Multiple Processes Generate Productivity-Diversity Relationships in Experimental Wood-Fall Communities

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Abstract

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

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

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   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   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 limnorid 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 ~160m^2 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 (m^2). 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* $\log_{10}$ 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* $\log_{10}$ 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.

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 $\beta_{SØR}$ (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.

Acknowledgements

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. Villeger, 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-biodiveristy
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.

Hurlbert, A. H., and W. Jetz. 2010. More than "more individuals": the nonequivalence of area and energy in the scaling of species richness. The American Naturalist **176**:E50-65.

Kaspari, M. 2001. Taxonomic level, trophic biology and the regulation of local abundance. Global Ecology and Biogeography **10**:229-244.

Kaspari, M., S. O'Donnell, and J. R. Kercher. 2000. Energy, density, and constraints to species richness: ant assemblages along a productivity gradient. American Naturalist **155**:280-293.

Kerekes, J., M. Kaspari, B. Stevenson, R. H. Nilsson, M. Hartmann, A. Amend, and T. D. Bruns. 2013. Nutrient enrichment increased species richness of leaf litter fungal assemblages in a tropical forest. Molecular Ecology **22**:2827-2838.

Mason, N. W. H., P. Irz, C. Lanoiselee, D. Mouillot, and C. Argillier. 2008. Evidence that niche specialization explains species– energy relationships in lake fish communities. Journal of Animal Ecology **77**:285-296.

McClain, C. R., and J. P. Barry. 2014. Beta-diversity on deep-sea wood falls reflects gradients in energy availability. Biology Letters **10**:20140129.

McClain, C. R., L. Lundsten, J. Barry, and A. DeVogelaere. 2010. Assemblage structure, but not diversity or density, change with depth on a northeast Pacific seamount. Marine Ecology **31**:1-12.

McClain, C. R., L. Lundsten, M. Ream, J. Barry, and A. DeVogelaere. 2009. Endemicity, biogeography, composition, and community structure on a Northeast Pacific seamount. PLoS One **4**:e4141.

McClain, C. R., J. C. Stegen, and A. H. Hurlbert. 2012. Dispersal, niche dynamics, and oceanic patterns in beta-diversity in deep-sea bivalves. Proceedings of the Royal Society B: Biological Sciences **279**:1933-2002.

McGlynn, T. P., M. D. Weiser, and R. R. Dunn. 2010. More individuals but fewer species: testing the 'more individuals hypothesis' in a diverse tropical fauna. Biology Letters **6**:490-493.

McKane, R. B., L. C. Johnson, G. R. Shaver, K. J. Nadelhoffer, E. B. Rastetter, B. Fry, A. E. Giblin, K. Kielland, B. L. Kwiatkowski, J. A. Laundre, and G. Murray. 2002. Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. Nature News **415**:68-71.

Mittelbach, G. C., C. F. Steiner, S. M. Scheiner, K. L. Gross, H. L. Reynolds, R. B. Waide, M. R. Willig, S. I. Dodson, and L. Gough. 2001. What is the observed relationship between species richness and productivity? Ecology **82**:2381-2396.

Mönkkönen, M., J. T. Forsman, and F. Bokma. 2006. Energy availability, abundance, energy use and species richness in forest bird communities: a test of the species–energy theory. Global Ecology and Biogeography **15**:290-302.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. M. Stevens, and H. Wagner. 2013. vegan: Community Ecology Package.

Post, D. M. 2002. The long and short of food-chain length. Trends in Ecology and Evolution **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   maitaining 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 Xylophagainae (Myoida: Pholoadidae). 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. Oecologica **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

		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.	productivity-diversity relationship. Communities at ends of productivity gradient represent nested subsets of communities at intermediate productivities	Communities on smaller wood falls (lower productivity) represent nested subsets of larger wood falls (higher productivities).	
More Specialization Theory/Niche Position Hypothesis	Schoener (1976), DeAngelis (1994), Evane et al. (1999, 2005)	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	Number of rare species increases with increasing productivity. Abundance increases with increasing productivity not equivalent among species.	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	Fig. 1F, 4, 7

				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 R^2 for wood-fall size ($\log_{10}$ 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 R^2	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 Residuals	-3.94***	2.54*	245*	0.94***	0.70	3.77E-08

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

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 verses 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 $\beta_{SØR}$ 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
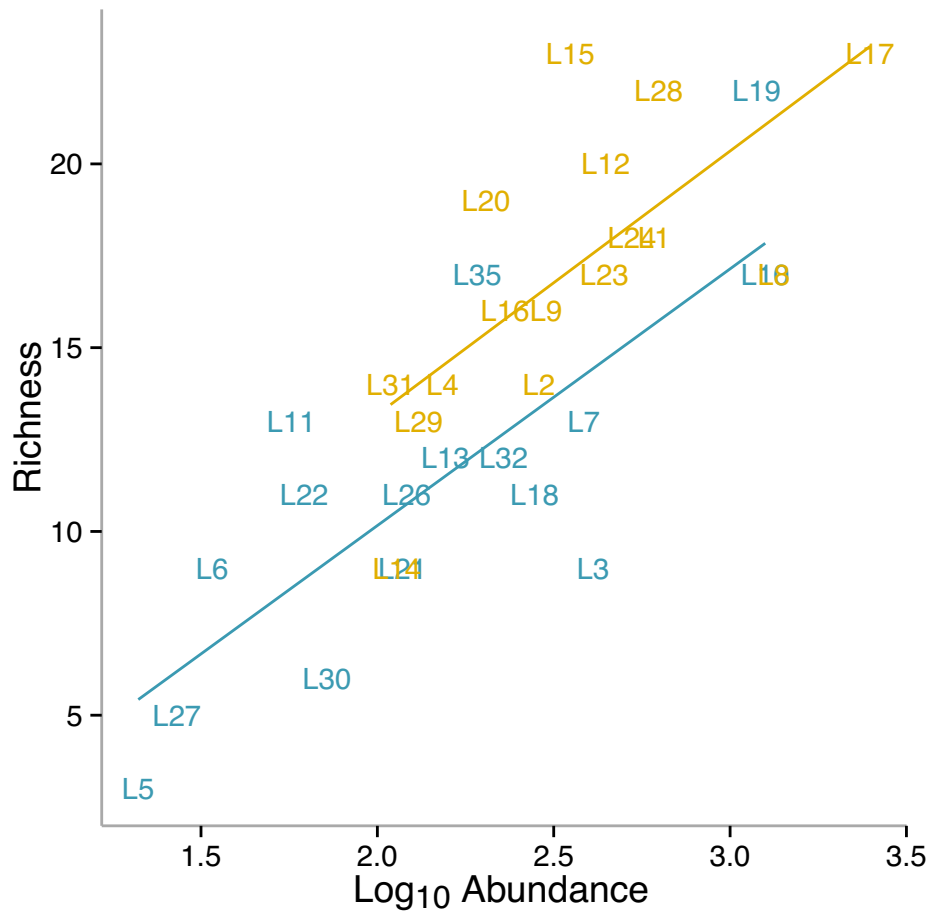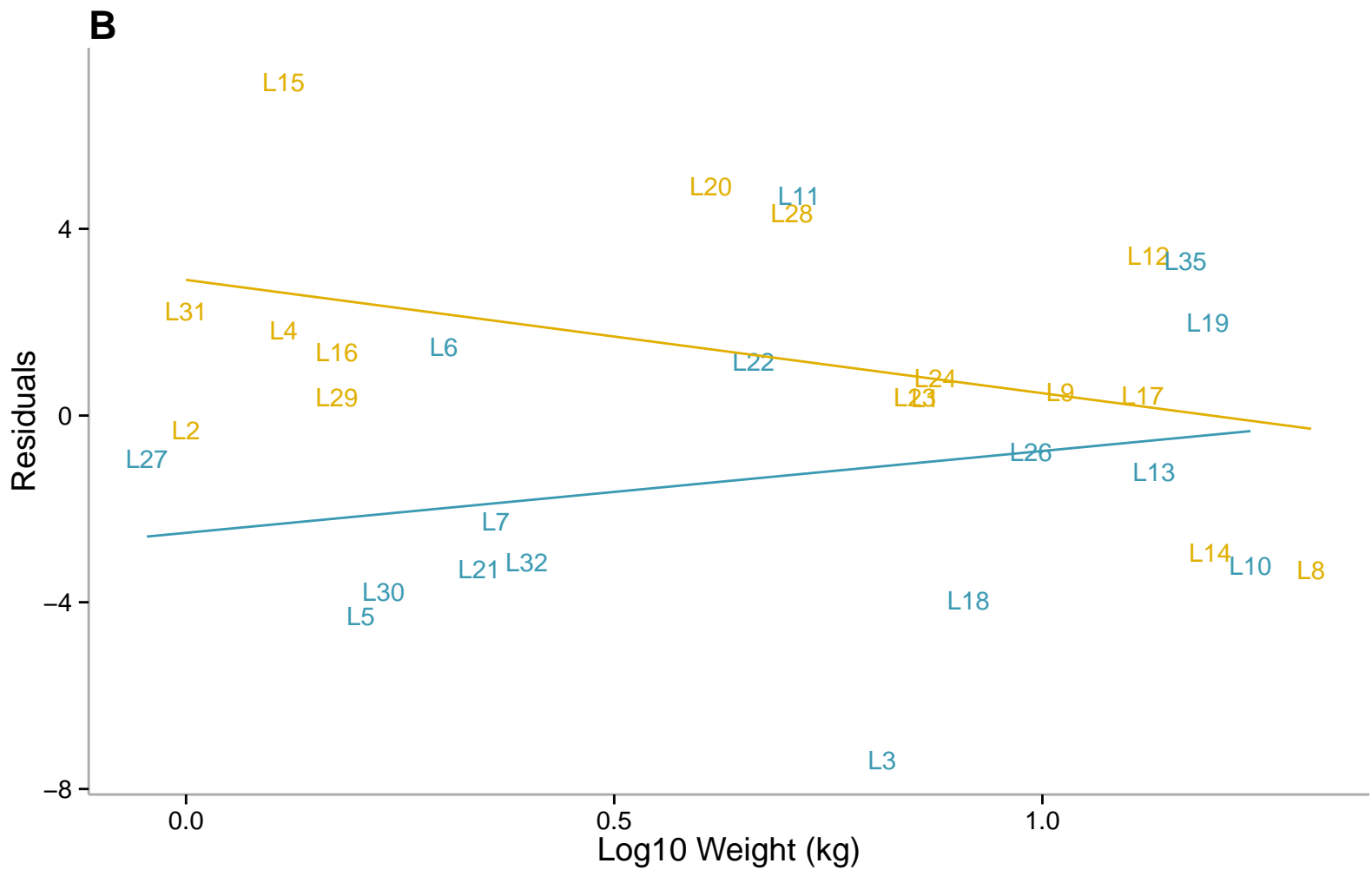
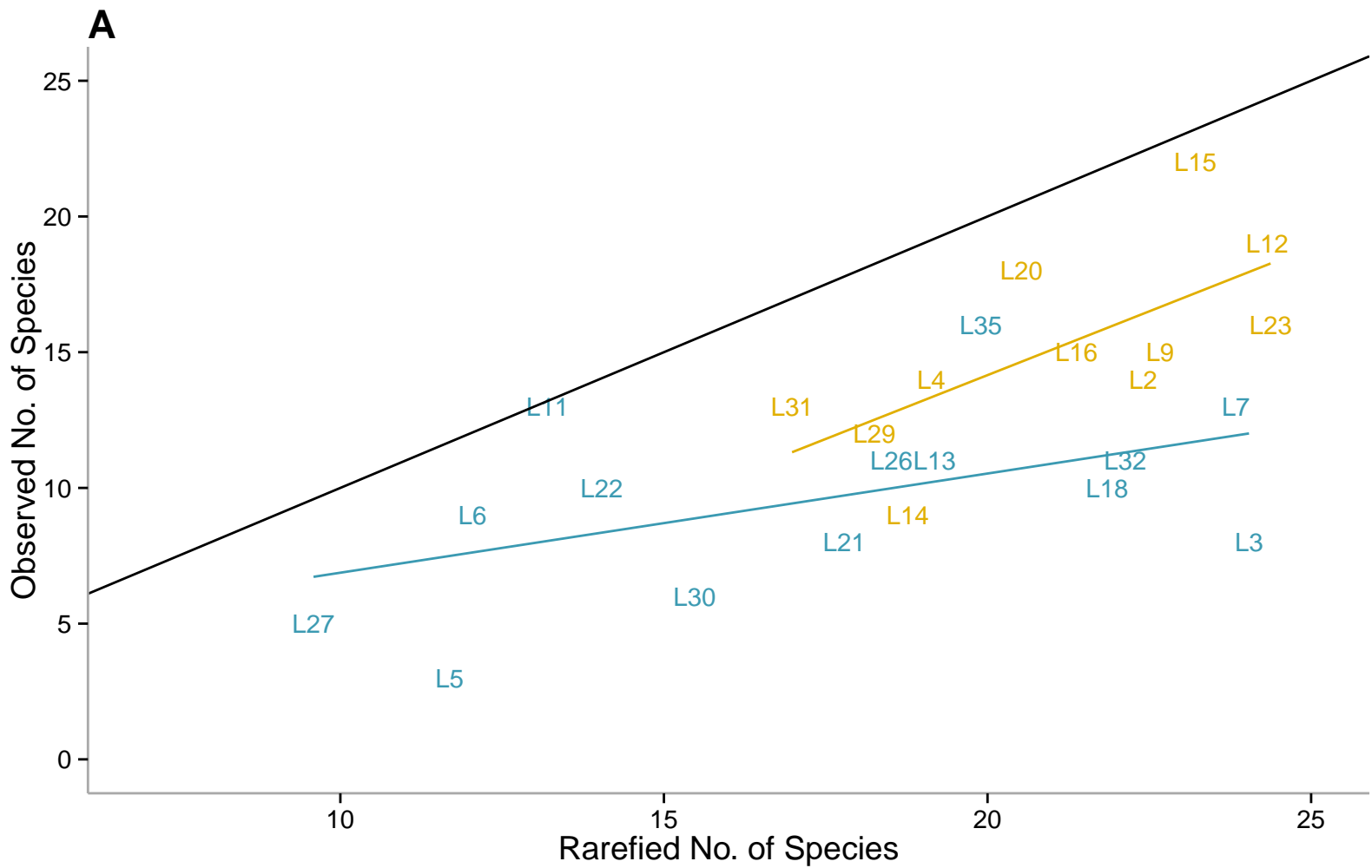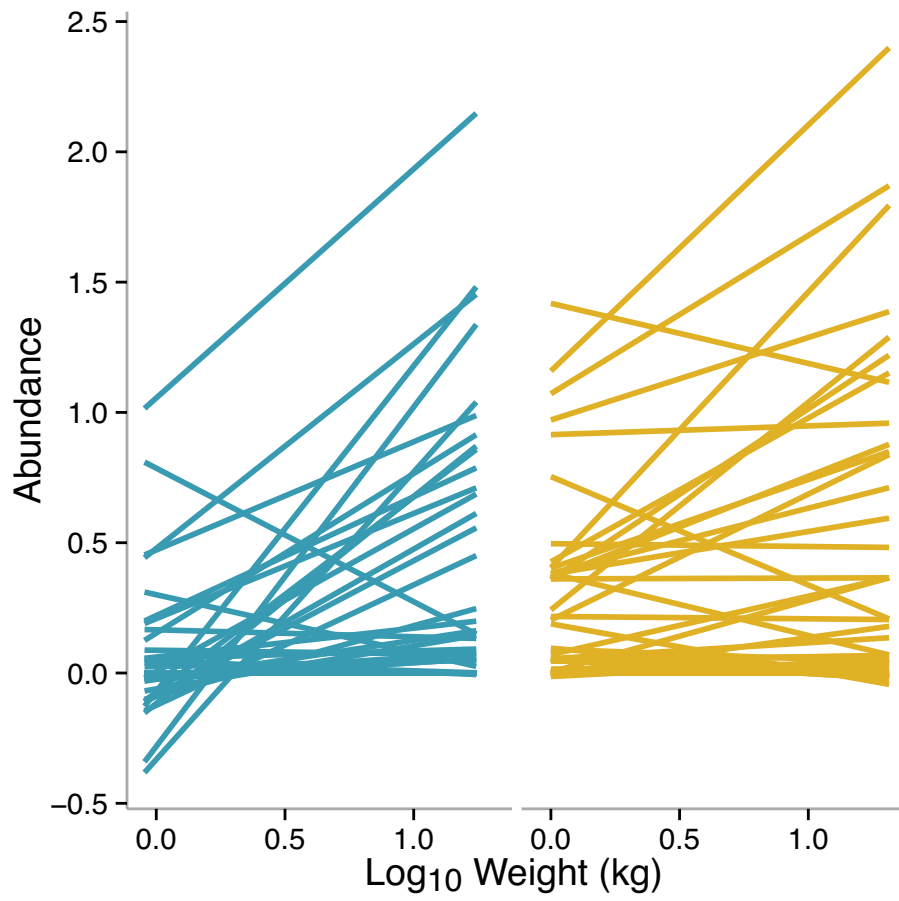12 October 2013 (7 years). Significant regression lines are also shown.

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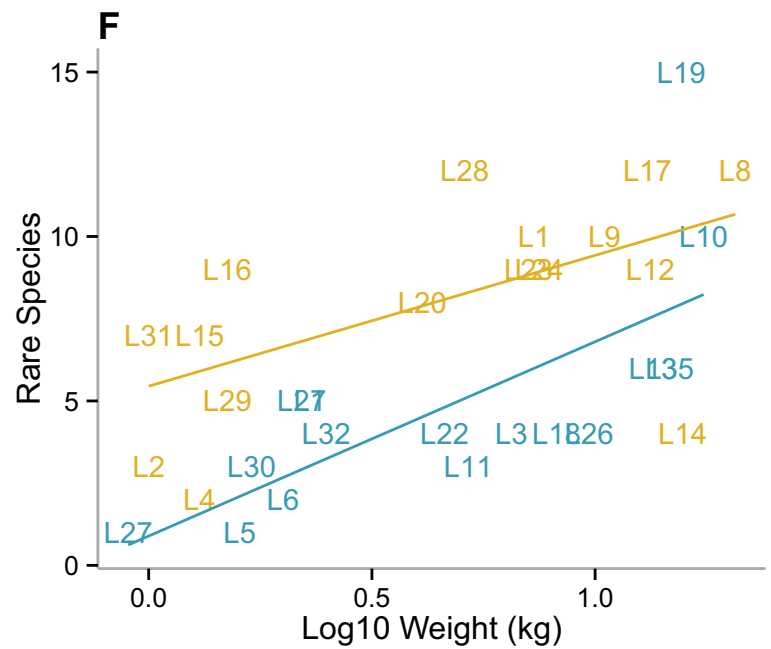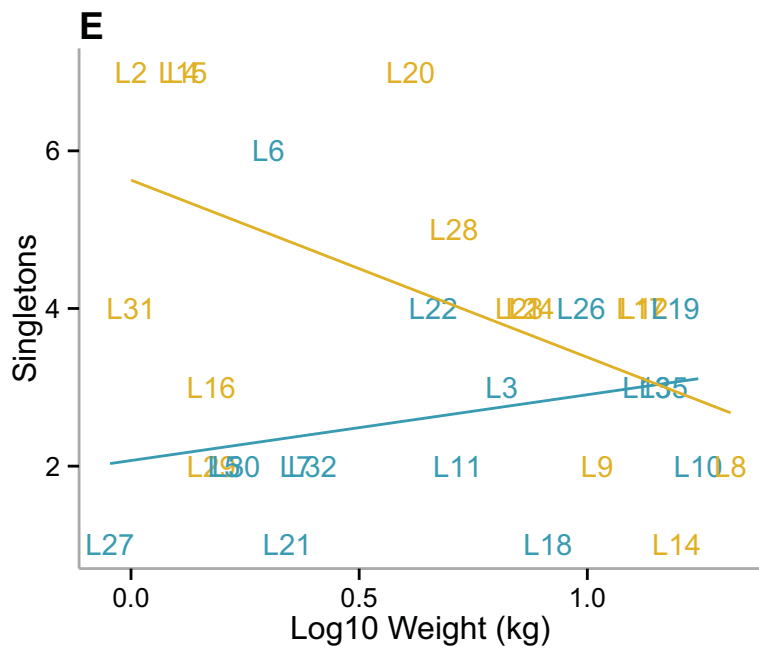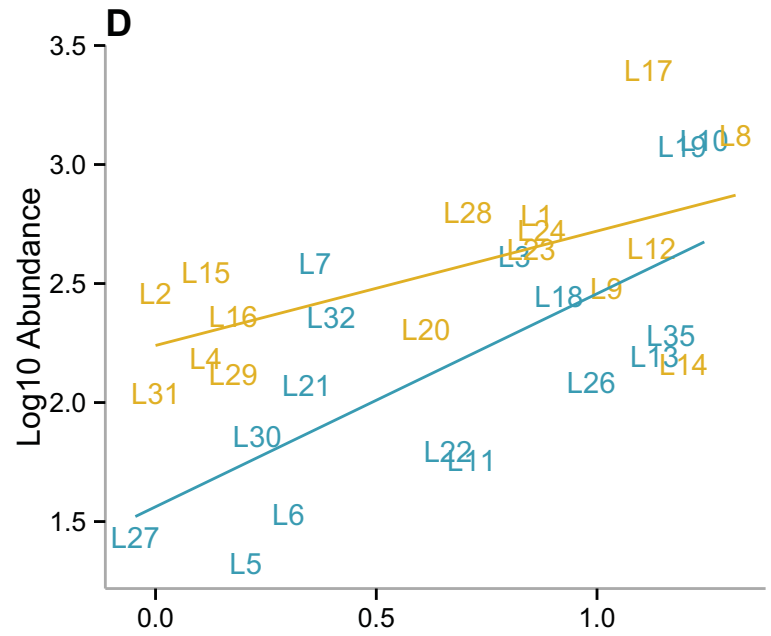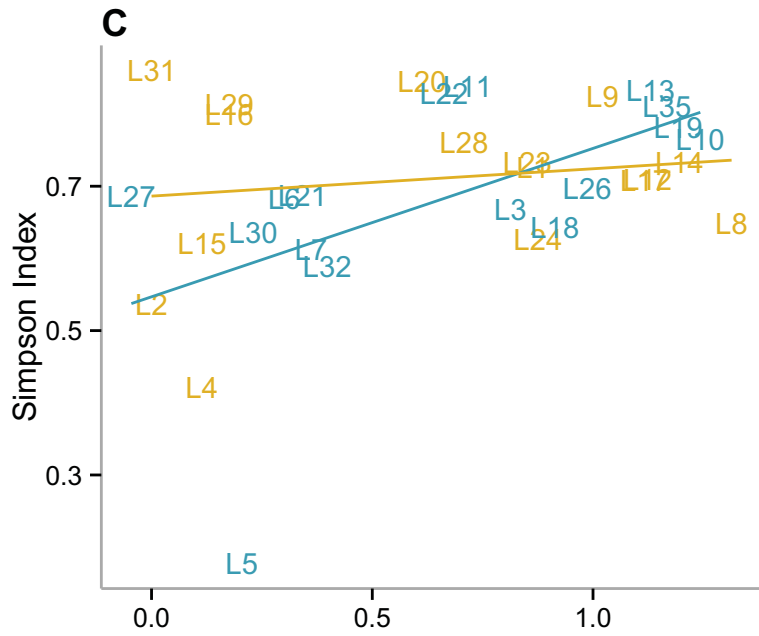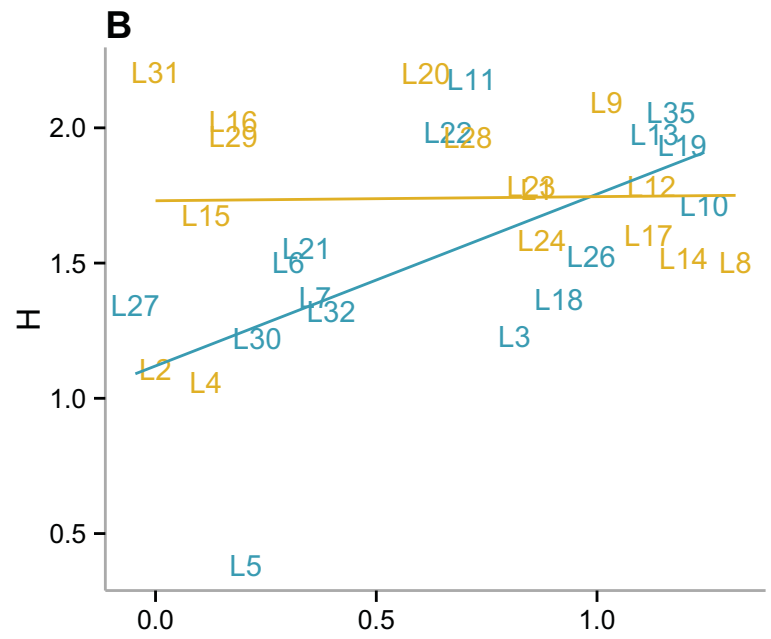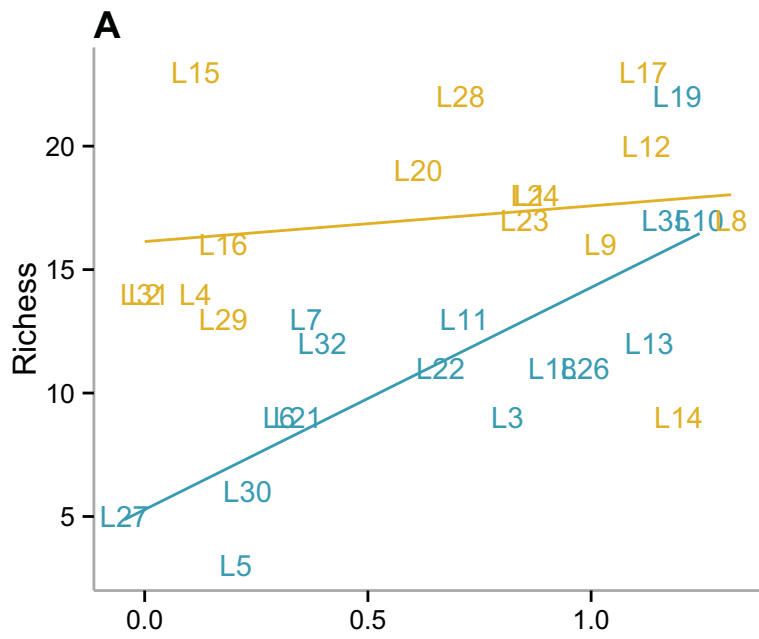
Figure 2

Figure 4

Figure 5a

Figure 5b

Figure 6

Figure 7