ***Diversity***

8 Linear relationships between \log_{10} wood-fall size (kg) and species richness, Shannon's
9 Diversity Index H' , Simpson's Index, number of singletons, and the number of species with
10 abundance less than 5 (a proxy for rarity) were examined. Model fits were conducted for the two
11 sets separately and combined with the factor *Set* and the interaction term *Set* log₁₀ wood-fall*
12 *size*.

13 ***Abundance***

14 For each wood fall, \log_{10} abundance was quantified. Model fits were conducted for the
15 two sets separately and combined with the factor *Set* and the interaction term *Set* log₁₀ wood-*
16 *fall size*. Additionally, the relationship between richness and \log_{10} abundance and wood-fall size
17 was quantified.

18 ***Random Assembly***

19 Simulations were also conducted in R. Random draws of individuals were taken from the
20 total regional pool without replacement, i.e. combined abundances of species across all wood

1 falls. Empirical species richness values for wood falls were compared to the mean species
2 richness across permutations of this model.

3 ***Composition and Community Structure***

4 Composition and community structural changes were examined through multivariate
5 methods. As the data were proportional abundances, Bray-Curtis similarities were computed on
6 the data. An MDS was conducted to visualize differences in community structure. A Constrained
7 Analysis of Principal Coordinates (CAP) analysis, related to a Redundancy Analysis but
8 allowing for non-Euclidean distances like Bray-Curtis, was used to analyze the effect of wood
9 weight and set number.

10 We also decomposed β -diversity over the wood falls into two distinct components;
11 species turnover and species loss leading to nestedness. The latter pattern being when smaller
12 communities form ordered subsets of the species composition of larger communities (Baselga
13 2010, Brault et al. 2013). Specifically, we used the *betapart* package (Baselga et al. 2013) in R to
14 decompose Sørensen's dissimilarity index $\beta_{SØR}$ into dissimilarity due to turnover measured as
15 Simpson's index β_{SIM} and a new index of dissimilarity due to species loss leading to nestedness
16 β_{NES} . We computed dissimilarity between pairs of sites against the difference in depth for each
17 pair (Baselga 2010). We used a Mantel test with 1,000 replicates (Pearson correlation) to assess
18 whether the components of β -diversity changed among sites along the gradient of wood-fall
19 sizes. Additionally we implemented the BINMATNEST in the *bipartite* package (Dorman et al.
20 2008) in R to test for nestedness among wood falls and the rank order of nestedness with wood-
21 fall size.

1 Results

2 A total of 13,024 individuals were assigned to 48 species. Species richness significantly
3 increased with increasing wood-fall size but only for Set 1 (Fig. 1A, Table 2). Set 2 also
4 contained significantly more species than Set 1 for a given wood-fall size particularly at smaller
5 wood-fall sizes (Fig. 1A, Tables 2, 3). Diversity, as measured as H' also increased with
6 increasing wood-fall size, but again only in Set 1 (Fig 1b, Tables 2, 3). Simpson's evenness
7 increased with increasing wood-fall size but was only significant in Set 1 (Fig. 1C, Tables 2, 3).
8 Larger wood falls also yielded more individuals equally on the two wood fall sets (Fig. 1D,
9 Tables 2, 3), though for the same wood-fall size more individuals were found on the older wood
10 fall Set 2.

11 No overall relationship existed among singletons and wood-fall size; however,
12 individually the two sets possessed contrasting relationships (Fig. 1E, Tables 2, 3). Set 1
13 exhibited no relationship while Set 2 exhibited a negative slope. Yet, for rare species, species
14 represented by less than five individuals on a wood fall (below the 50% percentile for
15 abundance), both sets exhibited increases in rare species with increasing wood-fall size (Fig. 1F,
16 Tables 2, 3). For a given size, Set 2 wood falls exhibited more rare species than Set 1.

17 Overall, richness increased with increasing abundance on individual wood falls ($p=3.3e^{-}$
18 07 , adjusted $R^2=0.65$, Fig. 2). Although Set 2 wood falls showed slightly more species for a given
19 level of abundance, the relationship did not differ significantly between the different sets
20 (interaction $p=0.92$, set $p=0.69$). In a full model incorporating wood-fall size and abundance,
21 wood-fall size is not significant. AIC values were lower for the model with abundance only

1 (169.64) versus models with abundance and wood-fall size (171.03), or wood-fall size only
2 (195.87).

3 Compared to the expected number of species predicted from a random draw from the
4 regional pool, both sets exhibited less species than predicted (Fig. 3A). The empirical slopes
5 were also shallower than the 1:1 line indicating increasing larger wood falls gained species
6 slower than expected from random sampling. Deviations from expected were greater in smaller
7 wood falls. In Set 1, small wood falls contained less species than predicted, and in Set 2 more
8 than predicted (Fig. 3B). Individual species did show varying changes in abundance with
9 increasing wood-fall size between the two sets (Fig. 4).

10 Considerable compositional and community structure differences were seen with changes
11 in wood-fall size and among sets. A CAP analysis revealed that wood-fall size was a significant
12 predictor of changes in both species presence/absence ($p=0.0011$) and abundances ($p=0.0013$) of
13 species (Fig. 5). Several gastropod species, e.g. *Xyloskenea* sp. nov., *Provanna pacifica*, and
14 *Provanna* sp. 1, reached peak abundances only on large wood falls (Fig. 6). The gastropod
15 *Hyalogyra* sp. 1, the amphipod *Seba* sp., and numerous polychaetes, e.g. Opheliidae sp. A, also
16 only occur on larger wood falls. Likewise, the presence/absence and proportional abundances of
17 species differed among wood fall sets ($p=0.0051$ and 0.0046 respectively). Several species only
18 occur on Set 2 such as the bivalves *Yoldiella* sp. 1, *Adontorhina lynnae*, and *Bathyarca frielei*. In
19 some cases, species are ubiquitous on Set 2 but rare in Set 1 (e.g. Opheliidae sp. A and *Seba* sp.).

20 Set 1 exhibited significant patterns in β -diversity across wood-fall size (Fig. 7). Most of
21 the pattern of β -diversity as measured by $\beta_{S\text{OR}}$ (Mantel: $r=0.3021$, $p=0.0050$) was related to a
22 significant pattern in β_{NES} ($r=0.3546$, $p=0.0010$) and not β_{SIM} ($r=0.0193$, $p=0.3885$). None of the

1 patterns of β -diversity with wood-fall size were significant for Set 2 ($p=0.0939-0.4448$). The
2 BINMATNEST yielded probabilities of $p<0.0001$ that Set 1 and 2 matrices were similar to null
3 random matrices suggesting considerable nestedness in each set. The nestedness pack order in
4 both sets was significantly related to wood-fall size (Fig. 7G, H).

5 **Discussion**

6 Our experiment suggests that multiple interacting mechanisms influence the PDRs. We
7 find partial support for all four of hypotheses, More-Individuals Hypothesis, Resource-Ratio
8 Theory, More Specialization Theory, and the Connectivity-Diversity Hypothesis. In Set 1,
9 species richness, H' , and Simpson's Index increased linearly with increased wood-fall size, and a
10 presumed increased in energy availability (Fig. 1A). In many local scale studies (less than <20
11 km), PDRs are often not present (Waide et al. 1999, Mittelbach et al. 2001). However, our
12 finding of a linear positive PDR is in agreement with the fraction of local scale studies that
13 exhibit significant PDRs (Waide et al. 1999, Mittelbach et al. 2001) and the prevalent pattern of
14 positive PDRs in plant and animal studies (Gillman and Wright 2006, Cusens et al. 2012).
15 However, our findings do contrast with aquatic invertebrate patterns that are concave down
16 unimodal (Mittelbach et al. 2001).

17 **More-Individuals Hypothesis**

18 A variety of the observed patterns are consistent with More-Individuals Hypothesis
19 (Wright et al. 1993, Srivastava and Lawton 1998). First, small wood fall communities are nested
20 within larger wood fall communities. At extreme low productivity, communities are often

1 impoverished subsets of larger communities (Brault et al. 2013). One hypothesis for this is low
2 productivity areas represent sink populations experiencing frequent Allee events (Wright et al.
3 1993, Srivastava and Lawton 1998, Rex et al. 2005) and should exhibit little endemism and
4 represent attenuations of higher productivity communities (Rex et al. 2005, Brault et al. 2013).
5 Second, consistent with the More-Individuals Hypothesis, abundance increases with increasing
6 wood-fall size (Fig. 1D) and is correlated with increases in diversity (Fig. 2). After accounting
7 for changes in abundance, wood-fall size is no longer a significant predictor of diversity. Third,
8 increases in abundance with time on Set 2 also result in increases in diversity (Figs. 1, 2). This
9 occurs despite an overall breakdown in the relationship between diversity and wood-fall size on
10 Set 2. Fourth, the number of singletons on small wood falls in Set 1 is exceptionally high,
11 indicating that many species may not be sustainable populations. Fifth, rare species should
12 exhibit stronger PDRs because they frequently experience localized extinctions at low levels of
13 productivity (Fig. 1F). More abundant species, buffered against localized extinction, should
14 exhibit weaker PDRs. However, the More-Individuals Hypothesis predicts that all species should
15 have positive slopes between abundance and productivity, a prediction not supported among
16 wood falls (Fig. 4).

17 The relationship between species-area and species-energy relationships has received
18 attention in the literature (Storch et al. 2005, Hurlbert 2006, Hurlbert and Jetz 2010). In the
19 experiments here increasing wood fall size increases both energy availability and area. Increases
20 in species richness with increasing area are posited to potentially reflect three different
21 mechanisms: sampling effort; increases in habitat diversity; dynamic equilibrium between
22 speciation, extinction, and extinction (Hurlbert 2006). Increases in habitat diversity with

1 increasing wood fall size are difficult to envision given the spatial scale of individual treatments
2 in the experiment. Likewise, the short temporal timespan of minimize the long-term
3 evolutionary dynamics of speciation and extinction.

4 Larger areas inherently contain larger number of individuals. However, increases in
5 abundance must require increases in local food supply, as each new individual into the
6 community has a metabolic demand. Indeed, Wright (1983) notes that species energy is a
7 special case of more general species-energy relationship. More recently experiments have
8 confirmed that abundance and species richness depends on the total quantity of resource
9 available, regardless of whether the resources are spread over small or large areas (Hurlbert
10 2006). “These results support the view that energetic constraints are of fundamental importance
11 in structuring ecological communities, and that such constraints may even help explain
12 ecological patterns such as the species–area relationship” (Hurlbert 2006).

13 The relationships between abundance and wood fall size may simply reflect a sampling
14 effect, i.e. larger wood falls may provide more area and receive a greater number of larval
15 recruits from the regional pool (Evans et al. 2008). Our randomizations drawing individuals at
16 random from the regional pool, however, exhibit a fundamentally different relationship from the
17 empirical patterns. Specifically, randomizations always overpredict the number of species that
18 should occur on any woodfall. The rate of increase in richness with increasing wood-fall was
19 also less than predicted. This overestimation of species richness arises because the model
20 assumes homogenous spatial distributions (Evans et al. 2008). The species in the study show
21 much more aggregated distributions and do not occur across all wood falls with equal

1 probability. This suggests the species here possess specific habitat requirements, e.g. wood fall
2 size.

3 Resource-Ratio Theory

4 We find that species turnover over the productivity gradient is not related strictly to
5 compositional shifts but rather due to species loss, i.e. nestedness (Figs. 7). Smaller wood falls
6 often possess mere subsets of the richer communities on larger wood falls. Indeed the nestedness
7 packing order strongly correlates with wood-fall size (Fig. 7G). In part this may support the
8 Resource Ratio Hypothesis (Tilman 1982, Tilman 2004). When resources are balanced at
9 intermediate productivities, species adapted to both ends of the spectrum can coexist because
10 neither is competitively superior. This would suggest that communities at high and low
11 productivities would be a nested subset of intermediate productivity communities. If our largest
12 wood falls represent only an intermediate productivity, then our findings support this hypothesis.
13 However, it is clear that the largest wood falls have reached asymptotic richness (Fig. 3). Further
14 increases in wood-fall size would likely not yield substantially more species, suggesting we have
15 captured the full productivity gradient.

16 More Specialization Theory

17 Additional energy may elevate the amount of rare resources, allowing rare or absent
18 niche-specialists to become abundant and raise overall community diversity, e.g. Niche Position
19 Hypothesis (Evans et al. 1999, Evans et al. 2005). At high productivities, greater specialization is
20 allowable and prevents competitive exclusion (Schoener 1976, DeAngelis 1994). Interestingly,
21 the number of rare species increases with wood-fall size (Fig. 1F). Much of the increases of

1 diversity with wood-fall size seem to stem from the addition of these species (Fig. 1). If rare
2 species are assumed to be more specialized this would support this hypothesis. However, this
3 results of increasing rare species with wood-fall size also corresponds, as note above, to the
4 More-Individuals Hypothesis. Abundance responses across wood-fall sizes are also not
5 equivalent among species (Fig. 4). This suggests processes beyond a basic More-Individuals
6 Hypothesis where strict positive increases in abundance might be expected among all species.

7 Connectivity-Diversity Hypothesis

8 Chase and Ryberg (2004) reported that positive linear relationships were greater when
9 connectivity between sites was low, resulting in strong compositional differences between sites.
10 This may explain the different patterns observed here between the two experimental sets. In Set
11 1, colonization of wood falls occurs mainly from the regional larval pool with little recruitment
12 among the wood falls in the experiment itself. This low connectivity generates a strong positive,
13 linear PDR, and as predicted, differences in species composition do exist among wood falls
14 (Figs. 5,7). With increased time, the wood falls begin to generate reproducing populations that in
15 turn seed nearby wood falls. This increased connectivity leads to a lack of compositional
16 differences among wood falls (Figs. 5,7) in Set 2 and the loss of a significant PDR (Fig. 1B).

17 Major changes are seen in β -diversity across the gradient of wood-fall sizes (Fig. 7)
18 similar to other studies (Chase and Ryberg 2004, Harrison et al. 2006, McClain et al. 2012).
19 However, the patterns are absent or reduced in Set 2. Three possible mechanisms are proposed to
20 account for compositional differences with productivity (Chase and Leibold 2002). One,
21 environmental heterogeneity among sites increases with mean productivity (but see Harrison et
22 al. 2006). Second, at higher levels of productivity more possible alternative stable states are

1 allowable. However, among our experimental wood falls, compositional differences appear to
2 be greater among small wood falls as opposed to large wood falls (Fig. 5,7) suggesting that there
3 is more heterogeneity at the lower end of the productivity gradient. Third, compositional
4 turnover rates may be higher at higher levels of productivity. Anecdotally, larger wood falls did
5 appear to transition through successional states more quickly (McClain and Barry 2014). Larger
6 wood falls also hit peak richness more quickly, i.e. maximum richness did not vary between Sets
7 1 and 2 at larger wood-fall sizes (Fig. 1A, B). In contrast, smaller wood falls differed
8 significantly in richness between Sets 1 and 2 suggesting turnover rates were indeed higher on
9 larger wood falls.

10 **Conclusions**

11 Here, we test the underlying mechanisms for PDRs (Table 1) finding that multiple
12 processes may lead increases in productivity causing increasing in diversity. A breakdown in
13 this relationship with time may reflect increased connectivity between wood-fall communities
14 (Connectivity Hypothesis). Major changes occurred in beta-diversity across the gradient of
15 wood-fall sizes; in part this may be related to higher compositional turnover rates among larger
16 wood falls. Compositionally, smaller wood falls were attenuations of larger wood falls
17 (Resource-Ratio Theory). Diversity increases were concordant with increases in abundance with
18 increasing wood-fall size. After accounting for changes in abundance, wood-fall size was no
19 longer a significant predictor of diversity (More-Individuals Hypothesis). The number of
20 singletons on smaller wood falls also was higher suggesting nonsustainable populations.
21 However, the number of rare species seems to increase with wood-fall size and account the

1 increases in diversity (Niche Position Hypothesis). Overall, we find that increases of diversity
2 with increasing productivity are a complex interplay of dispersal, population growth, and niche
3 dynamics. Future work will need to examine PDR hypotheses in unison and focus on the
4 interactions among them.

5 **Acknowledgements**

6 We thank Karl Evans, Tom Webb, and Solange Brault for input on the analyses. Janet Voight
7 provided invaluable assistance with the experimental design, taxonomic identification, and
8 review of the manuscript. Tom Webb, Jeff Nekola, Morgan Ernest, and Dan McGlenn provided
9 helpful comments on earlier versions of the manuscript. The crew of the RV *Western Flyer* and
10 ROV *Doc Ricketts* were invaluable for their help in deployment and retrieval. We also thank C.
11 Lovera, K. Buck, P. Whaling, and D. Honig for providing help with processing of the retrieved
12 logs. CRM was supported by the National Evolutionary Synthesis Center (NSF # EF-0905606).
13 This work was also supported by the Monterey Bay Aquarium Research Institute (projects
14 200002, 900703, 900608) and the David and Lucile Packard Foundation. Michelle Gaither-
15 McClain provided editorial assistance and loving patience with the first author.

16 **References**

- 17
18 2011. R: A language and environment for statistical computing. *in* R. D. C. Team, editor. R
19 Foundation for Statistical Computing, Vienna, Austria.
20 Abramsky, Z., and M. L. Rosenzweig. 1984. Tilman's predicted productivity-diversity
21 relationship shown by desert rodents. *Nature* **309**:150-151.
22 Arim, M., P. A. Marquet, and F. M. Jaksic. 2007. On the relationship between productivity and
23 food chain length at different ecological levels. *The American Naturalist* **169**:62-72.
24 Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. *Global*
25 *Ecology and Biogeography* **19**:134-143.

- 1 Baselga, A., D. Orme, S. Vileger, J. D. Bortoli, and F. Leprieur. 2013. betapart: Partitioning beta
2 diversity into turnover and nestedness components.
- 3 Behrenfeld, M. J., R. T. O'Malley, D. A. Siegel, C. R. McClain, J. L. Sarmiento, G. C. Feldman,
4 A. J. Milligan, P. G. Falkowski, R. M. Letelier, and E. S. Boss. 2006. Climate-driven
5 trends in contemporary ocean productivity. *Nature* **444**:752-755.
- 6 Belmaker, J., C. H. Sekercioglu, and W. Jetz. 2012. Global patterns of specialization and
7 coexistence in bird assemblages. *Journal of Biogeography* **39**:193-203.
- 8 Boyce, D. G., M. R. Lewis, and B. Worm. 2010. Global phytoplankton decline over the past
9 century. *Nature* **466**:591-596.
- 10 Brault, S., C. Stuart, M. Wagstaff, C. R. McClain, J. A. Allen, and M. A. Rex. 2013. Contrasting
11 patterns of α - and β -diversity in deep-sea bivalves of the eastern and western North
12 Atlantic. *Deep-Sea Research II* **92**:157-164.
- 13 Chase, J. M. 2010. Stochastic community assembly causes higher biodiversity in more
14 productive environments. *Science* **328**:1388-1391.
- 15 Chase, J. M., and M. A. Leibold. 2002. Spatial scale dictates the productivity-biodiversity
16 relationship. *Nature* **416**:427-430.
- 17 Chase, J. M., and W. A. Ryberg. 2004. Connectivity, scale-dependence, and the productivity-
18 diversity relationship. *Ecology Letters* **7**:676-683.
- 19 Cusens, J., S. d. Wright, P. D. McBride, and L. N. Gillman. 2012. What is the form of the
20 productivity--animal-species-richness relationship? A critical review and meta-analysis.
21 *Ecology* **2012**:2241-2252.
- 22 DeAngelis, D. L. 1994. Relationships between the energetics of species and large-scale species
23 richness. Pages 263-272 in C. G. Jones and J. H. Lawton, editors. *Linking Species and*
24 *Ecosystems*. Chapman & Hall, New York.
- 25 Dorman, C. F., B. Gruber, and J. Frueund. 2008. Introducing the bipartite Package: Analysing
26 Ecological Networks. *R News* **8**:8-11.
- 27 Evans, K. L., J. J. D. Greenwood, and K. J. Gaston. 2005. Dissecting the species-energy
28 relationship. *Proceeding of the Royal Society B: Biological Sciences* **272**:2155-2163.
- 29 Evans, K. L., N. A. James, and K. J. Gaston. 2006. Abundance, species richness and energy
30 availability in the North American avifauna. *Global Ecology and Biogeography* **15**:372-
31 385.
- 32 Evans, K. L., S. E. Newson, D. Storch, J. J. D. Greenwood, and K. J. Gaston. 2008. Spatial scale,
33 abundance and the species–energy relationship in British birds. *Journal of Animal*
34 *Ecology* **77**:395-405.
- 35 Evans, K. L., P. H. Warren, and K. J. Gaston. 1999. Species–energy relationships at the
36 macroecological scale: a review of the mechanisms. *Biological Reviews* **80**:1-25.
- 37 Gillman, L. N., and S. d. Wright. 2006. The influence of productivity on the species richness of
38 plants: A critical assessment. *Ecology* **87**:1234-1243.
- 39 Harrison, S., K. F. Davies, H. d. Safford, and J. H. Viers. 2006. Beta diversity and the scale-
40 dependence of the productivity-diversity relationship: a test in the Californian serpentine
41 flora. *Journal of Ecology* **94**:110-117.
- 42 Hurlbert, A. H. 2004. Species-energy relationships and habitat complexity in bird communities.
43 *Ecology Letters* **7**:714-720.
- 44 Hurlbert, A. H. 2006. Linking species–area and species–energy relationships in *Drosophila*
45 microcosms. *Ecology Letters* **9**:287-294.

- 1 Hurlbert, A. H., and W. Jetz. 2010. More than "more individuals": the nonequivalence of area
2 and energy in the scaling of species richness. *The American Naturalist* **176**:E50-65.
- 3 Kaspari, M. 2001. Taxonomic level, trophic biology and the regulation of local abundance.
4 *Global Ecology and Biogeography* **10**:229-244.
- 5 Kaspari, M., S. O'Donnell, and J. R. Kercher. 2000. Energy, density, and constraints to species
6 richness: ant assemblages along a productivity gradient. *American Naturalist* **155**:280-
7 293.
- 8 Kerekes, J., M. Kaspari, B. Stevenson, R. H. Nilsson, M. Hartmann, A. Amend, and T. D. Bruns.
9 2013. Nutrient enrichment increased species richness of leaf litter fungal assemblages in
10 a tropical forest. *Molecular Ecology* **22**:2827-2838.
- 11 Mason, N. W. H., P. Irz, C. Lanoiselee, D. Mouillot, and C. Argillier. 2008. Evidence that niche
12 specialization explains species–energy relationships in lake fish communities. *Journal of*
13 *Animal Ecology* **77**:285-296.
- 14 McClain, C. R., and J. P. Barry. 2014. Beta-diversity on deep-sea wood falls reflects gradients in
15 energy availability. *Biology Letters* **10**:20140129.
- 16 McClain, C. R., L. Lundsten, J. Barry, and A. DeVogelaere. 2010. Assemblage structure, but not
17 diversity or density, change with depth on a northeast Pacific seamount. *Marine Ecology*
18 **31**:1-12.
- 19 McClain, C. R., L. Lundsten, M. Ream, J. Barry, and A. DeVogelaere. 2009. Endemicity,
20 biogeography, composition, and community structure on a Northeast Pacific seamount.
21 *PLoS One* **4**:e4141.
- 22 McClain, C. R., J. C. Stegen, and A. H. Hurlbert. 2012. Dispersal, niche dynamics, and oceanic
23 patterns in beta-diversity in deep-sea bivalves. *Proceedings of the Royal Society B:*
24 *Biological Sciences* **279**:1933-2002.
- 25 McGlynn, T. P., M. D. Weiser, and R. R. Dunn. 2010. More individuals but fewer species:
26 testing the ‘more individuals hypothesis’ in a diverse tropical fauna. *Biology Letters*
27 **6**:490-493.
- 28 McKane, R. B., L. C. Johnson, G. R. Shaver, K. J. Nadelhoffer, E. B. Rastetter, B. Fry, A. E.
29 Giblin, K. Kielland, B. L. Kwiatkowski, J. A. Laundre, and G. Murray. 2002. Resource-
30 based niches provide a basis for plant species diversity and dominance in arctic tundra.
31 *Nature News* **415**:68-71.
- 32 Mittelbach, G. C., C. F. Steiner, S. M. Scheiner, K. L. Gross, H. L. Reynolds, R. B. Waide, M. R.
33 Willig, S. I. Dodson, and L. Gough. 2001. What is the observed relationship between
34 species richness and productivity? *Ecology* **82**:2381-2396.
- 35 Mönkkönen, M., J. T. Forsman, and F. Bokma. 2006. Energy availability, abundance,
36 energy use and species richness in forest bird communities: a test of the species–energy
37 theory. *Global Ecology and Biogeography* **15**:290-302.
- 38 Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson,
39 P. Solymos, M. H. M. Stevens, and H. Wagner. 2013. *vegan: Community Ecology*
40 *Package*.
- 41 Post, D. M. 2002. The long and short of food-chain length. *Trends in Ecology and Evolution*
42 **17**:269-277.

- 1 Rex, M. A., C. R. McClain, N. A. Johnson, R. J. Etter, J. A. Allen, P. Bouchet, and A. Waren.
2 2005. A source-sink hypothesis for abyssal biodiversity. *American Naturalist* **165**:163-
3 178.
- 4 Rosenzweig, M. L., and Z. Abramsky. 1993. How are diversity and productivity related? Pages
5 52-65 *in* R. E. Ricklefs and D. Schluter, editors. *Species Diversity in Ecological*
6 *Communities: Historical and Geographical Perspectives*. University of Chicago Press,
7 Chicago.
- 8 Schoener, T. W. 1976. Alternatives to Lotka-Volterra competition: models of intermediate
9 complexity. *Theoretical Population Biology* **10**:309-333.
- 10 Snelgrove, P. V. R., J. F. Grassle, and R. F. Petrecca. 1992. The role of food patches in
11 maintaining high deep-sea diversity: Field experiments with hydrodynamically unbiased
12 colonization trays. *Limnology and Oceanography* **37**:1543-1550.
- 13 Srivastava, D. S., and J. H. Lawton. 1998. Why more productive sites have more species: an
14 experimental test of theory using tree-hole communities. *American Naturalist* **152**:510-
15 529.
- 16 Storch, D., K. L. Evans, and K. J. Gaston. 2005. The species-area-energy relationship. *Ecology*
17 *Letters* **8**:487-492.
- 18 Tilman, D. 1982. *Resource Competition and Community Structure*. Princeton University Press,
19 Princeton, NJ.
- 20 Tilman, D. 2004. Niche tradeoffs, neutrality, and community structure: a stochastic theory of
21 resource competition, invasion, and community assembly. *Proceedings of the National*
22 *Academy of Sciences* **101**:10854-10861.
- 23 Tilman, D., and D. Wedin. 1991. Plant traits and resource reduction for five grasses growing on a
24 nitrogen gradient. *Ecology* **72**:685-700.
- 25 Venterink, H. O., M. J. Wassen, A. W. M. Verkroost, and P. C. De Ruiter. 2008. Species
26 richness-productivity patterns differ between n-, p-, and k-limited wetlands. *Ecology*
27 **84**:2191-2199.
- 28 Voight, J. R. 2007. Experimental deep-sea deployments reveal diverse Northeast Pacific wood-
29 boring bivalves of Xylophaginae (Myoida: Pholadidae). *Journal of Molluscan Studies*
30 **73**:377-391.
- 31 Waide, R. B., M. R. Willig, C. F. Steiner, G. C. Mittelbach, L. Gough, S. I. Dodson, G. P. Juday,
32 and R. Parmenter. 1999. The relationship between productivity and species richness.
33 *Annual Review of Ecology and Systematics* **30**:257-300.
- 34 Wallace, A. R. 1878. *Tropical Nature: And Other Essays*. Macmillan and Company, London.
- 35 Wright, D. H. 1983. Species-energy theory: An extension of species-area theory. *Oikos* **41**:496-
36 506.
- 37 Wright, D. H., D. J. Currie, and B. A. Maurer. 1993. Energy supply and patterns of species
38 richness on local and regional scales. Pages 66-74 *Species Diversity in Ecological*
39 *Communities: Historical and Geographical Perspectives*. University of Chicago Press,
40 Chicago.
- 41 Yee, D. A., and S. A. Juliano. 2007. Abundance matters: a field experiment testing the more
42 individuals hypothesis for richness-productivity relationships. *Oecologia* **153**:153-162.
- 43

1 **Table 1:** Theories of productivity-diversity relationships, their predictions, and support for them
 2 from this study.

3

Theory	Reference	Hypothesis/Prediction	Predictions	Results from this study	Figures
More-Individuals Hypothesis	Wright (1983), Wright et al. (1993), Srivastava and Lawton (1998)	Low productivity reduces population sizes and increases risk of stochastic extinction. As productivity and population levels increase, Allee effects are reduced and local coexistence increases	Positive relationship between energy and abundance, positive relationship between abundance and species richness. Number of singletons increases at lower productivities suggesting nonsustainable populations. Rarer species will exhibit stronger species-energy relationships	Abundance increases with wood fall size. Abundance and diversity related across wood falls. Number of singletons on small wood falls higher. After accounting for changes in abundance, no effect of wood-fall size on diversity.	Fig. 1A, 1D, 1F 2
Resource Ratio Theory	Tilman (1982)	With high levels of one resource (e.g. productivity)	Concave down unimodal	Linear PDR observed.	Fig. 5,7

		<p>another resource will be limiting. No single species can be competitively dominant at all resource ratios, i.e. species have trade-offs in the capture or utilization efficiency for different resources. When resources are balanced, e.g. intermediate productivities, species adapted to both ends of the spectrum, can coexist because neither is competitively superior.</p>	<p>productivity-diversity relationship. Communities at ends of productivity gradient represent nested subsets of communities at intermediate productivities</p>	<p>Communities on smaller wood falls (lower productivity) represent nested subsets of larger wood falls (higher productivities).</p>	
<p>More Specialization Theory/Niche Position Hypothesis</p>	<p>Schoener (1976), DeAngelis (1994), Evane et al. (1999, 2005)</p>	<p>A minimum amount of resource is needed to support specialist species. At low productivity some resources are too rare to support these species. At high productivities, greater specialization is allowable and prevents competitive exclusion</p>	<p>Number of rare species increases with increasing productivity. Abundance increases with increasing productivity not equivalent among species.</p>	<p>Number of rare species increases with increased in wood-fall size. Increases in diversity with increasing wood-fall size correspond to the addition of these rare species. Abundance responses across</p>	<p>Fig. 1F, 4, 7</p>

				wood-fall sizes are not equivalent among species.	
Connectivity Hypothesis	Chase and Ryberg (2004)	Scale-dependence in productivity–diversity relationships depend on the degree of connectivity among localities within regions	Positive PDRs are stronger when connectivity between sites is low, resulting in strong compositional differences	Increased connectivity in Set 2 corresponds with loss of PDR and lack of compositional differences among wood falls.	Fig. 1b, 5, 7

1

2

- 1 **Table 2:** Model coefficients, p-values, and adjusted R² for wood-fall size (log₁₀ weight in
 2 kilograms) and various dependent variables for experimental deep-sea wood falls. Significance
 3 for coefficient: *** 0.001, **, 0.01, and * 0.05

Dependent	Intercept	Coefficient Log10 Weight	Coefficient Set2	Coefficient Interaction	Adjusted R²	p-value
Richness	5.2**	8.26***	10.24***	-7.00*	0.53	2.23E-05
H'	1.11***	0.60*	0.57*	-0.58	0.18	3.67E-02
Simpsons	0.55***	0.20*	0.13	-0.16	0.11	9.92E-02
Abundance	1.56***	0.67**	0.89***	-0.41	0.48	7.26E-05
Singletons	1.78*	0.42	0.001**	0.02*	0.32	3.32E-03
Rare Species	0.95	5.73***	4.37*	-2.04	0.49	6.57E-05
Rarefaction	-3.94***	2.54*	245*	0.94***	0.70	3.77E-08
Residuals						

4

5

1 **Table 3:** Model coefficients, p-values, and adjusted R^2 for wood-fall size (\log_{10} weight in
 2 kilograms) and various dependent variables for Set 1 and Set 2 individually.

3

Dependent	Set	Intercept	Coefficient Log10 Weight	Adjusted R^2	p-value
Richness	1	5.20	8.26	0.55	0.0006
	2	15.44	1.20	-0.04	0.5430
H'	1	1.12	0.60	0.29	0.0186
	2	1.69	0.02	-0.07	0.9133
Simpsons	1	0.55	0.20	0.23	0.0338
	2	0.68	0.04	-0.05	0.5724
Abundance	1	1.56	0.89	0.44	0.0031
	2	2.23	0.48	0.33	0.0112
Singletons	1	1.78	0.81	-0.01	0.3874
	2	5.53	-2.49	0.29	0.0183
Rare Species	1	0.95	5.73	0.43	0.0033
	2	5.32	3.69	0.33	0.0121
Rarefaction Residuals	1	-6.03	5.70	0.39	0.0054
	2	1.19	1.65	-0.03	0.4543

4

5

1 **Figure Legends**

2 **Figure 1:** Relationship between wood-fall size (\log_{10} weight in kilograms) and species richness
3 **(A)**, Shannon's Diversity Index H' **(B)**, Simpson's Index **(C)**, \log_{10} abundance **(D)**, number of
4 singletons **(E)**, and number of rare species (abundance less than five corresponding to a
5 percentile of 50%) **(F)**. Numbers refer to wood fall identification number, e.g. L29. Blue refers to
6 Set 1 collected in October 2011 (5 years) and orange to Set 2 collected in October 2013 (7
7 years). Significant regression lines are also shown.

8 **Figure 2:** Relationship between \log_{10} abundance and species richness per wood fall. Blue refers
9 to Set 1 collected in October 2011 (5 years) and orange to Set 2 collected in October 2013 (7
10 years). Significant regression lines are also shown.

11 **Figure 3: A.** The number of species predicted from random draws from the regional pool versus
12 the observed number of species per wood fall. Black line is $y=x$. **B.** Residuals of relationship of
13 A versus wood-fall size (\log_{10} weight in kilograms). Blue refers to Set 1 collected in October
14 2011 (5 years) and orange to Set 2 collected in October 2013 (7 years). Significant regression
15 lines are also shown.

16 **Figure 4:** Regression lines for abundance and wood-fall size (\log_{10} weight in kilograms) for each
17 individual species. Blue refers to Set 1 collected in October 2011 (5 years) and orange to Set 2
18 collected in October 2013 (7 years).

19 **Figure 5: A.** Non-metric multidimensional scaling plot based on arcsine-transformed
20 abundances for wood fall communities. **B.** Non-metric multidimensional scaling plot based on
21 presence-absence for wood fall communities. Circles denote individual wood falls. Dashed lines

1 indicate direction of change in wood-fall size. Wood falls are linked together base on Sets. Blue
2 refers to Set 1 collected in October 2011 (5 years) and orange to Set 2 collected in October 2013
3 (7 years).

4 **Figure 6:** Violin plots for each species showing changes in abundance and presence/absence
5 changes with wood-fall size (\log_{10} weight in kilograms). Blue refers to Set 1 collected in October
6 2011 (5 years) and orange to Set 2 collected in October 2013 (7 years).

7 **Figure 7: A. and B.** Simpson's index β_{SIM} of dissimilarity due to turnover versus difference in
8 wood-fall size. **C. and D.** Dissimilarity due to species loss leading to nestedness β_{NES} verses
9 difference in wood-fall size. **E. and F.** Sørensen's dissimilarity index β_{SOR} versus difference in
10 wood-fall size. **G. and H.** wood-fall size (\log_{10} weight in kilograms) versus nestedness pack
11 order. Blue refers to Set 1 collected in October 2011 (5 years) and orange to Set 2 collected in
12 October 2013 (7 years). Significant regression lines are also shown.

13

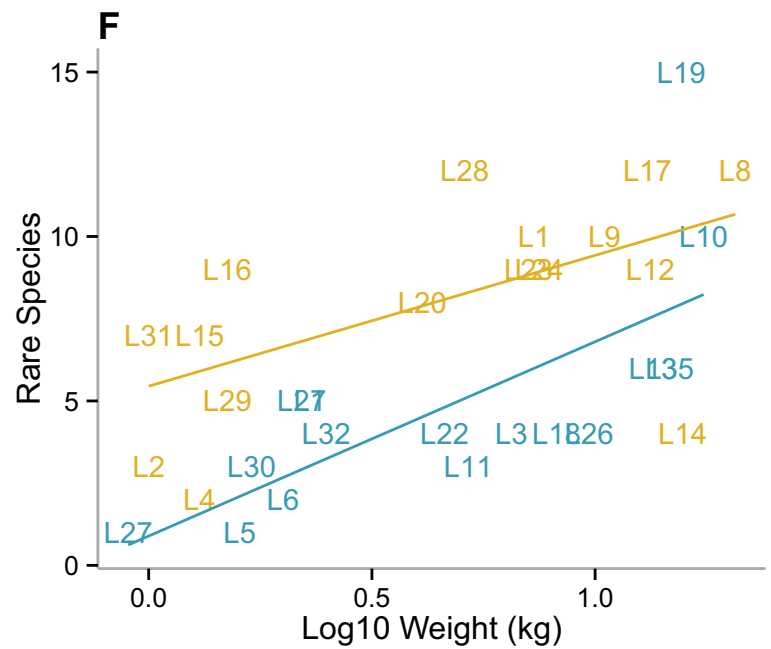
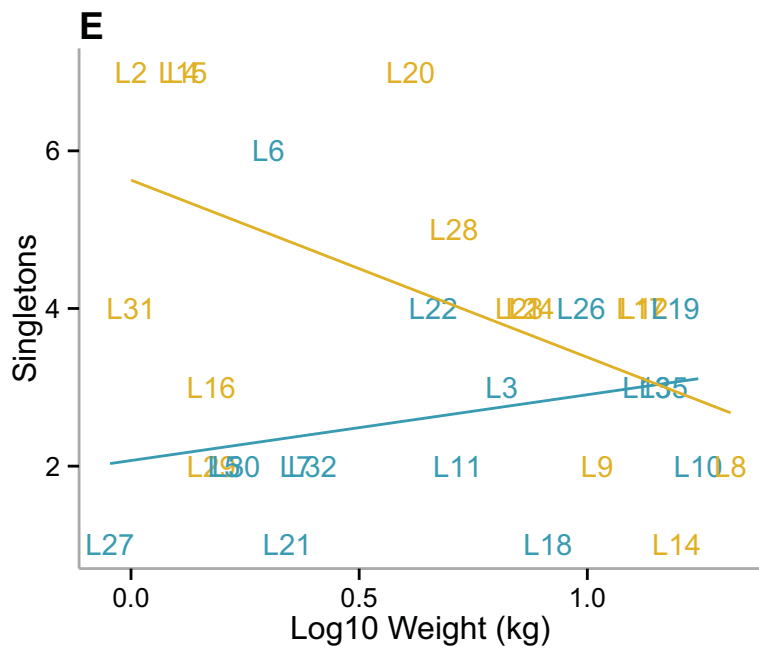
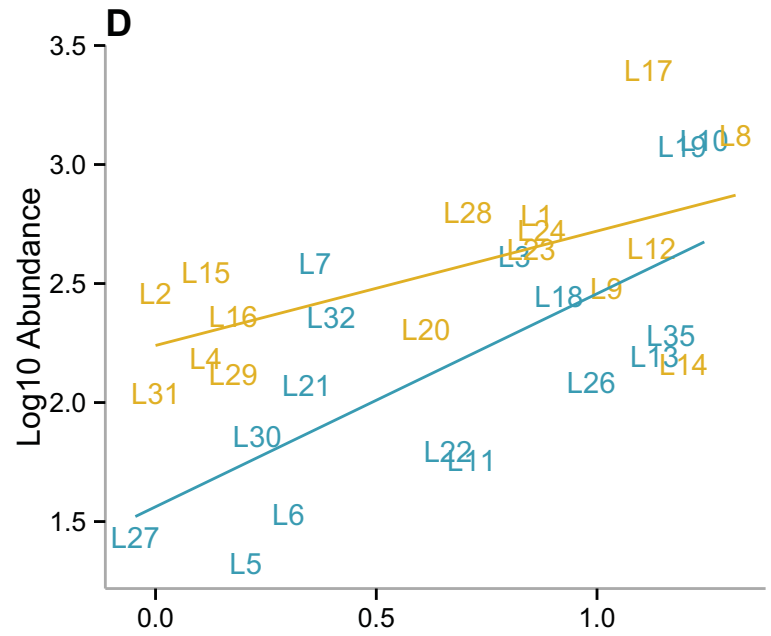
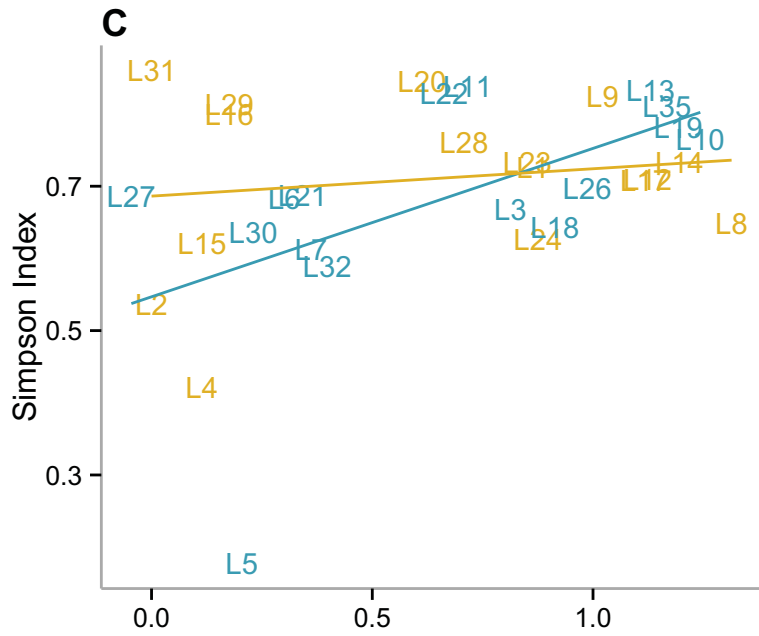
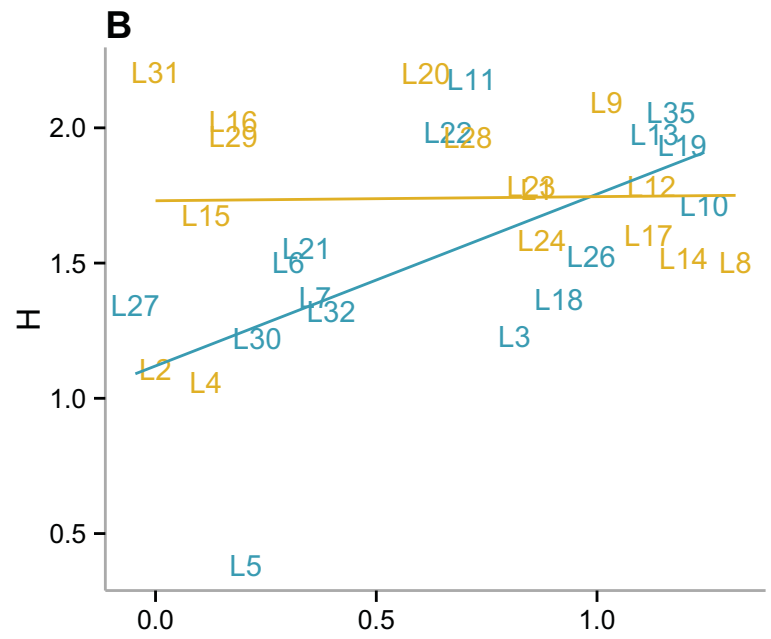
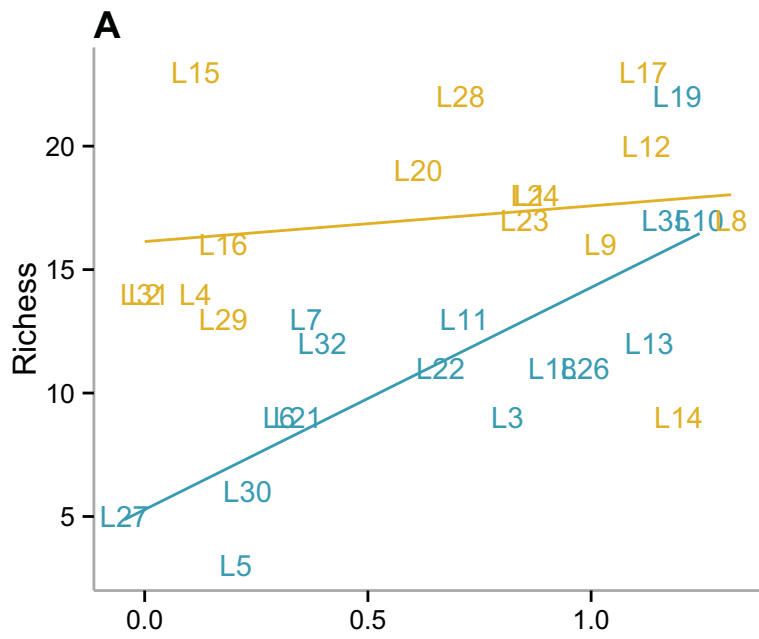
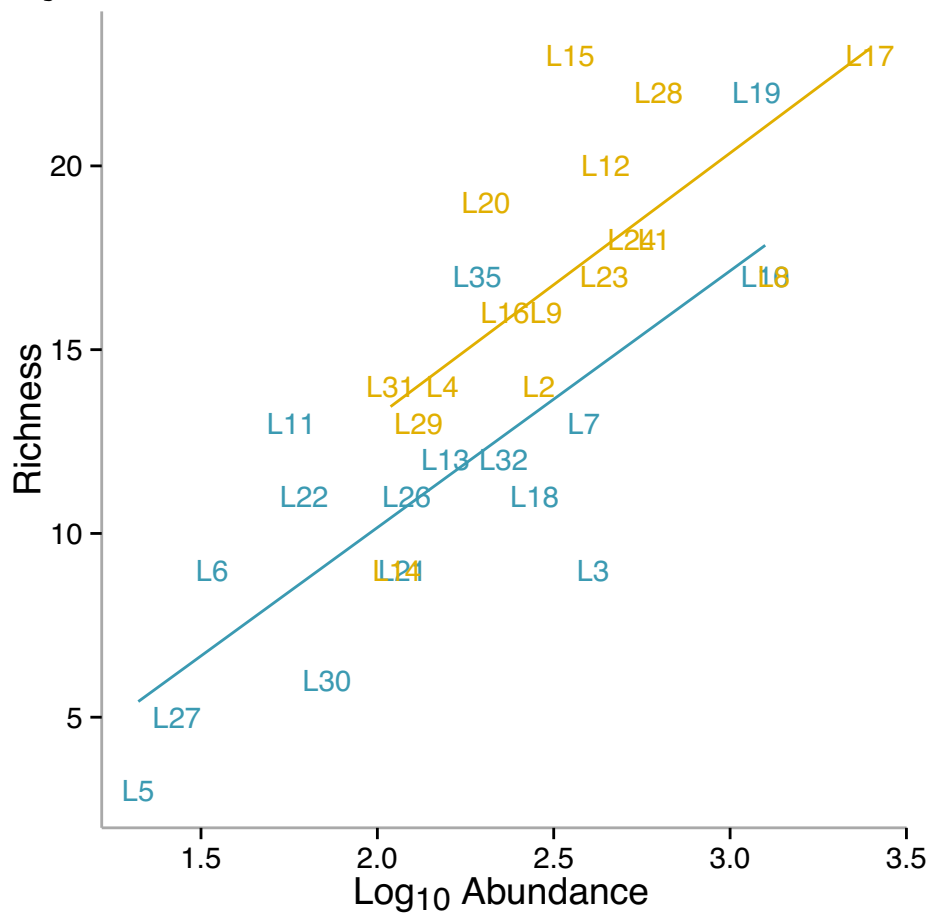


Figure 2



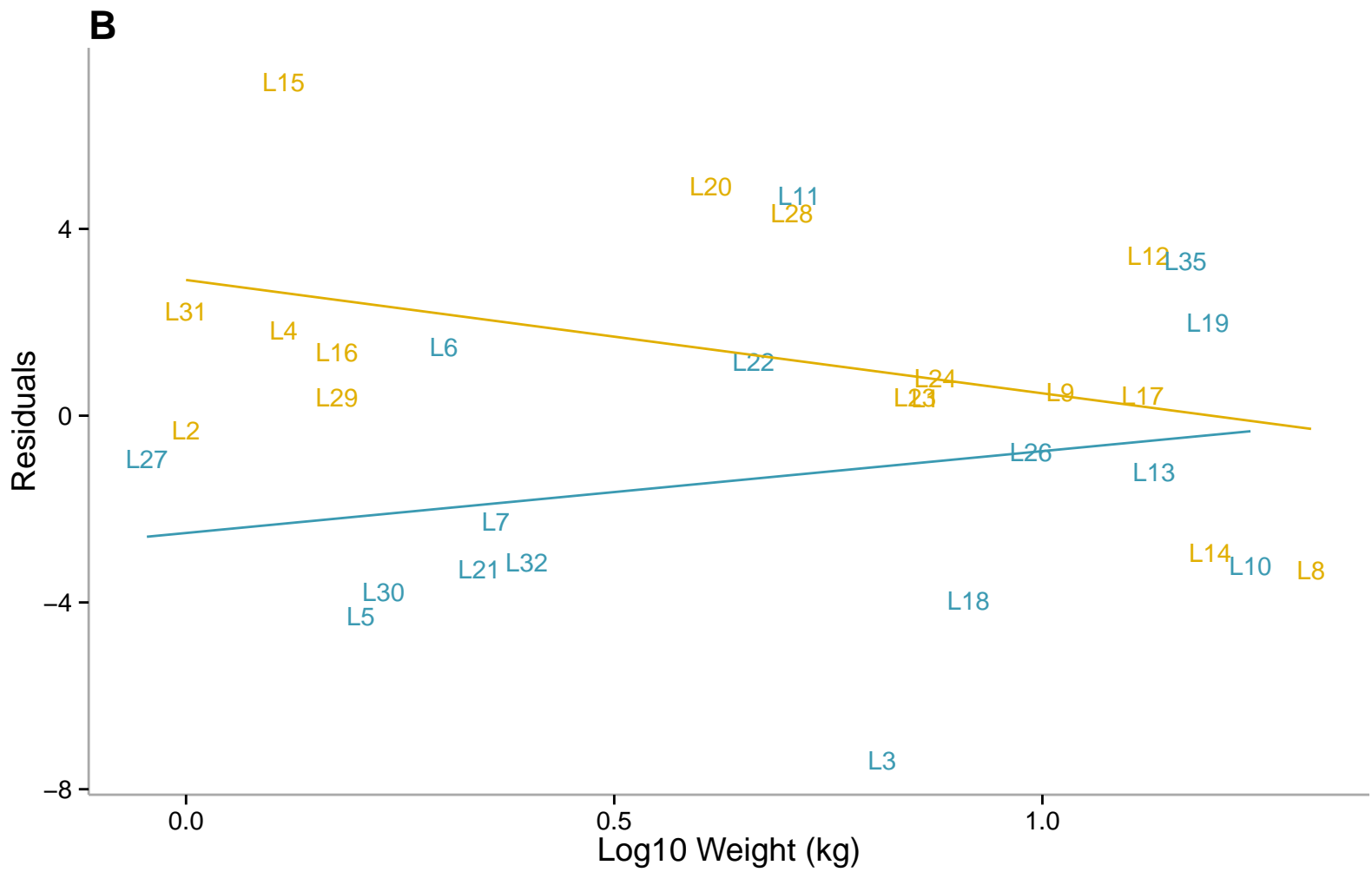
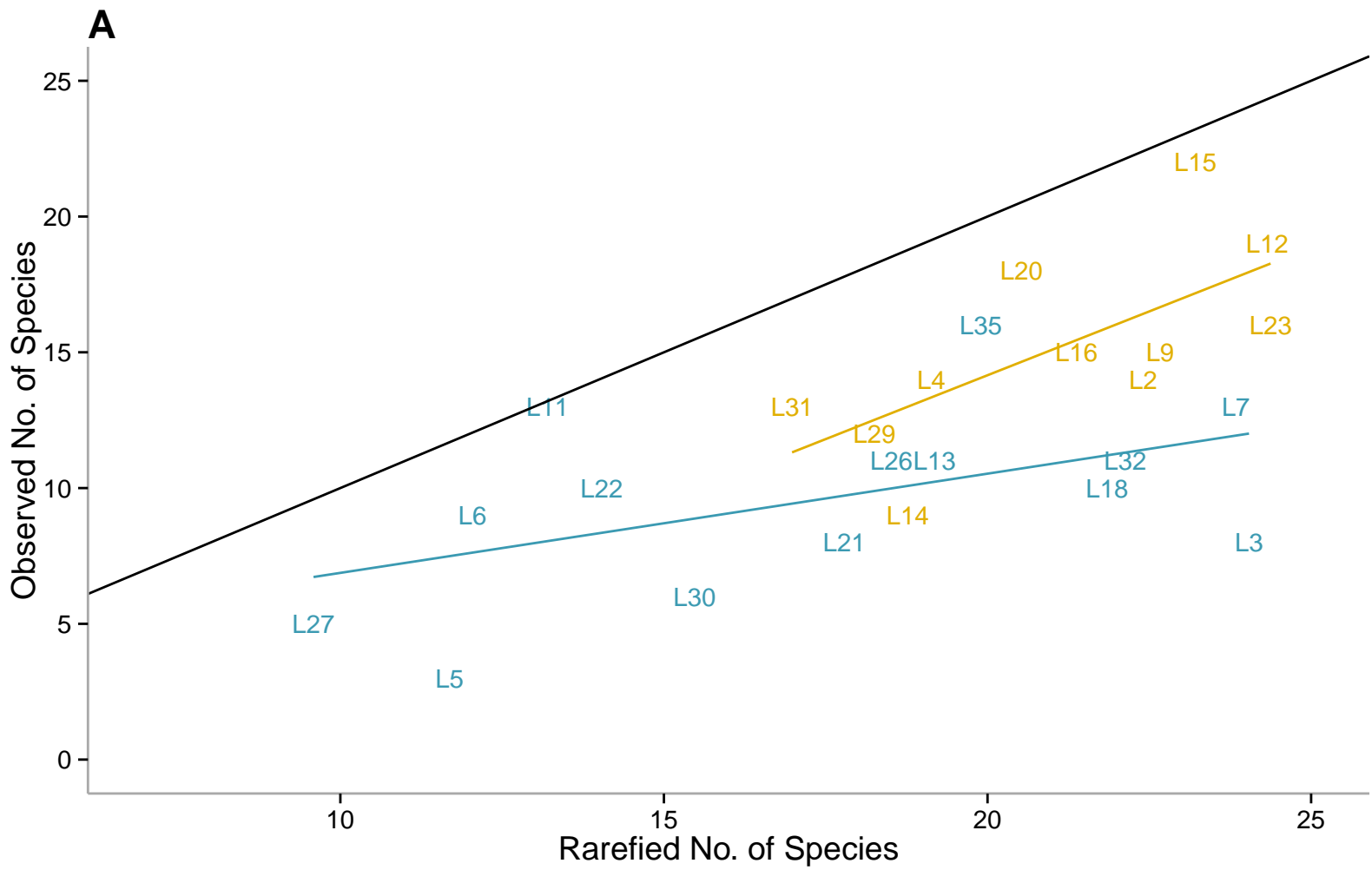


Figure 4

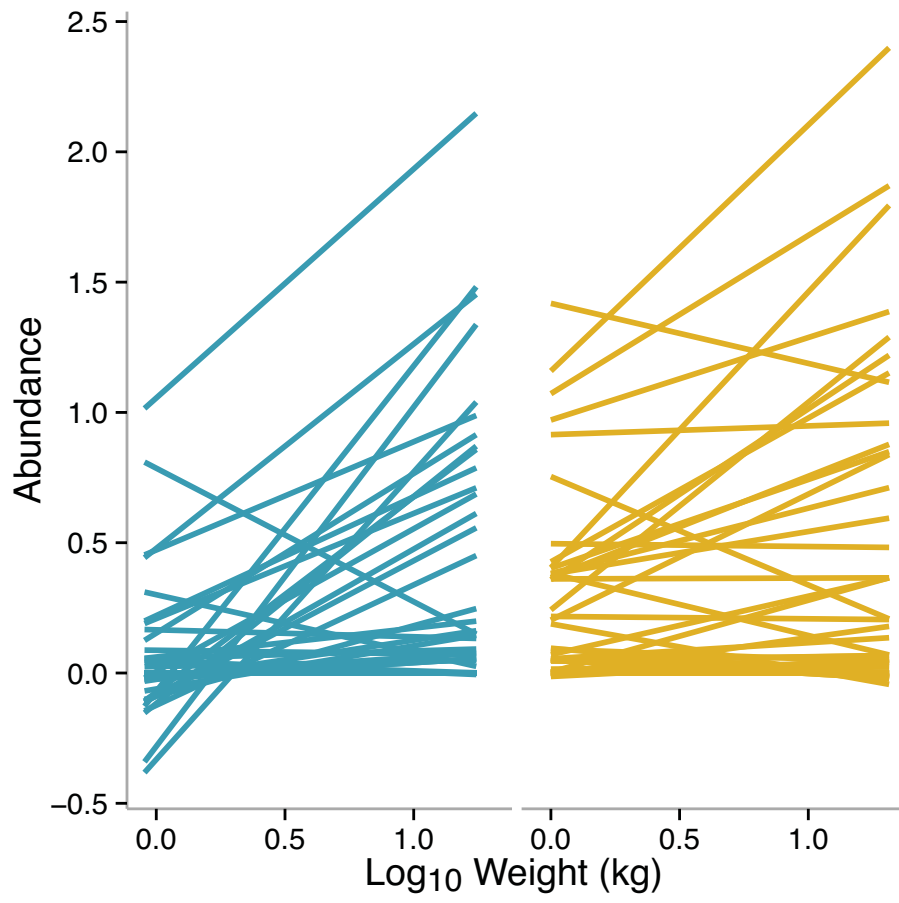


Figure 5a

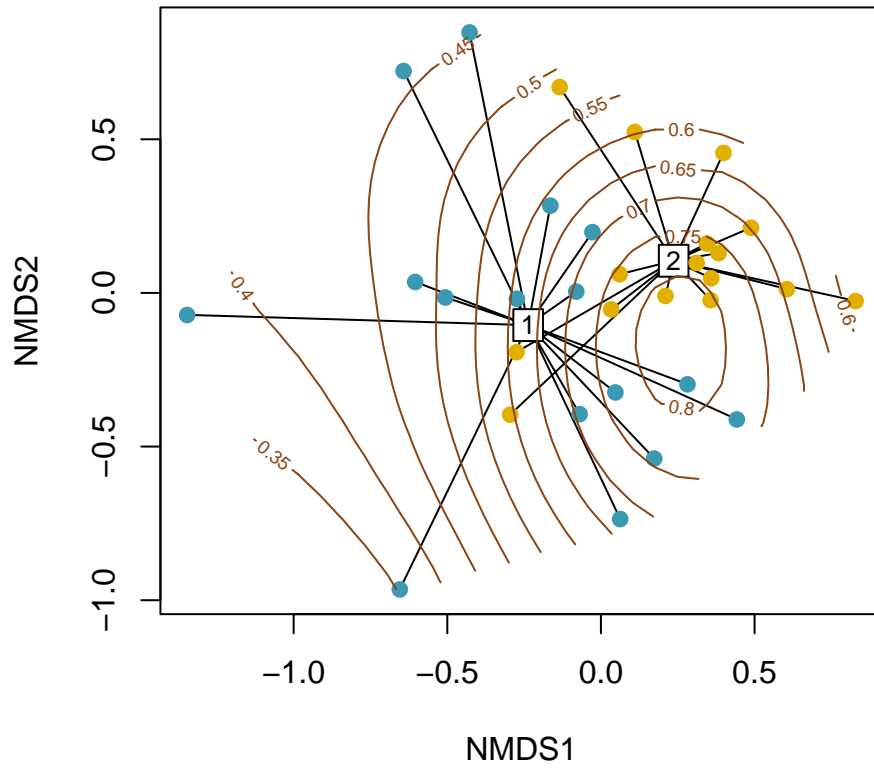


Figure 5b

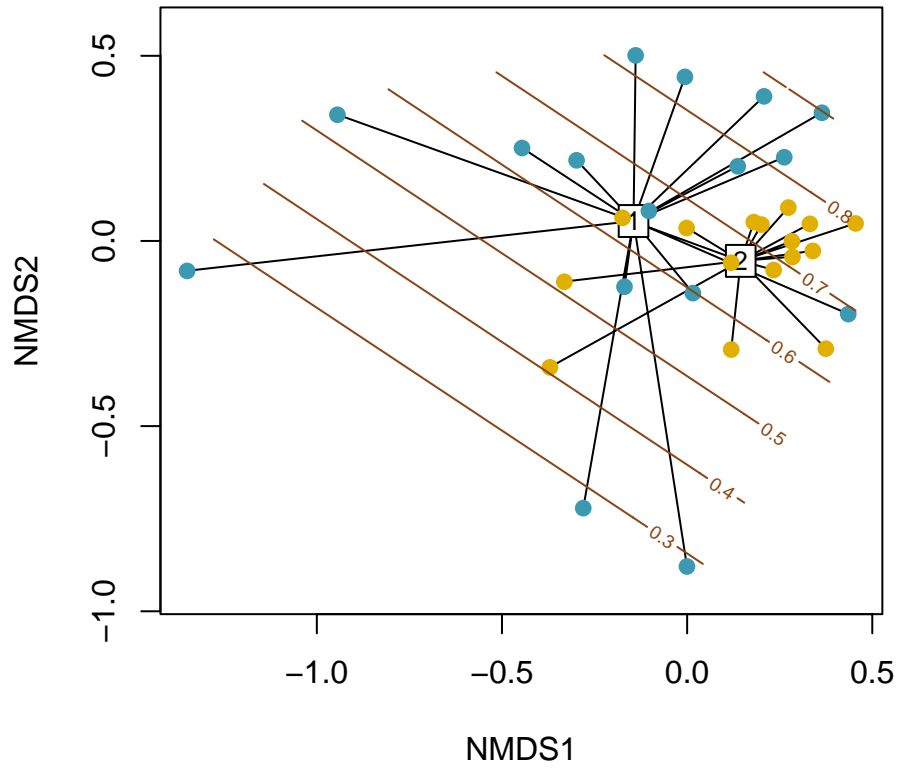


Figure 6

