

**EXAMINATION OF THE RELATIVE STRENGTH OF TROPHIC
INTERACTIONS ON SPECIES ABUNDANCE**

by

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ABSTRACT

Trophic cascades occur when the predation of prey has indirect effects on taxa at lower trophic levels in the same food chain (top-down effects), or the direct effect of primary productivity on herbivores has indirect effects on taxa at higher trophic levels (bottom-up effects). To assess whether top-down or bottom-up effects are stronger and/or more common across natural systems, I obtained the mean correlation between interacting species-pairs, then quantified the proportion of positive versus negative correlations. I found weak support for bottom-up effects. From my analyses of 3-species food chains, I found no support for either top-down or bottom-up cascades. There was, however, evidence of species that reduced prey abundance but increased predator abundance, preventing the possibility of cascading effects in either direction. If 'blocker' species are ubiquitous in natural food webs, it would be one explanation for why I didn't find evidence that trophic cascades were strong or common.

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1) BACKGROUND

Ecologists have long debated the forces shaping ecosystems that result in a green world, or a world where plants are abundant and intact (Hairston et al., 1960; Polis et al., 2000; Van der Putten, 2003). Although the availability of CO₂, water, and sunlight can partially explain the abundance of chlorophyll, the interaction between herbivores and plants might be expected to reduce plant abundance. However, examples of herbivores inducing desertification of a green world into a brown world is rare (Wilkinson & Sherratt, 2016). Therefore, it is uncertain if herbivores are regulating primary production or if primary production regulates herbivores.

While food webs in natural systems include complex interactions, simple top-down and bottom-up effects have played a prominent role in the history of food web research. Top-down effect refers to taxa at the higher trophic levels influencing the community of those below them via predation or herbivory, and bottom-up refers to the influence exerted by lower-level taxa on those above them via resource restriction (Li et al., 2020) Top-down and / or bottom-up effects and trophic cascades are discussed in most introductory ecology textbooks and several meta-analyses have been conducted on top-down and bottom-up effects over the last three decades (Brett & Goldman, 1996; Mäntylä et al., 2011; Vidal & Murphy, 2018). Further, the concept of trophic cascades has been applied in managing aquatic ecosystems (Bunnell et al., 2013; Galimany et al., 2020; Kao et al., 2016). Top-down and bottom-up forces are acknowledged as crucial in understanding food webs, but more research is needed to ascertain the relevance of these forces in natural systems.

1.1) Trophic Cascades

Theory on top-down trophic cascades provides an early explanation for why herbivores fail to reduce plant abundance (Hairston et al., 1960). The theory asserts that indirect species interactions originate with predators and spread downward through a food web (Ripple et al., 2016). More specifically, consumers negatively affect their prey which in turn positively affects the abundance of organisms eaten by the prey. A study conducted by Mäntylä et al. (2011) supported this theory when plants experienced significantly more leaf damage, mortality, and biomass loss when birds were excluded compared to plants grown where birds could prey on herbivorous insects. Small scale natural studies have also shown top-down control in natural ecosystems including ungulates exerting a top-down control on soil microbial communities (Peschel et al., 2015) and marine zooplanktivores affecting zooplankton populations in the Baltic Sea (Rudstam et al., 1994).

However, top-down trophic cascades are driven not only by consumptive effects, but also by nonconsumptive forces; this can include changes in prey traits or behaviours in response to the risk of predation. For example, the presence of predators can force prey to make a choice between feeding and avoiding contact with predators (Schmitz et al., 2004). Catano et al. (2016) discovered that in the presence of piscivorous black grouper (*Myxeroperca bonaci*) decoys, herbivorous fishes consumed less food at a faster rate. Morphology of prey is also affected by predation; aphids are capable of exhibiting polymorphism for either winged or unwinged form, and Weisser et al. (1999) found that presence of predators enhances the proportion of winged aphids over unwinged aphids. Despite the combination of consumptive and nonconsumptive effects,

predators often do not exercise enough control over herbivore abundance to turn a green world into a brown one, even when predators of herbivores are removed from the system (Wilkinson & Sherratt, 2016). Wilkinson & Sherratt (2016) have noted cases where more herbivores result in predation-resistant plants, suggesting that the top-down model is insufficient in explaining why the world remains green.

One alternative theory to top-down trophic cascades is the bottom-up force on food webs, in which the resource has a positive effect on the consumer (Ripple et al., 2016). More specifically, bottom-up effects emphasize that the productivity and abundance of populations at any given trophic level are controlled or limited by the productivity and abundance of populations in the trophic level below them (Smith & Smith, 2015). A traditional example of bottom-up forces is increased abundance of primary producers as a result of nutrient inputs, causing increased consumer abundance. For example, Fujita et al. (2019) found that discharging nutrient-rich submarine groundwater increased the biomass of primary producers, primary consumers, and secondary consumers. Furthermore, Matsuzaki et al. (2018) found that pond smelt abundance was positively correlated with the abundance of zooplankton, and zooplankton abundance was positively influenced by primary producers, but no top-down control was detected between zooplankton and phytoplankton.

However, response times may vary across trophic levels, and this may explain why bottom-up effects are weaker when time-lags are not accounted for (Pace et al., 1998; Salomon et al., 2010). For example, Matveev (1995) found that zooplankton density had a delayed response to the density of phytoplankton. Yamamoto (2003) also noted a time-lag between phosphorus discharge and the number of red tides. A similar time-lag was also found between phosphorus discharge and fisheries, with fish catch

increasing with increasing phosphorus discharge. Similarly, Specziár and Vörös (2001) noted a one-year time-lag of chironomids to phytoplankton production in Lake Balaton, Hungary. Thus, evidence from the literature suggests bottom-up trophic interactions will not have an immediate effect on species higher up in a food web, and time-lags should be considered when measuring the strength of bottom-up effects.

1.2) Alternating Between Top-Down and Bottom-Up Cascades

However, there are other plausible forms of top-down and bottom-up that can occur where a linear relationship may not be seen in nature. For example, a simple Lotka-Volterra predator-prey model can lead to oscillating dynamics where neither top-down nor bottom-up effect are dominant over long time periods (Smith & Smith, 2015). If the population growth of the predator is dependent on the amount of prey consumed, fluctuations in the predator population lag those of the prey population. The lag between a predator and prey population can result in alternation between top-down and bottom-up forces through time (Benincà et al., 2009). Under those circumstances, short-term top-down or bottom-up effects might be observed but the long-term average effects of top-down or bottom-up drivers can be very small.

1.3) Practical Value of the Trophic Cascade Concept

The discussion and research surrounding top-down cascade has led to these concepts being used as solutions for controlling lake and river eutrophication. Eutrophication occurs when nutrient inputs lead to increased algal growth (Hoover et al., 2006; Price & Hunter, 2005), which can result in reduced dissolved oxygen levels (Gooday et al., 2009; Khan & Ansari, 2005). Top-down cascades have been proposed to

counteract the bottom-up effects from nutrient runoff by manipulating the predators of grazers as a means of eliminating nuisance algae (Liu et al., 2018; Östman et al., 2016). For example, Schindler (2006) noted that removing zooplanktivorous fish has reduced algal blooms in tritrophic systems. Similarly, Beklioğlu (1999) reported an increase in cladoceran biomass and reductions in algae. Thus, understanding the relative strength of top-down and bottom-up cascades in natural systems may have management implications.

1.4) Gap in Trophic Cascade Literature

Although there is extensive research assessing trophic interactions and notably the relative importance of top-down versus bottom-up effects, previous work has been largely limited to manipulative experiments (Bell et al., 2003; Brett & Goldman, 1996; Romero & Koricheva, 2011). For example, Burkholder et al. (2013) demonstrate that top-down control by large herbivores such as sea cows and turtles is a determinant to plant biomass and are controlled by predators such as tiger sharks. Pinnegar et al. (2000) reviewed 21 tri-trophic or larger food chains of coastal habitats such as lobster-urchin-kelp and oystercatcher-limpet-algae, all of which experienced top-down trophic cascade. In addition, Bell et al. (2003) found that the strength of top-down cascade did not diminish with increasing experiment duration. From 67 manipulation studies, Romero and Koricheva (2011) found that carnivores increased plant fitness by suppressing herbivores. However, there is also plentiful evidence of bottom-up effects from experimental studies (Masters et al., 2001; Nakamura et al., 2005; Walde 1995); for example, Gratton & Denno (2003) found that the addition of nutrients resulted in greater

biomass of *Spartina* plants, which carried over into the higher trophic levels relative to plots that did not receive nutrients.

Meta-analyses into trophic interactions using natural systems is scarce and are typically focused on a specific type of ecosystem (Harrison & Banks-Leite, 2020; Kling et al., 1992). For this study, I have used empirical evidence from natural systems to assess how well the experimental evidence transfers to the ‘real world’.

1.5) Objectives & Hypotheses

While numerous studies have examined trophic interactions in natural systems, or systems where there was no manipulation nor control of confounds, these studies focused on isolated cases of interaction between two or a few species in a consumer-producer context. Examples include studies that have captured the interaction between the snowshoe hare *Lepus americanus* and Canada lynx *Lynx canadensis* (Ivan & Shenk, 2016; Sheriff et al., 2010; Yan et al., 2013), Fox *Vulpes vulpes* and numerous different rabbit species (Scroggie et al., 2018), wolf and moose (McLaren & Peterson, 1994; Vucetich & Peterson, 2004; Peterson et al., 2014), and between fish species that interact in a predator-prey fashion (Essington & Hansson, 2004; Nilsson et al., 2019; Tsehaye et al., 2014). In addition, there have been several meta-analyses of experimental research (Bell et al., 2003; Hu et al., 2022; Romero & Koricheva, 2011). However, to date there has not been a systematic review of trophic interactions across natural systems. A large-scale synthesis that summarizes the results from many natural systems regarding top-down and bottom-up is needed to assess the relative strength of top-down and bottom-up forces across different natural settings. Therefore, the objective of my study is to assess whether top-down or bottom-up forces are more prevalent and / or stronger across

different natural settings. In addition to studying adjacent top-down and bottom-up, I assessed the relative prevalence of top-down and bottom-up cascades across natural systems. I used the distribution of correlations between species that are one and two trophic levels apart to assess the relative prevalence of communities dominated by top-down versus bottom-up effects and the strength of each.

For top-down effects to be deemed more common in nature, negative correlations for species-pairs that were 1 trophic level apart, would have to be stronger and / or more common than expected by chance. On the other hand, bottom-up effects would be stronger and / or more common in nature if positive correlations were stronger than expected by chance. For species-pairs that were 2 TLA, top-down or bottom-up would be more common if positive correlations were stronger than expected by chance (i.e. a mean correlation statistically significantly greater than zero). Note that the predictions for top-down and bottom-up effects are the same so correlation two levels apart cannot be used to distinguish between top-down and bottom-up systems:

A. The top-down hypothesis makes the following predictions:

1. There will be a negative correlation in abundance between taxa that are 1 trophic level apart.
2. There will be a positive correlation in abundance between taxa that are 2 trophic levels apart.

B. The bottom-up hypothesis makes the following predictions:

1. There will be a positive correlation in abundance between all taxa from different trophic levels although the correlation will weaken as the distance between trophic levels increases.

C. Lagged data results in the following predictions:

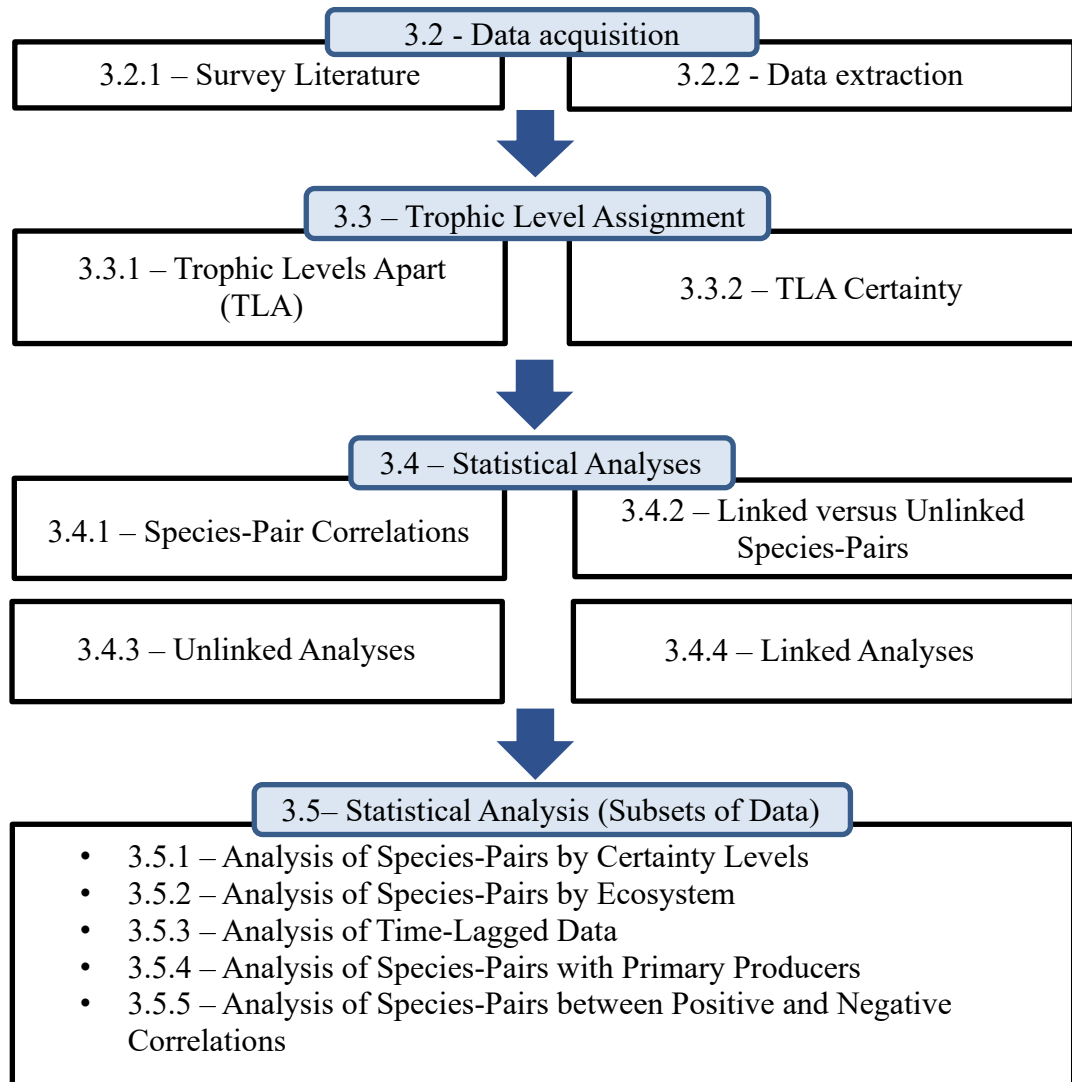
1. Correlations expected of top-down will not show stronger correlations than unlagged data.
2. Correlations expected of bottom-up will show stronger correlations than lagged data, with the correlation being weaker as distance between trophic levels increase.

Note that the rationale for prediction A3 is that the effects of increased predation are likely to be almost immediate because the act of predation instantaneously reduces prey abundance. By contrast, the rationale for prediction B2 is that bottom-up effects on predator abundance may be delayed because the effects of reduced resources on (1) predator mortality will only occur after prolonged starvation and (2) predator birth rates will only decline as less energy is directed towards reproduction over time. There are other more complex time-varying models of trophic dynamics (e.g. oscillating top-down and bottom-up effects), but I will not be testing for them here.

2) METHOD

2.1) Method Flowchart

Figure 1: A roadmap and summary of the methodology.



2.2) Data Acquisition

2.2.1) Survey of Published Literature

To test if top-down or bottom-up effects are common and / or strong in natural systems, I collected species abundance time-series in pairs of taxa that were one or two trophic levels apart. I found articles containing abundance time-series using the journal indexing databases Wildlife & Ecology Studies Worldwide and Canadian Journal of Fisheries and Aquatic Sciences. I also collected abundance time series from Dryad and the Long-Term Ecological Research Network data archive (Table 1).

Table 1: Search terms used for Dryad and literature indices during data collection.

Literature Indices Ecosystem Type	Search Terms
All Literature Indices	Predator-Prey OR Prey-Predator OR Prey AND Predator AND Abundance Trophic Interaction AND Abundance
Terrestrial	Carnivores AND Ungulates AND Abundance Abundance OR population AND Hare AND lynx
Aquatic	Phytoplankton OR Zooplankton AND Abundance OR Richness OR Population AND Years Fish AND phytoplankton OR zooplankton AND abundance OR richness OR population

2.2.2) Data Extraction

I extracted data from tables or figures in publications or directly from databases stored in data repositories. The following variables were considered primary variables of interest:

- Taxonomic unit – This was usually species or genus information, but if the study provided broad identifiers (e.g., avian predators, mesopelagic fish, etc.) or taxa (e.g., family, order, etc.), this was collected instead.
- Abundance – This was measured in a variety of ways including track counts, spotlight counts, trapping, plankton netting, trawling, exported fur data, etc.
- Year – The data must contain at least three years of data to avoid the calculation of perfect correlations.
- Trophic level – Relative trophic levels apart, or the trophic distance between two taxa. Note that most datasets lacked the trophic distance between two species.

The process by which trophic distance is established can be found in section 2.3.

If there were 2 or fewer years, the study was excluded from collection. If trophic level could not be established based on the taxonomic unit, the study was later excluded. I extracted data contained in figures using ImageJ software.

The following variables were considered ancillary variables. Even if one or more of these variables were missing, the data were still included.

- The type of ecosystem studied (freshwater, marine, or terrestrial).
- The country, continent, or ocean where the ecosystem was studied.
- Presence or absence of confounding variables within a study capable of affecting trophic dynamics (e.g. a drought in an ecosystem, an infection affecting a population, or human intervention such as habitat destruction and overexploitation).
- Whether or not the researchers conducted multiple censuses within a year.

Time-series were excluded if:

- Studies involved a control and treatment group (i.e. experimental studies).
- Species were detritivores.
- There was no overlap in season or months despite overlap in years (e.g. data collection has occurred from 1996 to 2000 and the predators were collected in spring, but the prey were collected in the fall).

In studies where data were collected at finer than annual temporal scales (e.g. weekly, monthly, or seasonally) they were aggregated to provide annual measures of abundance. However, if there was a difference in temporal scale between two time series, the study or metadata must provide additional information to compare the temporally finer time-series data to the temporally broader data. For example, if the study had given the abundance of the prey in months and the abundance of predators in seasons, and the author has provided additional information on what months constitute a particular season, the time-series pair would be kept for analysis. When there was temporal overlap between the estimates of the two species' abundance, but it was unclear whether there was complete overlap, I reduced the certainty category by one level (see description of certainty levels in Section 2.3.2). For example, if predator abundance was estimated only in the spring whereas the prey was collected yearly without specification of season, the certainty was reduced by one level (e.g., from high to moderate).

Species-pairs had to co-occur at the same site (e.g., same lake, river, or overlapping areas for terrestrial organisms). In many cases there was no precise information about sampling locations but so long as each of the time series came from a single dataset from the same site it was assumed that the sampling locations were close

enough to each other or occurring over a broad enough scale that the species were considered to be co-occurring. Differences in location between two interacting organisms due to habitat choice were ignored (e.g., benthic vs. pelagic, inshore vs. offshore, etc.). The final dataset included time series for 777 species-pairs, with 439 unique groups of organisms (Appendix A1).

2.3) Relative Trophic Level Assignment

2.3.1) Trophic Level Apart (TLA)

Precisely identifying the trophic level of an individual species requires a complete understanding of the trophic interactions of the system the species is embedded in so trophic levels are difficult to assign. In some cases, I was not able to identify absolute trophic levels, but was only able to identify an integer value representing the ‘trophic distance’ between two species. To test my hypotheses, species pairs had to be assigned to a ‘trophic level apart’ (TLA) category. For example, in the three-way interaction among lynx, snowshoe hare and plants, snowshoe hare and plants are 1 TLA because all primary producers are assigned to trophic level 1 and all herbivores to trophic level 2; lynx and snowshoe hares are 1 TLA because lynx are assigned to trophic level 3 as direct consumers of snowshoe hare, so lynx and plants are 2 TLA.

In journal indices, the authors or owners of a dataset explicitly identified the trophic levels of both species in a species pair. In those cases, I used the TLA assigned by the authors or owners. When dataset owners/authors did not explicitly assign trophic levels to the censused species, I used published information to identify the food preferences of all taxa in my dataset. In data repositories, there was no published information on a specific species and for those I used published information provided at

a higher taxonomic level (e. g. genus or family). Species that were identified as possibly consuming across trophic levels (i.e. omnivory) were assigned to the relative trophic level associated with their preferred food. For example, if one species in a species pair was identified as carnivorous (despite occasionally eating fruits or berries) and the other as herbivorous (despite occasionally eating carrion) they were assigned as being one trophic level apart.

2.3.2) Certainty Levels

The feeding habits of living organisms are rarely completely understood so there is often uncertainty about the absolute and relative trophic levels of particular species. In cases where the dataset owners or authors did not explicitly identify the trophic levels of censused species, I used published information to assign certainty levels to interactions between two organisms. Interactions were assigned with ‘high’ certainty when there was published evidence that the two specific species in the species pair interacted with each other. I assigned moderate certainty when there was published evidence that one species interacted with the broader group that included the other organism. I assigned low certainty when I used relative body size comparisons to assign predator-prey relationships (Table 2).

Table 2: Rules for designating certainty levels for interactions between organisms.

Certainty Levels	Criteria to Reach Certainty Level
High certainty	Published evidence that Species A is a predator of Species B or Species B is prey for Species A. This includes observed attempts of predation, predation of a prey, presence of prey species in gut content, and studies that found a species to eat another species. For example, <i>P. pediculus</i> prefers feeding on <i>B. longirostris</i> (Monakov, 1972).
	If Species A is only a predator of Species B at a specific life stage or stages, the time series had to identify the life stage. Likewise, if my time-series identified species A as a predator of species B at a specific life stage, the evidence had to identify the life stage too. Otherwise, the certainty level is reduced by a level. For example, my data specifies barnacles in the nauplii and cyprid stages, but the evidence broadly states that barnacle <i>Elminius modestus</i> is capable of eating phytoplankton and zooplankton (Rainbow & Wang, 2001).
	Published evidence that a species is a herbivore feeding on primary producers. For example, “an abundance of small, digestible algal species is important to the foraging success of <i>H. gibberum</i> ” (Tessier, 1983, p. 75).
Moderate certainty	When there is no published evidence that Species A eats Species B, but there is published evidence that individuals from genus A eat individuals from genus B and species A belongs to genus A and species B belongs to genus B.
	Broader groups may be identified by genus, family or order or by more generic terms such as planktivory, clams, barnacles which indicate a general group of predators or prey. For example, Catano et al. (2016) found that <i>Acartia tonsa</i> is a predator of <i>Oithona colcarva</i> , but my species-pair was <i>Acartia tonsa</i> and <i>Oithona similis</i> .
Low certainty	When the only evidence of a species’ diet is broadly described to be a carnivore, raptorial, omnivore, and other broad terms that fail to narrow down a group to the species or genus level. For example, a zooplankton can be an obligate predator, but this could indicate that it eats rotifers, bacteria, or zooplankton.
	For two species that are considered carnivorous, it is plausible based on body size comparison that Species A could eat Species B or vice-versa. An example would be that <i>Heterocope septentrionalis</i> and <i>Polyphemus pediculus</i> are identified as predatory zooplankton (O'Brien et al., 1979; Primicerio, 2000). <i>H. septentrionalis</i> is not only bigger than <i>P. pediculus</i> , but the <i>P. pediculus</i> size fell into the range of prey <i>H. septentrionalis</i> ate (O'Brien et al., 1979; Robidoux et al., 2015).

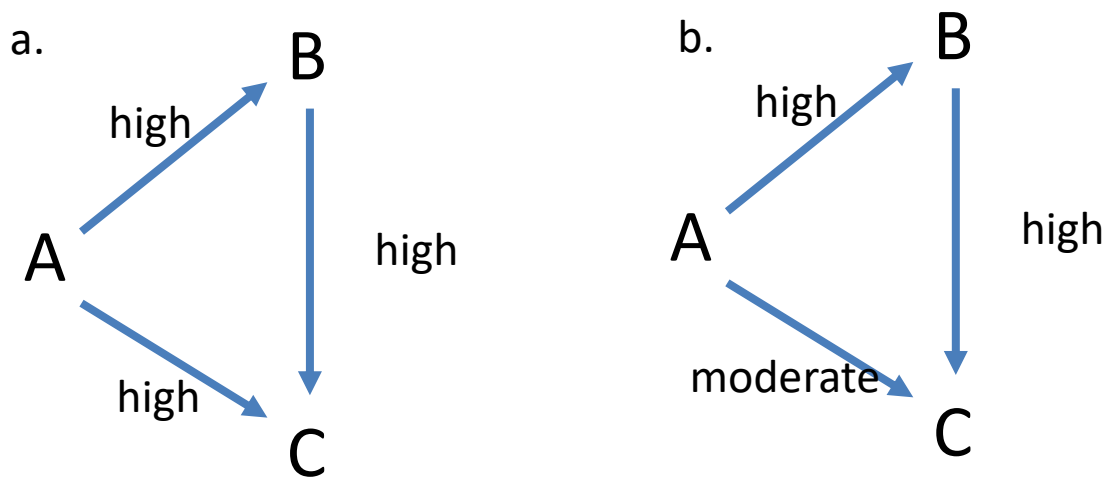
For species-pairs that were two trophic levels apart, assigning certainty levels depended on the evidence about two interactions – the certainty that the taxon at the top trophic level consumed the taxon at the middle level and the certainty that the taxon at the middle level consumed the taxon at the lower level. The lower of these two certainty levels was always assigned to the 2 TLA species-pair. For example, if the herbivore *H. gibberum* interaction had high certainty when interacting with phytoplankton, but *H. gibberum* interaction had moderate certainty when interacting with the predator *H. septentrionalis*, then the 2 TLA interaction between *H. septentrionalis* and *H. gibberum* would be assigned to the moderate certainty category.

2.3.2.1) Ambiguity caused by potential predation across trophic levels.

Each species pair could only be assigned to a single ‘trophic-level-apart’ (TLA) category. Taxa that were identified as (1) consuming a particular prey as well as (2) consuming a predator of that prey were assigned either to 1 or 2 TLA – they could not be assigned to both. That is, it is possible for Species A to feed directly on Species C but also feed on Species B that feeds directly on Species C (e.g., a fish capable of eating zooplankton and planktivorous fish). When a species-pair could plausibly be assigned to more than one TLA category, it was assigned to the category with the higher certainty level. In the case of a tie, the species pair was assigned to the lower TLA category. In the above example (assuming equal certainty for all three pairwise direct interactions), the species A-B pair would be assigned 1 TLA, the species B-C pair would be assigned 1 TLA, and the species A-C pair would be assigned 1 TLA (Figure 2a). However, if the A-B and B-C direct interactions were ‘high’ certainty and the direct interaction between A-C was ‘moderate’ certainty, the species A-B pair would be assigned 1 TLA, the species

B-C pair would be assigned 1 TLA and the species A-C pair would be assigned 2 TLA (Figure 2b).

Figure 2: Schematic of trophic interactions among species A, B and C. Arrows identify direct consumption. a. A-B (1 TLA); B-C (1 TLA); A-C (1 TLA). b. A-B (1 TLA); B-C (1 TLA); A-C (2 TLA).



2.3.2.2) Assigning Relative Trophic Levels based on Body Size.

When both species of a species pair were identified to be carnivores, but no evidence existed to determine which predated on the other, a body-size comparison was done to assess the direction of the interaction (note that this approach was only necessary for carnivorous zooplankton). I used published information to obtain the range of prey sizes for both species. If one of the two species fell into the prey body-size range of the other, it was identified as prey for that species. However, if neither or both species fell into the other's prey body-size range, the interaction was omitted. Even with these

trophic level assignment rules, limited information and omnivorous feeding behavior led to uncertainty in “trophic level apart” assignments.

2.4) Statistical Analyses (All Data)

All: My entire dataset consisted of a final total of 777 species-pairs. All species pairs had to be at least one trophic level apart (see Section 3.3 for description of how species-pairs were assigned to TLA categories). Each species-pair has been assigned to one of three categories 1 TLA, 2 TLA or 3 TLA. Species-pairs that were 1 TLA represent a direct trophic interaction between species (e.g. primary predator-prey, herbivore-plants, etc.). Species-pairs that were 2 TLA represent an indirect trophic interaction between species (e.g. primary predator and the plant of the herbivore it eats). Species-pairs that were 3 TLA also represent an indirect trophic interaction between species but with an additional trophic level of separation (e.g. secondary predator and the plant of the herbivore the primary predator eats); however, this was excluded as it only represented 1 species-pair in my data.

Subsets: I also analyzed subsets of the data, filtering for (i) certainty levels (see Section 3.5.1) (ii) ecosystem types (see Section 3.5.2), (iii) whether a species-pairs included a primary producer or not (see Section 3.5.4) and (iv) the strength of the correlation between taxa in a species-pair (see Section 3.5.5).

2.4.1) Species-Pair Correlations

I calculated Pearson correlations for each of the 777 species-pairs to estimate the distribution of correlations for species-pairs that were one trophic level apart and two trophic levels apart. Because there was only one correlation for species-pairs three

trophic levels apart, I have not included that correlation here. I calculated Pearson correlations for each species-pair both with the prey species abundance lagged by one year and without the 1-year lag.

I used the distribution of species-pair correlations to test whether evidence of top-down or bottom-up effects was stronger and/or more common in natural systems than we would expect by chance and to test whether evidence for trophic cascades of either kind was more common in natural systems than we would expect by chance.

I estimated the relationship between mean correlation and the number of years in the species-pair time series across all 777 pairs. I also estimated the mean weighted correlation for each species-pairs, weighting correlations by the number of years in the time series. I did this for both unlinked and linked species-pairs (below for definition of unlinked versus linked species-pairs).

2.4.2) Unlinked Species-Pairs Analyses

2.4.2.1) Frequency of positive versus negative correlations.

I used a binomial test to find the difference in the proportion of negative versus positive correlations for both 1 and 2 TLA species-pairs. For species-pairs that were 1 TLA, top-down effects would be supported to occur more commonly in nature if there were more negative correlations than would be expected by chance (i.e. significantly > 50 % negative correlations). However, bottom-up effects would be supported if there were more positive correlations than would be expected by chance (i.e. significantly > 50 % positive correlations). For species-pairs that were 2 TLA, top-down or bottom-up would be supported if there were more positive correlations were obtained than expected by chance. Note that the predictions for top-down and bottom-up effects are the same so

correlation two levels apart cannot be used to distinguish between top-down and bottom-up systems.

2.4.2.2) Mean Correlation

I used Monte Carlo simulations to test if the mean correlation between co-existing species was significantly different from zero. Simulated correlations were chosen from a normal distribution with $mean = 0$, $variance = observed\ variance$ (for set/subset being tested) and $n = observed\ n$ (i.e. number of species-pairs in set/subset being tested). I compared the observed mean correlation to the distribution of simulated mean correlations to estimate the probability that the observed mean correlation came from a distribution with a mean of zero. The probability was calculated as the number of simulated mean correlations that were greater than or equal/less than or equal (depending on the one-tailed hypothesis) to the value of the observed mean correlation divided by the number of simulated values. For all Monte Carlo analyses, I ran 10,000 Monte Carlo simulations.

$$p_{value} = \frac{\# \text{ of simulated mean correlations } \geq \text{ or } \leq \text{ observed mean correlation}}{10,000}$$

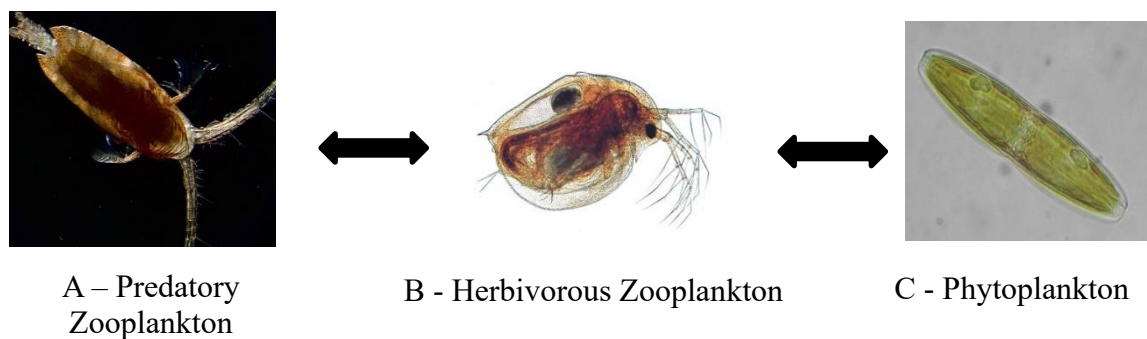
For example, for all 1 TLA species-pairs ($n = 713$) simulated correlations were chosen from a normal distribution with $variance = 0.443$ and $n = 713$. None of the 10000 simulated values were as large or larger than the observed mean correlation of 0.0565.

$$p_{value} = \frac{0}{10,000} = < 0.0001$$

2.4.3) Defining Linked and Unlinked Species-Pairs

Single species-pairs correlations – either 1 TLA or 2 TLA – were defined as ‘unlinked’. This is because the correlations were not used in tandem with correlations of other species-pairs to provide insights for the occurrence of cascading top-down or bottom-up effects. The following section will explain linked species-pairs by examining an example of an interaction across two trophic levels for three species (Figure 3).

Figure 3: An example of a tri-trophic food chain, with arrows representing the direct influence of species for both predatory (A-B) or herbivory (B-C) interactions.



Each individual species-pair correlations, one between the predatory zooplankton and the herbivorous zooplankton (A-B), another between the herbivorous zooplankton and phytoplankton (B-C), and between the predatory zooplankton and phytoplankton (A-C) - provides information in isolation; they are considered ‘unlinked’ because the individual correlations are not placed in a food chain created using other species-pairs.

Unlinked correlations for species-pairs that are 1 TLA can only provide evidence for or against top-down or bottom-up effects in adjacent taxa and thus, do not address the existence of cascading effects. Unlinked correlations for species-pairs that are 2 TLA

can provide evidence for or against cascading effects but cannot distinguish between top-down and bottom-up effects because both top-down and bottom-up hypotheses predict a positive correlation between species that are 2 TLA. By linking a species-pair to create a triplet, it can identify the type of trophic cascade if there is evidence of a cascade.

Linked species-pair correlations are required to directly address whether cascading effects are common and the relative frequency of top-down versus bottom-up cascading effects. Correlations between predatory zooplankton and herbivorous zooplankton (A-B), herbivorous zooplankton and phytoplankton (B-C), and predatory zooplankton and phytoplankton (A-C) such as one seen in figure 3 is assessed in the context of a proposed chain can provide valuable information about the frequency of cascades and the relative frequency of top-down versus bottom-up cascades. When I examine and interpret A-B/B-C/A-C correlations as ‘triplets’ I consider the species-pairs to be linked. Linked species pairs allow me to test more directly for upward or downward trophic cascades (see Section 2.4.4).

2.4.4) Linked Species-Pair Correlations

2.4.4.1) Linked species-pair correlation combinations.

To test for trophic cascades, I used linked tri-trophic interactions to ascertain if either top-down or bottom-up cascades were more prevalent than expected by chance across ecosystems. In a trophic interaction between three organisms A-B-C (e.g. fish “A” predating zooplankton “B”, and zooplankton “B” grazing on phytoplankton “C”), where A predate on B, A indirectly interacts with C, and B predate on C in a food chain, there were eight possible combinations of correlations. Note that only the **first**

and eighth combination are consistent with my hypotheses, with (+ / + / +) being consistent with a bottom-up trophic cascade and (- / + / -) being consistent with a top-down trophic cascade.

1. Positive correlation for all interactions, resulting in positive interactions for A-B, A-C, and B-C, denoted as (+ / + / +), **consistent with bottom-up trophic cascade.**
2. Negative correlation for all interactions, resulting in negative correlations for A-B, A-C, and B-C, denoted as (- / - / -).
3. Negative correlation for the adjacent interaction between A-B, but positive correlations for A-C and B-C, denoted as (- / + / +).
4. Negative correlation for the indirect interaction between A-C, but positive correlations for all interactions that are 1 TLA, denoted as (+ / - / +).
5. Negative correlation for the interaction between B-C, but positive correlations for the interaction between A-B and A-C, denoted as (+ / + / -).
6. Negative correlations for the interaction between A-B and A-C, but a positive correlation for B-C, denoted as (- / - / +).
7. Negative correlations for the interaction between A-C and B-C, but a positive interaction between A-B, denoted as (+ / - / -).
8. Negative correlations for direct interactions A-B and B-C, but a positive correlation for the indirect interaction A-C, denoted as (- / + / -), **consistent with top-down cascade.**

Note that the order of interaction within the bracket are (A-B interaction / A-C interaction / B-C interaction) in the A-B-C food chain. Once all possible correlations

were compiled, I used the frequency of each combination to assess whether top-down or bottom-up cascades were stronger and more prevalent than expected by chance.

2.4.4.2) Randomizations for linked species-pair correlations.

I used randomizations to test whether combinations of species-pair correlations occur more frequently than expected by chance. I assumed that, if correlations between species were random (i.e. the abundances of the species in a species-pair were independent of each other), the probability of a positive correlation would be 0.5 and the probability of a negative correlation would be 0.5. Below is the process by which I have performed the randomization:

1. I assigned a random number from a uniform distribution between 0 and 1 to each simulated species – pair in a simulated A-B/A-C/B-C ‘triplet’.
2. All random values greater than 0.5 were assigned to the POSITIVE category and all random values less than 0.5 were assigned to the NEGATIVE category. Thus, each simulated triplet was assigned to one of the eight possible ‘triplet’ combinations.
3. For each simulation, the frequency of occurrences of each of the eight possible ‘triplet’ combinations was saved.
4. The expected value in each of the eight cells was calculated as $Expected = \frac{N}{8}$, where N is the number of ‘observed’ triplets.
5. For each simulation I calculated:
 - I. $\sum |Observed - Expected|$
 - II. Maximum frequency across all eight possible combinations

- III. Minimum frequency across all eight possible combinations
 - IV. Frequency of triplet expected for top-down cascades
 - V. Frequency for triplet expected for bottom-up cascades
6. The simulation was repeated 1,000 times
 7. The probabilities for I., II., IV., and V. were estimated as:

$$\frac{\text{Frequency of Simulated Values} \geq \text{Observed Values}}{1,000}$$

and for III. were estimated as:

$$\frac{\text{Frequency of Simulated Values} \leq \text{Observed Values}}{1,000}$$

Example: For the linked species-pairs, there were a total of 235 three-species chains.

Thus, each of the three correlations in a ‘triplet’ would be assigned a random value between 0 and 1 from a uniform distribution. This would be repeated for each of the 235 three-species chains. Each of the random values in a ‘triplet’, would be assigned a ‘positive’ or a ‘negative’ based on the value of the random number. This would be repeated for each of the 235 three-species chains. Each ‘triplet’ would be assigned to one of the eight possible correlation combinations (Table 3). $Expected = \frac{N}{8} = 235/8 = 29.375$ for each of the eight cells. This would be repeated 1000 times to provide a distribution of simulated values.

Table 3: The eight possible triplet combinations for the linked analysis.

A-B		A-C		B-C	
				+	-

	+	+/+/+	+/+/-
+	-	+/-/+	+/-/-
	+	-/+/+	-/+/-
-	-	-/-/+	-/-/-

2.4.4.3) Predictions for the linked species-pair correlations.

I tested two competing predictions, top-down cascades and bottom-up cascades. For there to be support for top-down cascade, I must have observed more negative A-B / positive A-C / negative B-C correlation pairs than would be expected by chance (i.e. significantly > 12.5% or > 29.375 observations for - / + / - correlations). For there to be support for bottom-up cascade, I must have observed more positive A-B / positive A-C / positive B-C correlations are found than would be expected by chance (i.e. significantly > 12.5% or > 29.375 observations for + / + / + correlations).

2.5) Statistical Analyses: Subsets of Data

I analyzed subsets of the complete dataset to address questions related to (1.) the ambiguity about TLA assignments, (2.) variation across ecosystem types, (3.) time-lagged correlations, (4.) variation based on where interactions fell in the food web, and (5.) variation between strong versus weak correlations. Note that the in the following, it does not test for cascades.

2.5.1) Analysis of Species-Pairs by Certainty Levels

To test for effects of trophic-level assignment ambiguity, I tested for a difference in mean species-pair correlations among high, moderate, and low certainty levels using ANOVA. This was done for both the 1 and 2 TLA data. In cases where I had to combine the moderate and low certainty to make up for insufficient data ($n \leq 10$), I used a t-test to

determine if there was a mean difference between high certainty versus moderate-low certainty mean correlations. For statistically significant ANOVA results, I used the post-hoc Tukey test to assess which mean correlations were statistically significant among the three groups.

2.5.2) Analysis of Species-Pairs by Ecosystem

Because the strength of top-down and bottom-up effects has been hypothesized to vary among ecosystem types (Shurin et al., 2006; Strong, 1992), I tested for a difference in mean species-pair (1 TLA) correlations among freshwater, terrestrial, and marine ecosystems using an ANOVA. Most of the species-pairs were from aquatic systems, but there were enough from terrestrial systems to repeat the unlinked analyses separately for aquatic versus terrestrial systems (figures 8-10). I used the post-hoc Tukey test to assess which mean correlations were significant if the overall ANOVA result was significant. I performed a t-test to test for a difference in mean correlation between terrestrial and freshwater ecosystem at 2 TLA. Marine species-pairs were excluded due to the lack of data.

2.5.3) Analysis of Time-Lagged Data

Because I predict that bottom-up effects may be lagged I tested for differences between lagged and unlagged correlations. For time-lagged data, I obtained the correlations by adding a one-year lag for the species at the lower trophic level (Predator t against Prey $t+1$). However, note that this eliminated species-pairs with only three data points prior to lagging the data. Similar statistical techniques were used as to the ones mentioned for the unlinked species-pairs; I used a Monte-Carlo simulation to test if the

difference in correlation was significant for 1 TLA and 2 TLA data, an ANOVA for comparison by certainty level, and a binomial test to assess if positive or negative correlations were more prevalent than expected by chance.

2.5.4) Analysis of Species-Pairs with Primary Producers

Because top-down and bottom-up effects may be more important at different levels of the food chain, I analyzed species-pairs including a primary producer separately from those not including a primary producer. Similar statistical techniques were used as to the ones mentioned for the unlinked species-pairs. I performed a Monte-Carlo simulation to test if the difference in correlation was significant for 1 TLA and 2 TLA data and a binomial test to assess if bottom-up or top-down was more prevalent than expected by chance. Lastly, I used t-tests to determine if there was a difference in mean correlation between the primary producers versus the non-primary producers.

2.5.5) Analysis of Species-Pairs by Strength of Correlation

I used the binomial test to test for the proportion of positive versus negative correlations after filtering the data to only include correlation of ± 0.2 , ± 0.4 , and ± 0.6 or stronger (e.g. comparing count of positive correlations that are $\geq +0.2$ relative to negative correlations that are ≤ -0.2). The randomization process for the linked triplet was carried out again after filtering the data to only include correlations with strength of ± 0.1 , ± 0.2 , and ± 0.3 , or greater (Table 5 in section 5.9). The sample sizes for correlations $\geq \pm 0.1$, $\geq \pm 0.2$ and $\geq \pm 0.3$ were 122, 67 and 39 respectively. Thus, the expected values for each triplet were 15.25 for correlations $\geq \pm 0.1$, 8.375 for correlations $\geq \pm 0.2$, and 4.875 for correlations $\geq \pm 0.3$.

3) RESULTS

3.1.1) Descriptive Statistics: All data

After data collection and cleaning I was left with 777 total time-series pairs. There were 713 pairs that were 1 TLA, 63 pairs that were 2 TLA and one 3 TLA species-pair. The average number of years in a time-series was 12 ± 7.9 years (minimum = 3, maximum = 42) (Figure 4; Appendix A1). There was no evidence of a relationship between mean correlation and the number of years in a time series ($R^2 = 0.00045$, $F(1, 775) = 0.349$, $p = 0.555$) (Figure 5). Six hundred and forty-two of the species-pairs were from US data sets (Appendix A2). There were 654 species-pairs from freshwater ecosystems, 46 from marine ecosystems, and 80 from terrestrial systems. Overall, there were 487 time-series pairs with high certainty, 251 pairs with moderate certainty, and 39 pairs with low certainty. There were 123 species-pairs with a primary producer as the “prey”.

Figure 4: The frequency of time-series pair with a certain number of years, ranging from 3 to 42 years of data.

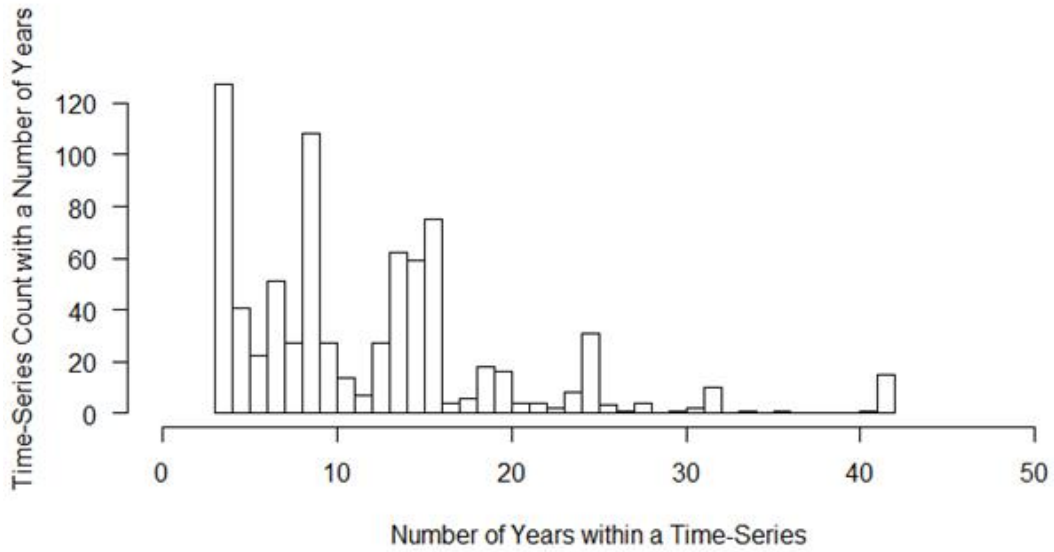
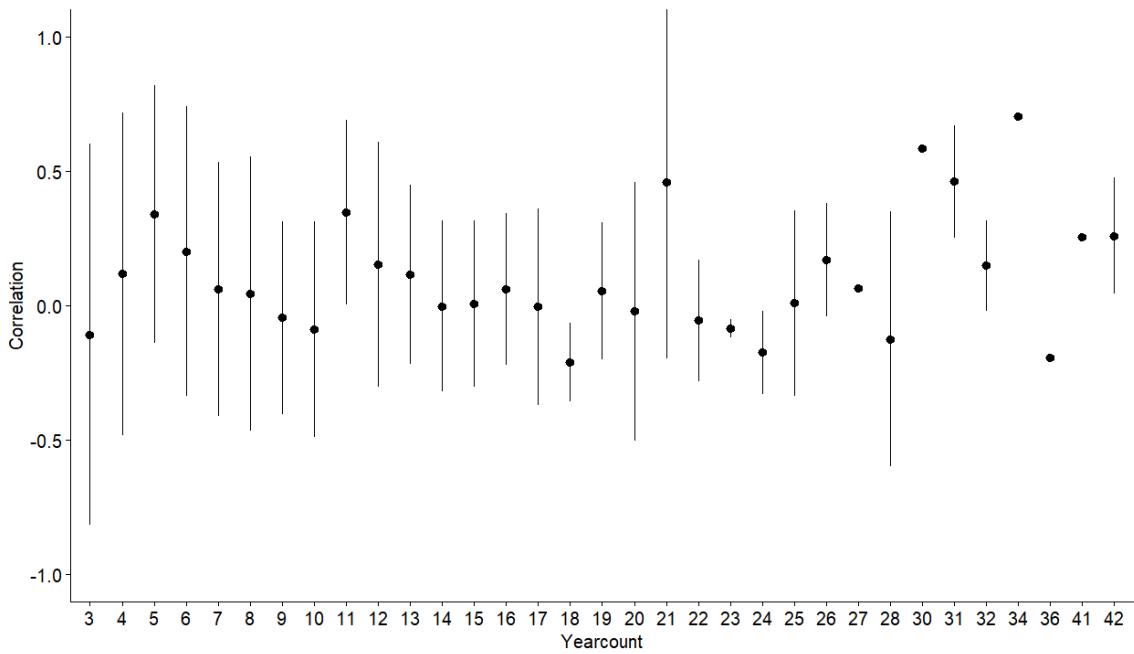


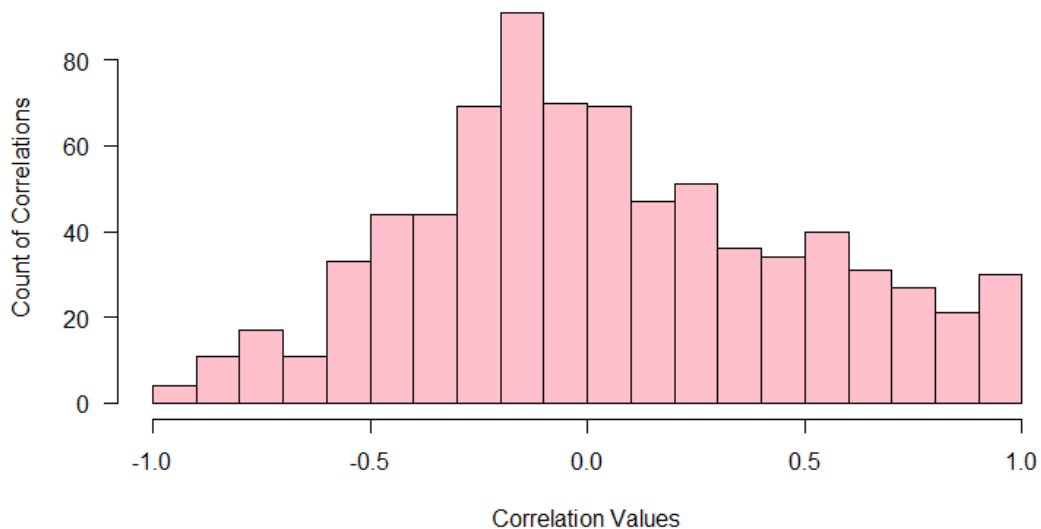
Figure 5: Mean correlation versus length of time series – All data. Mean (filled circle) and standard deviation (vertical line).



3.1.2) Unlinked Species-Pairs: All Data

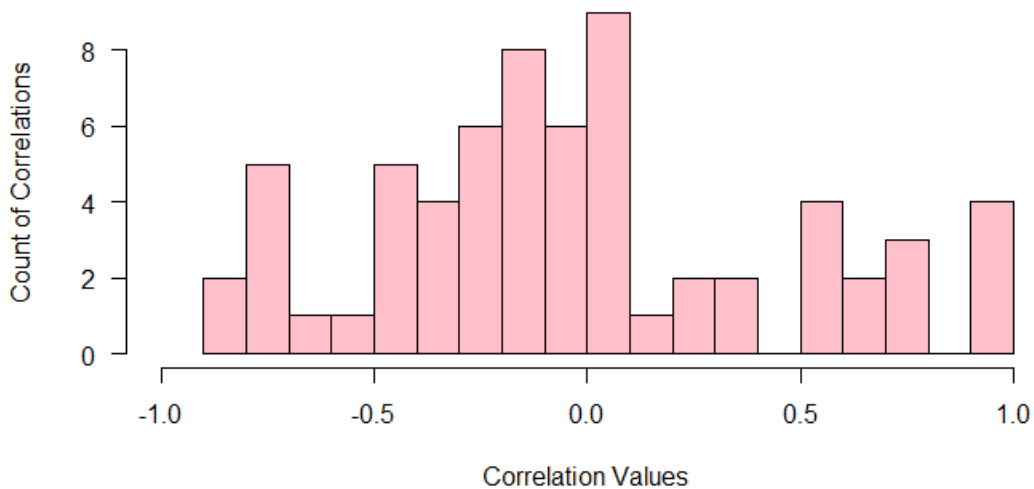
For species-pairs that were 1 TLA, the average correlation for the 713 species-pairs was 0.0575 ± 0.439 ($p < 0.01$), which was statistically significantly larger than zero, (Figure 6). The weighted average correlation was 0.0629. There were 358 positive and 352 negative correlations, which was not significantly different from the proportion expected by chance ($p = 0.851$). There was no statistically significant difference in mean correlation among high, moderate, and low certainty species pairs, $F(2,710) = 1.363$, $p = 0.257$ (Appendices B1:B5).

Figure 6: The distribution of correlations for time-series pairs one trophic level apart (n = 713).



The mean correlation for the sixty-three 2 TLA species-pairs was not statistically significantly different from zero ($r = -0.0374 \pm 0.474$; $p = 0.269$). The weighted correlation was -0.0478 . There were 26 positive correlations and 37 negative correlations (Figure 7) which was not significantly different from the proportion expected by chance ($p = 0.207$). I analyzed high certainty versus the combination of the moderate and lowest certainty due to insufficient data. There was no statistically significant difference between the high certainty data and the moderate / low certainty data ($t(1.321) = 26.293$, $p = 0.229$) (Appendix C1:C5).

Figure 7: The distribution of correlations for time-series pairs that were two trophic levels apart (n = 63).



3.1.3) Linked Species-Pairs: All Data

For the linked species-pairs, the frequency of the eight correlation combinations was different than we would have expected by chance ($p < 0.01$). However, the only

combination of correlations that was found more often than expected by chance was + AB / - AC / - BC ($p < 0.01$), which is not consistent with either top-down or bottom-up cascades (Table 4). This combination is consistent with a ‘middle’ taxon that has top-down effects on its prey and bottom-up effects on its predator. Neither of the combination of correlations expected for top-down or bottom-up cascades was found more frequently than would be expected by chance ($p = 0.323$ and $p = 0.559$, respectively).

Table 4: The frequency of observed triplet combinations. Combinations that differed significantly at $p < 0.01$ from the expected frequency are noted with **.

		n	%
Direction of correlations	+r A-B, +r A-C, +r B-C	29	12.3
	-r A-B, -r A-C, -r B-C	33	14.1
	-r A-B, +r A-C, +r B-C	13**	5.5
	+r A-B, -r A-C, +r B-C	29	12.3
	+r A-B, +r A-C, -r B-C	27	11.5
	-r A-B, -r A-C, +r B-C	20	8.5
	+r A-B, -r A-C, -r B-C	52**	22.2
	-r A-B, +r A-C, -r B-C	32	13.6
	Total	235	100

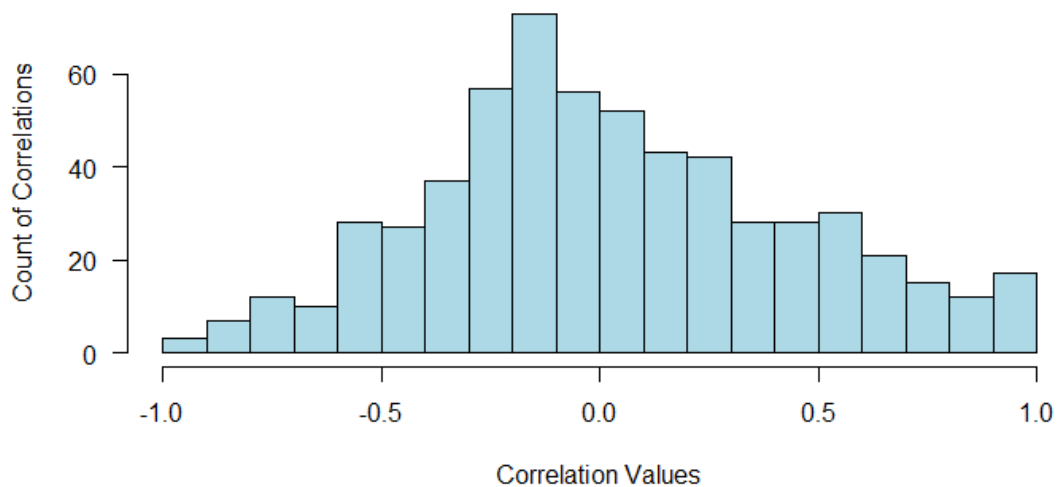
3.2) Comparison of Ecosystem Types

3.2.1) Unlinked 1 TLA Species-Pairs: Freshwater

The average correlation for the 598 freshwater species-pairs that were 1 TLA was 0.0285 ± 0.421 ($p = 0.0497$). The weighted correlation was 0.0532. There were 288 positive correlations and 307 negative correlations (Figure 8), which was not statistically

significantly different than what would be expected by chance ($p = 0.391$). There was a statistically significant difference between the three certainty categories, $F(2,595) = 4$, $p = 0.0207$ (Appendix D1:D5). The average correlations of the moderate certainty pairs ($M = 0.0941$, $SD = 0.432$) were significantly greater than the high certainty pairs ($M = -0.00511$, $SD = 0.419$), $p = 0.0188$, but not low certainty species-pairs ($M = -0.0181$, $SD = 0.320$), $p = 0.317$.

Figure 8: The distribution of correlations for freshwater time-series pairs that are 1 TLA (n = 598).

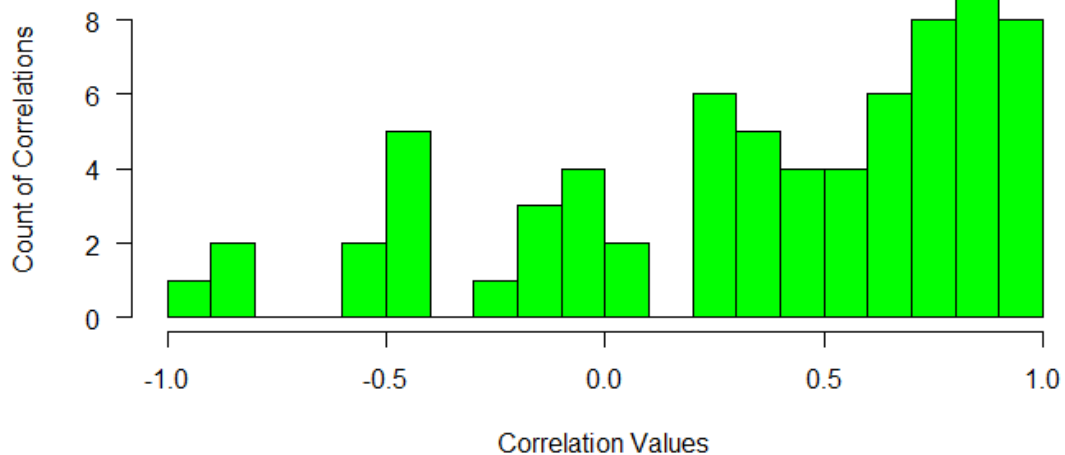


3.2.2) Unlinked 1 TLA Species-Pairs: Terrestrial

The average correlation of the 70 terrestrial time-series pairs that were one trophic level apart was 0.358 ± 0.519 ($p < 0.01$). The weighted average correlation was 0.257. There were 52 positive correlations and 18 negative correlations (Figure 9),

which was significantly different from what would be expected by chance ($p < 0.01$). I did not carry out an analysis of certainty due to the lack of moderate and low certainty species-pairs.

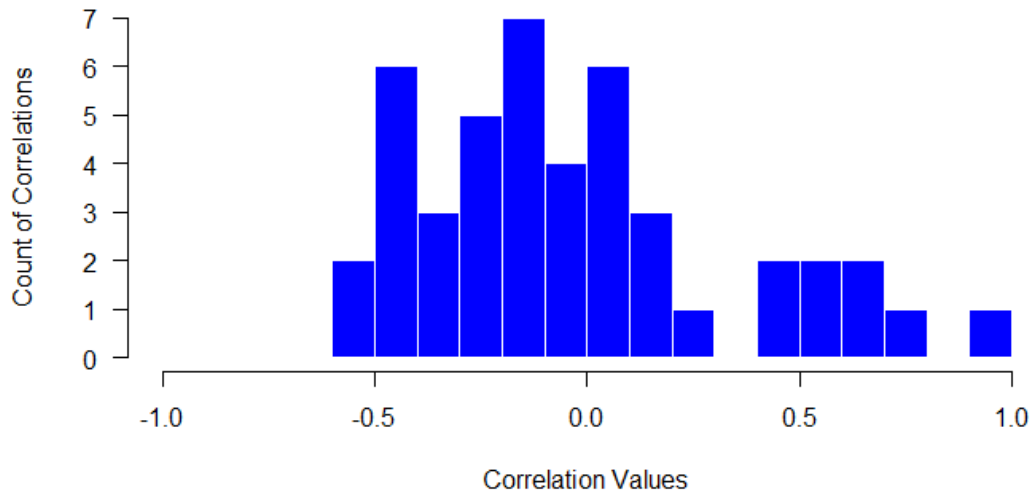
Figure 9: The distribution of correlations for terrestrial time-series pairs that are 1 TLA in trophic level (n = 70).



3.2.3) Unlinked 1 TLA Species-Pairs: Marine

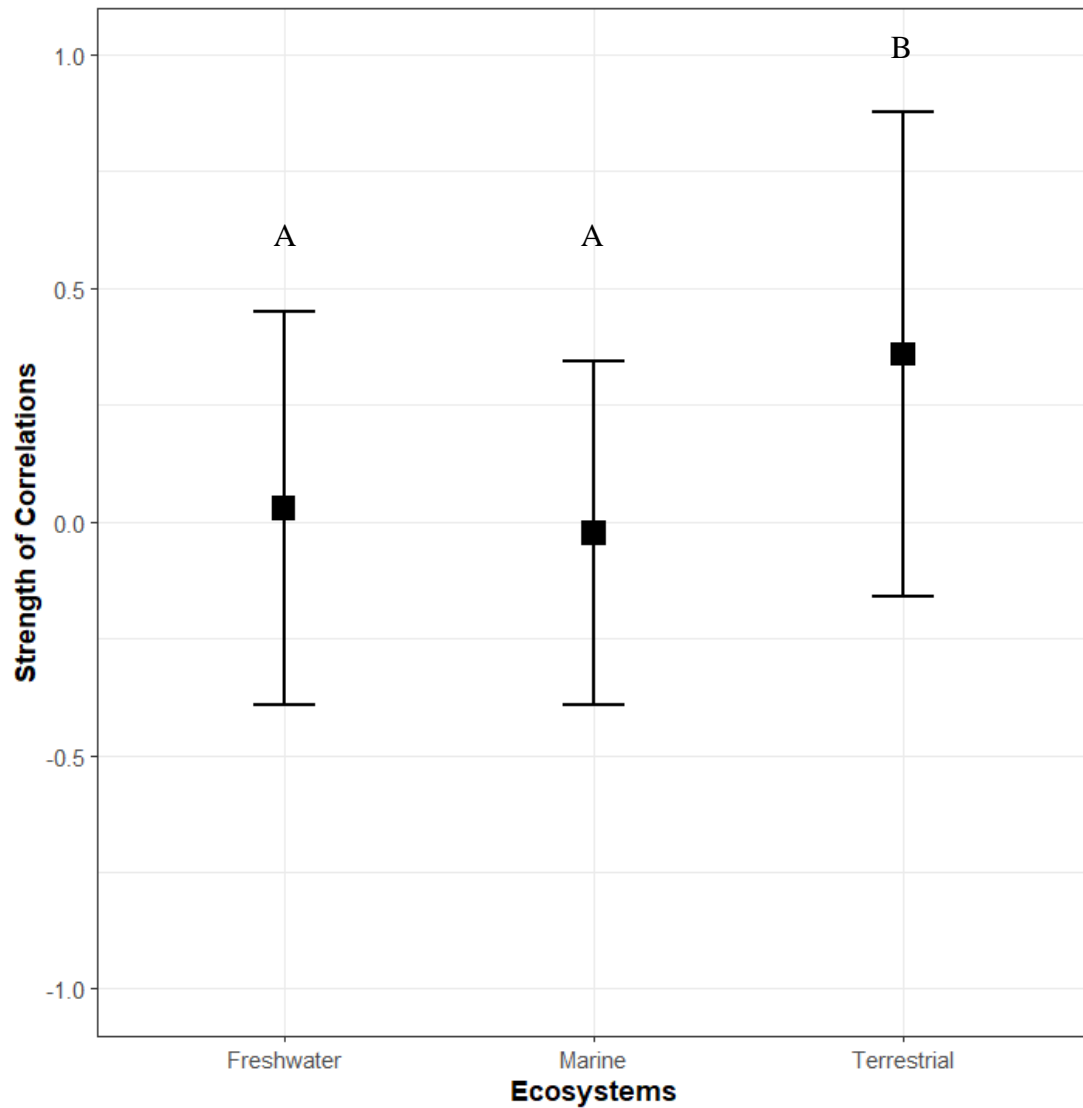
The average correlation of the 45 marine species-pairs was -0.0250 ± 0.363 ($p = 0.321$) and the weighted correlation was -0.0162 . There were 18 positive correlations and 27 negative correlations (Figure 10), which was not significantly different from that expected by chance ($p = 0.233$). I did not carry out an analysis of certainty due to the lack of moderate and low certainty species-pairs.

Figure 10: The distribution of correlations for marine time-series pairs that are 1 TLA trophic level (n = 45).



There was a statistically significant difference in average correlation among the three ecosystem types, $F(2,710) = 19.39$, $p < 0.01$. The average correlation of terrestrial ecosystems (mean $r = 0.358$, $SD = 0.519$) was significantly larger than that of marine (mean $r = -0.0242$, $SD = 0.421$), $p < 0.01$, and freshwater ecosystems (mean $r = 0.0242$, $SD = 0.367$) ecosystems, $p < 0.01$ (Figure 11, Appendix E1).

Figure 11: The mean (filled box) and standard deviation (vertical ‘whiskers’) of correlations for aquatic, terrestrial, and marine ecosystems for 1 TLA species-pairs. Letters identify statistically significant differences among groups.



3.2.4) 2 TLA Species-Pairs by Ecosystem

For the freshwater data, there were 52 species-pairs with a mean correlation of -0.0799 ± 0.472 (Appendix F1) which was not statistically significant than what was

expected by chance ($p = 0.111$). There were 20 positive correlations and 32 negative correlations which was also not a statistically significant difference ($p = 0.126$).

For the terrestrial data, there were 10 species-pairs with a mean correlation of 0.186 ± 0.471 , which was not statistically significant ($p = 0.109$). The weighted mean correlation was 0.0863. There were 6 positive correlations and 4 negative correlations (Appendix F2) which was not a statistically significant difference ($p = 0.754$). I did not carry out an analysis comparing certainty groups for terrestrial or freshwater species-pairs due to the lack of data. Likewise, I did not analyze marine 2 TLA species-pairs separately.

There was no statistically significant difference between the terrestrial and freshwater 2 TLA species-pairs, $t(1.638) = 12.727$, $p = 0.126$ (Appendix F3).

3.3) Position in Food Web

3.3.1) Unlinked 1 TLA Species-Pairs: Primary Producers

The mean correlation for the 78 species-pairs with a primary producer was -0.0383 ± 0.375 , which was not statistically significantly different than what was expected by chance ($p = 0.088$). The weighted mean correlation was -0.0479 . There were 31 positive species-pairs and 47 negative species-pairs (Appendix G1) which was not found to be a statistically significant difference ($p = 0.185$).

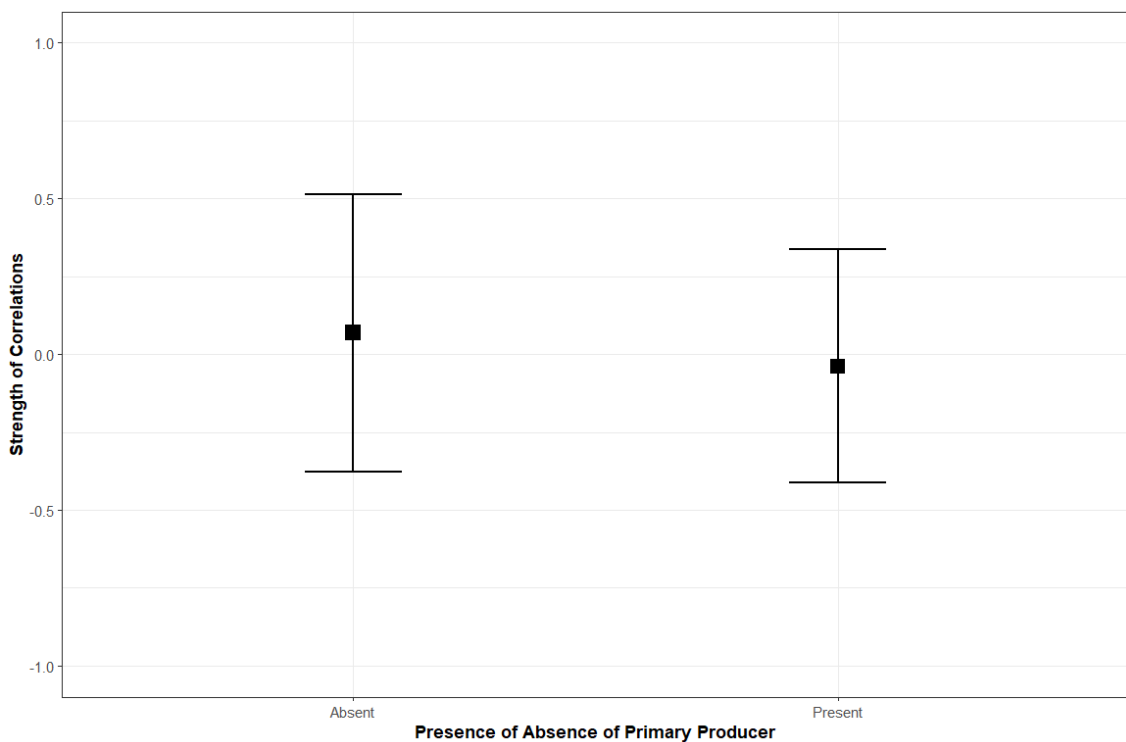
3.3.2) Unlinked 1 TLA Species-Pairs: Non-Primary Producers

The mean correlation for the 635 species pairs without a primary producer was 0.0692 ± 0.445 which was statistically different than what was expected by chance ($p < 0.01$). The weighted mean correlation was 0.0756. There were 305 positive correlations

and 330 negative correlations of the species-pairs (Appendix G2) which was not a statistically significant difference ($p = 0.341$).

The difference between the mean correlations of 1 TLA species-pairs with a primary producer (mean $r = -0.0383$, $SD = 0.375$) versus without a primary producer (mean $r = 0.0692$, $SD = 0.445$) at low trophic level was statistically significant, $p = 0.0213$ (Figure 12; Appendix G3).

Figure 12: The mean (filled box) and standard deviation (vertical ‘whiskers’) of correlations of species-pairs that were 1 TLA with and without a primary producer present.



3.3.3) Unlinked 2 TLA Species-Pairs: Primary Producers

The mean correlation for the 45 species-pairs with a primary producer was -0.0791 ± 0.483 , which was not statistically significant ($p = 0.142$). The weighted mean correlation was -0.0728 . There were 18 positive correlations and 27 negative correlations (Appendix G4) which was not found to be statistically significant ($p = 0.233$).

3.3.4) Unlinked 2 TLA Species-Pairs: Non-Primary Producers

The mean correlation for the 18 species-pairs without a primary producer was 0.0670 ± 0.448 , which was not statistically significant ($p = 0.264$). The weighted mean correlation was -0.0179 . There were 8 positive correlations and 10 negative correlations (Appendix G5) which was not found to be statistically significant ($p = 0.814$).

The difference between the mean correlations of 2 TLA species-pairs with and without a primary producer at low trophic level was not statistically significant, $t(1.143) = 33.617$, $p = 0.261$ (Appendix G6).

3.4) Lagged Analyses

3.4.1) Unlinked 1 TLA Species-Pairs

The mean correlation for the 698 1 TLA time-lagged species-pairs was -0.00665 ± 0.459 which was not found to be statistically significant ($p = 0.352$). There were 304 positive correlations and 394 negative correlations ($p < 0.01$). There was no significant difference among certainty categories ($F(2,695) = 0.89$, $p = 0.411$) (Appendix H1).

3.4.2) Unlinked 2 TLA Species-Pairs

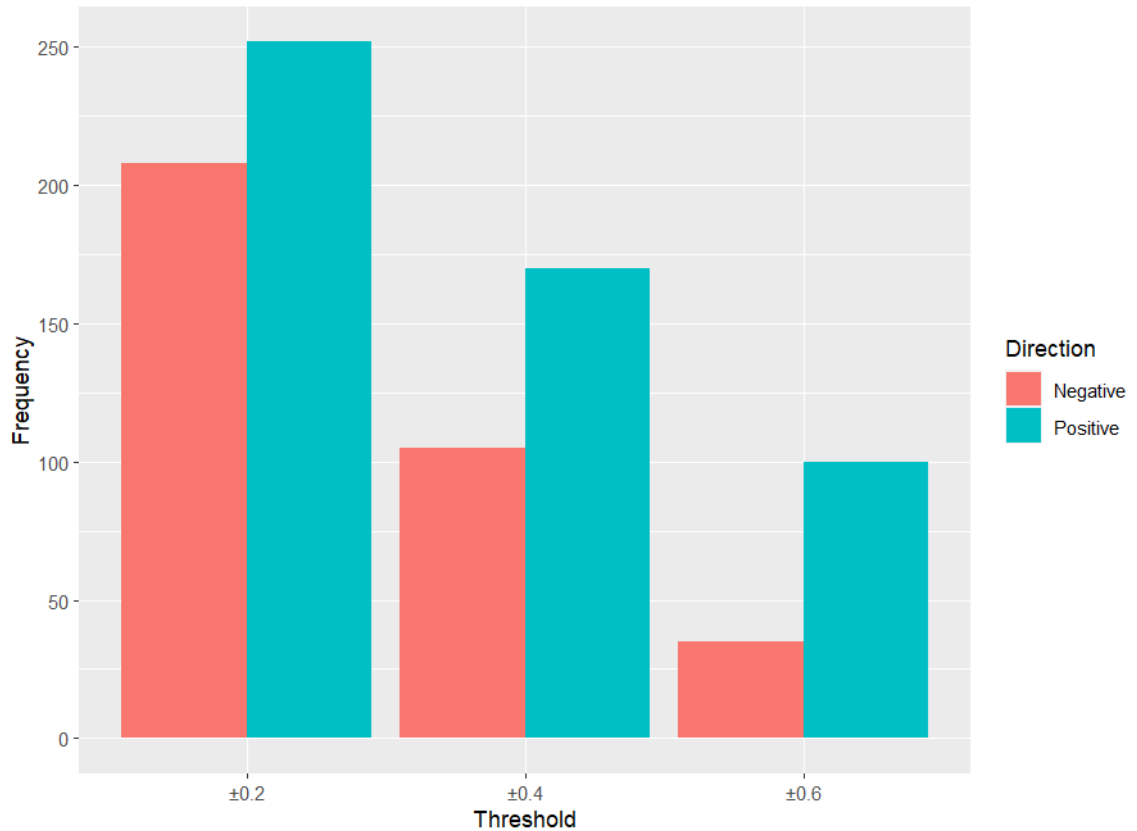
The mean correlation of time-lagged species-pairs two trophic levels apart was -0.0606 ± 0.477 ($p = 0.160$). There were 25 positive correlations and 39 negative correlations ($p = 0.103$). There was a no statistically significant difference between species-pairs of the two certainty categories, $p = 0.245$ (Appendix H2).

3.5) Correlation Strength

3.5.1) Correlation Thresholds of 0.2, 0.4 and 0.6 for 1 TLA Species-Pairs

There were 252 species-pairs with correlations $\geq +0.2$ and 208 species-pairs with negative correlations ≤ -0.2 , 170 species-pairs with correlations $\geq +0.4$ and 105 species-pairs with negative correlations ≤ -0.4 and 100 species-pairs with correlations $\geq +0.6$ and 35 species-pairs with negative correlations ≤ -0.6 . For each of the three thresholds the proportion of negative and positive correlations was significantly different from that expected by chance ($p = 0.0449$; $p < 0.01$; $p < 0.01$ respectively). The relative frequency of positive correlations increased with the threshold size, demonstrating that the positive tail is heavier than the negative tail (Figure 13).

Figure 13: The number of positive and negative correlations of species-pairs that were 1 TLA at thresholds of correlations $\geq \pm 0.2$, ± 0.4 , and ± 0.6 .



3.5.2) Correlation Thresholds of 0.2, 0.4 and 0.6 for 2 TLA Species-Pairs

There were 16 species-pairs with correlations $\geq +0.2$ and 24 species-pairs with negative correlations ≤ -0.2 , 12 species-pairs with correlations $\geq +0.4$ and 14 species-pairs with negative correlations ≤ -0.4 and 8 species-pairs with correlations $\geq +0.6$ and 8 species-pairs with negative correlations ≤ -0.6 . The proportion of negative and positive correlations was not statistically significantly different from that expected by chance, ($p = 0.268$; $p = 0.846$; $p = 1$, respectively) (Appendix I1).

3.5.3) Correlation Thresholds of 0.1, 0.2 and 0.3 for Linked Triplets

For the linked species-pairs with correlations at all thresholds ($\geq \pm 0.1$, $\geq \pm 0.2$, and $\geq \pm 0.3$), the frequency of the eight correlation combinations was different than we would have expected by chance ($p < 0.01$, $p < 0.01$, and $p = 0.019$ respectively). The only combination of correlations that was found more often than expected by chance was + AB / - AC / - BC at all thresholds ($p < 0.01$, $p < 0.01$ and $p = 0.027$, respectively), which was not consistent with either top-down or bottom-up cascades (Table 5). The triplet combinations for top-down and bottom-up cascades were not found to be statistically significant ($p = 0.117$, $p = 0.205$, and $p = 0.196$; $p = 0.77$, $p = 0.473$, and $p = 0.205$ for top-down and bottom-up, respectively) for any of the correlation thresholds.

Table 5: The frequency of observed triplet combinations at thresholds for correlations stronger than or equal to ± 0.1 , ± 0.2 , and ± 0.3 . Combinations that differed significantly at $p < 0.05$ from the expected frequency are noted with *, and $p < 0.01$ are denoted with **.

Direction of correlations	$r \geq \pm 0.1$		$r \geq \pm 0.2$		$r \geq \pm 0.3$	
	n	%	n	%	n	%
+r A-B, +r A-C, +r B-C	13	10.7	9	13.4	7	18
-r A-B, -r A-C, -r B-C	13	10.7	3	4.5	2	5.1
-r A-B, +r A-C, +r B-C	5*	4.1	3	4.5	0*	0
+r A-B, -r A-C, +r B-C	15	12.3	11	16.4	5	12.8
+r A-B, +r A-C, -r B-C	12	9.8	6	9	4	10.3
-r A-B, -r A-C, +r B-C	7	5.7	3	4.5	2	5.1
+r A-B, -r A-C, -r B-C	37**	30.3	21**	31.3	12*	30.8
-r A-B, +r A-C, -r B-C	20	16.4	11	16.4	7	17.9
Total	122		67		39	

Table 6: Summary of key findings from my analysis.

Section	Key Findings
Unlinked Species-Pairs from Overall Data (3.1)	<ul style="list-style-type: none"> • Statistically significant positive mean correlation for 1 TLA species-pairs, but no evidence of positive or negative correlations being more common than the other for 1 TLA species-pairs. • Mean correlation of 2 TLA species-pairs were not statistically significant and no evidence of positive or negative correlations being more common than the other for 2 TLA species-pairs.
Linked Species-Pairs from Overall Data (3.1)	<ul style="list-style-type: none"> • I observed 32 top-down (-/+/-) triplets and 29 bottom-up (+/+/) triplets; both were not statistically significantly more frequent than would be expected by chance. • The +/-/- triplet was observed 52 times, which was statistically significantly more than would be expected by chance. • Including only linked triplets where each of the three species-pairs had relatively strong correlations did not change my conclusions
Unlinked Species-Pairs by Ecosystem Type (3.2)	<ul style="list-style-type: none"> • The mean correlation for species-pairs that were 1 TLA was statistically significantly larger for terrestrial species-pairs than for either freshwater or marine species-pairs. • The mean correlation for 2 TLA species-pairs were not statistically significantly different across ecosystem types.
Unlinked Species-Pairs with and without a primary producer (3.3)	<ul style="list-style-type: none"> • The mean correlation for species-pairs that were 1 TLA was statistically significantly larger for pairs without a primary producer than for pairs with a primary producer
Species-Pairs by Certainty (3.1 – 3.3)	<ul style="list-style-type: none"> • There was no statistically significant difference in mean correlations among certainty levels except that for freshwater species-pairs that were 1 TLA the moderate certainty species-pairs had a larger mean correlation than either the high certainty or low certainty species-pairs. However, this did not affect my conclusions.

4) DISCUSSION

My key findings were (1) there was no evidence of trophic cascades in these natural systems, (2) there was weak evidence for bottom-up effects between taxa one trophic level apart and (3) the evidence for bottom-up effects between adjacent taxa was stronger for terrestrial species-pairs than aquatic species-pairs. It was also weaker for herbivore – primary producer pairs than species-pairs higher in the food web. There was no effect of a one-year time lag.

4.1) Trophic Cascades Summary

I found no evidence of trophic cascades ($n = 235$). If cascades were common or strong, I would have expected the negative effects of predation on prey abundance to reverberate to taxa two trophic levels beneath the predator or the positive effects of prey abundance to cascade to taxa two trophic levels above the prey. That is, in a 3-species top-down cascade we would observe negative correlations in abundance between A-B and B-C species pairs and a positive correlation in abundance between the A-C species pairs. By contrast, in a 3-species bottom-up cascade we would observe positive correlations between all three species pairs. I did not observe these combinations more often than one would expect by chance. Furthermore, for both top-down and bottom-up cascades I would expect correlations between species two trophic levels apart to be predominately positive and they were not.

4.2) Evidence for Cascades in Literature

Top-down trophic cascades are widely accepted by ecologists to be a prominent driver of changes in species' abundance (Baum & Worm, 2009; Ripple et al., 2016; Strong, 1992). Ellis et al. (2011) found that the introduction of a zooplanktivorous opossum shrimp *Mysis diluviana* altered the zooplankton community from large to smaller sizes, which in turn affected the grazing efficiency on phytoplankton. This effect resulted in increased primary production after the introduction of opossum shrimp *Mysis diluviana*, supporting a top-down cascade. Shurin et al. (2002) found a similar result - that predators had a strong effect on plants by eating the herbivores, and this was stronger in aquatic systems relative to terrestrial systems. Tronstad et al. (2010) also found evidence in favour of top-down trophic cascades; the introduction of lake trout *Salvelinus namaycush* resulted in decreased abundance and increased mean body size of Yellowstone cutthroat trout *Oncorhynchus clarkii bouvieri*, which in turn increased the abundance of zooplankton leading to a decrease in phytoplankton biomass. Meta-analyses of freshwater food webs have also found support for top-down trophic cascades; Brett & Goldman (1996) found that in 54 freshwater experimental studies examining interactions among zooplanktivorous fish, zooplankton, and phytoplankton, the presence of fish resulted in increased phytoplankton biomass due to the decreased zooplankton biomass. In addition, a review done by Pace et al. (1999) noted that top-down trophic cascades are ubiquitous, occurring not only in terrestrial and aquatic ecosystems, but also in microbial communities.

There are also studies that have found bottom-up effects to be common and / or strong. In freshwater systems, Li et al. (2015) found that increased nutrients were able to

induce a bottom-up cascade on phytoplankton and zooplankton. Similarly, Du et al. (2015) discovered that elevated nutrients in the Yangtze River increased the biomass of phytoplankton, rotifers, and planktivorous fish, consistent with a bottom-up trophic cascade. Terrestrial systems were also reported to experience bottom-up cascades in response to the presence or absence of fertilization; Gruner (2004) found that the tri-trophic relationship between plant *M. polymorpha*, herbivorous insects, and birds was influenced more by bottom-up than by top-down effects. Likewise, Dickson and Whitham (1996) found support for bottom-up effects among cottonwood trees, aphids, and birds.

Most of the research that contradicts my findings is from systems that were manipulated experimentally. For example, from 67 studies that have involved manipulation of carnivores, Romero & Koricheva (2011) found that carnivores increased plant fitness by suppressing herbivores and found that carnivores were also capable of decreasing fitness of plants by consuming pollinators. Bell et al. (2003) analyzed 90 top-down trophic cascade experiments involving fish-zooplankton-phytoplankton and found that not only do top-down cascades occur in most studies, but the effect does not decline over time. Similarly, Brett and Goldman (1996) analyzed 54 freshwater experiments involving fish-zooplankton-phytoplankton tri-trophic systems and found that phytoplankton biomass increased in the presence of fish. Lastly, a meta-analysis performed by Vidal and Murphy (2018) found that top-down forces were significantly stronger than bottom-up forces for birds-insects-plants interactions as birds increased plant quality by reducing insect abundance.

Although my results are inconsistent with many examples from the ecological literature, there are studies that also did not find support for trophic cascades. For example, Mikola and Setälä (1998) tested for the presence of trophic cascades across leaf litter, bacteria, and bacterivorous nematode, but were not able to detect either a top-down or a bottom-up cascade in their system. Malakhoff & Miller (2021) were also unable to find trophic cascades in the tri-trophic relationship among kelp, sea urchin, and sea stars.

4.3) Explanations for Lack of Trophic Cascades

4.3.1) Experimental versus Observational Studies

A possible explanation for the discrepancy between manipulation and observation studies is that cascading effects are obscured by the effects of other drivers of abundance embedded in natural systems (Bell et al., 2003; Romero & Koricheva, 2011; Vidal and Murphy, 2018). However, the lack of generalizability from experiments to nature is not a novel issue in ecology. For example, Major and Kendal (1996) found there was poor correspondence between the results of ~80 artificial bird nest studies to natural nests that it was emulating. Researchers have attempted to develop experimental designs to better reflect natural systems, but there is an inherent trade-off between controlled manipulations and realism (Moore & Robinson, 2004; Roe & Just, 2009). Thus, the difference between the results from my study relative to experimental manipulation studies could be caused by the trade-off between controlled experiments and the ‘noisy’ realism of observational studies.

4.3.2) Species Diversity dampens Cascades

I may not have detected trophic cascades in my data because diverse communities of predators and plants are known to dampen the effects of trophic cascades (Finke & Denno, 2004; Scherber et al., 2010; Schmitz et al., 2000). Natural food webs are often quite complex, and this may make such systems relatively stable. In other words, diverse natural systems could be unresponsive to minor changes at the top or bottom of food webs (Ripple et al., 2016). In addition, Finke & Denno (2004) demonstrated that increasing the diversity of arthropod predators diminished their impact on herbivores, thus dampening the top-down trophic cascade from arthropod predators to the primary producers. I did not measure predator or prey diversity so do not know what proportion of species-pairs in my data are from diverse systems. However, it is unlikely that all interacting species were censused. Because my data are only a subset of all interacting organisms, they may not capture the taxa that are the key drivers of trophic cascades. However, one would expect that in systems where trophic cascades are common or strong, a random sample of interacting organisms would detect those cascades.

4.3.3) Omnivory dampens Trophic Cascades

Many studies have found omnivory is capable of dampening trophic cascades. Species capable of feeding across trophic levels create ambiguity in the flow of energy in an ecosystem, (Benkendorf & Whiteman, 2021; Compte et al., 2012; Johnson et al., 2014). This dampening effect occurs because if predators are having direct effects on the prey of their prey, the indirect effects will be more difficult to detect. Many species in my dataset have been found to be capable of feeding across one or more trophic levels.

Therefore, it is plausible for omnivory to be a factor that resulted in my failure to detect trophic cascades.

4.3.4) Oscillating Dynamics

A plausible explanation for the lack of detectable trophic cascades in my study is oscillating predator-prey dynamics. Oscillating population dynamics cause fluctuations of predator and prey populations to be out of phase, typically with the prey population lagging behind the predator population (Smith & Smith, 2015). To observe alternation of bottom-up and top-down, predator-prey populations must be slightly out of phase (Benincà et al., 2009). For example, models with a quarter-delay or three-quarter delay of the prey population relative to the predator population demonstrate fluctuations involving alternation of top-down and bottom-up effects. Benincà et al. (2009) noted that coupled predator-prey systems in nature typically demonstrate these kinds of oscillating dynamics. If the nature of a trophic cascade is periodic and non-linear, it may make cascading effects difficult to detect because top-down and bottom-up effects alternate in importance over time so that the ‘mean’ effect is close to zero.

4.3.5) Dispersal Dampens Trophic Cascades

Howeth and Leibold (2008) found that trophic cascades were dampened in communities with high dispersal as compared to those with little or no dispersal. This is because dispersal increased grazer biomass independent of predator abundance. In comparison, closed communities will allow for top-down cascades to occur from increased fish abundance to reduced zooplankton to increased phytoplankton abundance. Most of my species-pairs were from freshwater systems where dispersal would have been

variable but occurring. I was unable to quantify dispersal in these systems. Dispersal remains a plausible explanation for the lack of evidence of trophic cascades in my data.

4.3.6) Variability in Predator Abundance

As noted by Ripple et al. (2016), while trophic cascades are important in determining the distribution and abundance of species, they will be undetectable when there are no changes to the predators; only by perturbing the predator abundance will the consequences of trophic cascade be seen. By analogy, in natural systems top-down effects will only be detectable when there is variation in predator abundance over time. There was variation in predator abundance across all species-pairs, but I have not examined the relationship between the magnitude of variation in predator abundance and evidence of top-down effects. It is plausible that top-down effects will be difficult to detect below some threshold of predator variability and thus, top-down effects may be difficult to detect across many species-pairs in natural systems.

4.3.7) Measurement Error masking Trophic Cascades

Perhaps the simplest explanation for my inability to detect cascading effects is measurement error. For example, researchers have used aerial counts to estimate population sizes of elephants, giraffes, and zebras, but they underestimate abundance due to a combination of foliage, topography, and variation in the distribution of a target population (Eikelboom et al., 2019; Jachmann, 2001). Beyond ecosystem-specific problems, Elphick (2008) noted issues associated with population sampling which included compromised availability (e.g. individuals not present for detection), compromised detection (e.g. missing detectable individuals, individuals imaged), or

compromised counting (e.g. misidentification, counting errors despite detection).

Counting errors can also occur when estimating a population through samples of plankton as demonstrated by Heyman et al. (1982). An additional form of ‘measurement’ error is a mismatch between the scale at which organisms are sampled and the scale at which they interact. Such spatial variation can also lead to measurement error if the individuals of interest are not present within the sampled area (Elphick, 2008; Power, 1992). Thus, measurement error remains a plausible explanation for my inability to detect trophic cascades.

Many of the caveats described above are caused by searching for evidence in ‘noisy’ natural versus ‘controlled’ experimental systems. Thus, the absence of detectable top-down trophic cascades does not imply that top-down trophic cascades do not exist in natural systems, but it does suggest that top-down trophic cascades may be a minor factor relative to other drivers of predator and prey abundance.

4.4) Evidence of Bottom-Up effects between Adjacent Taxa

Despite finding no evidence of trophic cascades, I found support of a weak positive correlation between taxa one trophic level apart. This is consistent with the occurrence of bottom-up effects between taxa at adjacent trophic levels, which have been reported for zooplankton-phytoplankton pairs in several studies (Carney & Elser, 1990; Gamito et al., 2019; Silvia et al., 2019). In addition, Hoover et al. (2006) found that the addition of macronutrients nitrite and nitrate resulted in the blooming of phytoplankton which in turn increased zooplankton growth, supporting a bottom-up effect between adjacent pairs of species. In terrestrial systems, Karr et al. (1992) found that the decline

of flying insects was a predictor in the decline of birds, supporting bottom-up between insects and birds. Similarly, Price & Hunter (2005) found that when precipitation promoted willow growth there was higher reproduction of sawflies, a consumer of willows.

However, there are several explanations for positive correlations between taxa at adjacent trophic levels other than bottom-up effects. A positive correlation between two species can be caused by any common or similar response to a third factor. For example, droughts are known to contribute to the decline of most or all species in ecosystems which will lead to positive correlations among most species-pairs (Machado-Silva et al., 2021; Tyree et al., 1994). Similarly, the exposure to a contaminant such as a heavy metal may cause declines of populations of all species in an ecosystem (Ali et al., 2014; Ebrahimi & Taherianfard, 2011; Kerrison et al., 1988). This would cause all species to co-vary positively in response to heavy metal fluctuations and provide evidentiary support for bottom-up effects even though they were not occurring. It is also possible that the observed correlation between two species is because both are resources for a third species. For example, bears eat ungulates and berries (i.e. ungulate food), and can cause a positive correlation between ungulate and berry abundance that is not caused by an interaction between ungulates and berries (Bastille-Rousseau et al., 2011; Mattson, 1997; Ripple et al., 2014). Thus, while a positive mean correlation is consistent with bottom-up effects it is also consistent with several other plausible processes and so should be seen as weak and inconclusive evidence that bottom-up effects are stronger than top-down effects in natural systems.

4.5) Evidence of Top-Down effects between Adjacent Taxa

However, there are also many ecological studies showing top-down effect between adjacent species in trophic level. For example, Hoover et al. (2006) noted that following the bloom of both zooplankton and phytoplankton, they observed strong top-down control of phytoplankton by the zooplankton. Likewise, Olli et al. (2007) noted that phytoplankton experienced strong grazing pressure by the zooplankton community in the Arctic Ocean. In terrestrial systems, Rogers et al. (2012) found that birds could exert strong top-down effects on spiders, and the decline of birds resulted in larger spider webs being formed independent of the season. Carson and Root (1999) also found support of top-down effect of herbivorous insects on plant biomass.

In my data, there was a similar proportion of negative correlations as positive correlations between species one trophic level apart. A superficially reasonable explanation for this pattern is that half of these systems are governed by top-down effects and the other half by bottom-up effects. However, that explanation implies a bimodal distribution of correlations rather than the unimodal distribution centered on a small positive value, which I found. So, I have chosen to treat the equal proportion of positive and negative correlations as evidence for neither top-down nor bottom-up effects. However, it is possible that some of these negative correlations are caused by top-down effects.

4.6) Freshwater versus Terrestrial Systems

Though neither freshwater nor terrestrial systems showed evidence of cascades, the strength of bottom-up effects between species at adjacent trophic levels was much stronger in terrestrial than freshwater systems. While there has been little discussion in

the ecological literature of bottom-up effects being stronger in terrestrial systems than aquatic, there has been much discussion of top-down effects being stronger in aquatic than terrestrial systems. Shurin et al. (2006) noted that top-down effects were weaker in terrestrial than in freshwater systems because autotrophs in aquatic ecosystems are typically smaller than the herbivores, but autotrophs in terrestrial ecosystems can be larger or smaller than the herbivores that target it. The size difference is important as top-down effects were greatest when the ratio of consumer-to-producer size was highest, so freshwater herbivores should have stronger top-down effects than terrestrial herbivores as aquatic herbivores are consistently larger than their algal resource. It was also demonstrated that spatially confined consumers can have stronger top-down effects than ecosystems supporting wider ranging organisms (McCann et al., 2005). The last explanation provided by Shurin et al. (2006) for why top-down effects were stronger in freshwater versus terrestrial systems is the impediment to the vertical flow of energy in terrestrial systems. Furthermore, terrestrial plants could be better defended than freshwater primary producers (Strong, 1992) likely due to loss of biomass being more costly in terrestrial than freshwater systems, as freshwater autotrophs are typically replaced more quickly than autotrophs in terrestrial systems (Shurin et al., 2006). If top-down effects might, in the aggregate, obscure bottom-up effects then we would expect that bottom-up effects would be more easily detected in terrestrial systems. This may explain why I found stronger evidence for bottom-up effects in terrestrial systems than in aquatic systems.

Despite assertions that top-down effects were weaker in terrestrial systems, there are several notable contradictory examples (Chase, 1998; Letourneau & Dyer, 1998;

Moran & Hurd, 1997). McLaren & Peterson (1994) showed a positive response in tree growth to wolf predation on moose. Top-down cascades were also detected in the tri-trophic relationship between spiders-insects-soybeans, in which soybean leaf damage declined with increasing spider density (Carter & Rypstra, 1995). By contrast, numerous studies have also found terrestrial ecosystems dominated by bottom-up forces. For example, Elmhagen and Rushton (2007) found that improving habitat quality via expansion in agricultural activity positively impacted red foxes. Scherber et al. (2010) in particular found no evidence of top-down control of carnivores on herbivores, rather higher plant diversity had bottom-up effects on the higher trophic levels. Sánchez-Piñero and Polis (2000) found that seabirds are responsible for incurring a bottom-up effect by importing organic material and nutrients from the ocean onto islands. Thus, there is evidence in the literature that supports top-down effects in terrestrial systems despite explanations that suggest top-down effects will be weaker in such systems.

Bottom-up effects have also frequently been observed in freshwater systems. For example, Li et al. (2020) demonstrated that phytoplankton had a statistically significant bottom-up effect on zooplankton. Similar findings were reported by Finlay et al. (2007), where the increased nutrients had a greater effect on zooplankton abundance than predation by fish. Lastly, Yoshida et al. (2003) also found that the impact of nutrients on rotifer abundance was much greater than the abundance of zooplankton that predate the rotifers.

4.7) Cascade-Blocking Species

Although my study did not find evidence of trophic cascades there was evidence suggesting the existence of “cascade blockers”. The combination of correlations in my 3-species chains that was most frequent and more common than expected by chance, was a combination with the ‘middle’ species having a negative effect on the taxon below it and a positive effect on the taxon above it. That is, a species that both drives the abundance of species below it by predation and species above it as a resource. Species that play important roles as both predator and prey prevent cascades in either direction by ‘blocking’ changes in their prey abundance from cascading upwards (because they are a key driver of any changes in abundance of the prey) and preventing changes in their predator abundance from cascading downwards (because they are the key driver of changes in abundance of their predator).

The possibility of a trophic cascade blocker has been noted by Li et al. (2020), but their definition of ‘blocking’ referred only to blocking top-down cascades. Here, I am referring to ‘middle’ species that prevent the transfer of energy across more than one trophic level because they control the abundance of their prey and their predator. Many taxa have been identified as both prey and predator. For example, spiders trap and eat insects but are captured and eaten by birds or reptiles (Carter & Rypstra, 1995; Dickson & Whitham, 1996; Karr et al., 1992); carnivorous zooplankton both eat herbivorous zooplankton and are eaten by planktivorous fish (Brett & Goldman, 1996; Ellis et al., 2011; Tronstad et al., 2010); browsing ungulates both consume plants and are eaten by large carnivores (Flagel et al., 2016; Martin et al., 2020; Ripple et al., 2014). However, the role of intermediate consumers such as spiders, carnivorous zooplankton or deer and

moose has been predominately viewed through the lens of top-down trophic cascades. That is, ecologists have asked “does the top-down effect of a predator on an intermediate consumer ‘cascade’ to the prey of the intermediate consumer?”. The assumption is that if the negative top-down effects due to the top predator or the bottom-up effects of primary producers are strong enough, we should see a cascading effect (Du et al., 2015; Ripple et al., 2016; Vidal & Murphy, 2018). However, what if the intermediate consumer has a bottom-up effect on its predators and a top-down effect on its prey? When that is true, cascades will be blocked in both directions. Top predators have generally been identified as ‘keystone’ species because of their putative ability to cause changes in abundances of species at lower trophic levels (Elmhagen & Rushton, 2007; Prugh et al., 2009; Ripple et al., 2016). However, the concept of cascade ‘blockers’ suggest that intermediate consumers may play important ‘keystone’ roles by preventing cascades within food webs. I have not seen the concept of a cascade ‘blocker’ explicitly addressed in the ecological literature. The importance of intermediate consumers may have received little attention in the ecological literature because there has been little reason to expect that a species is likely to have both top-down and bottom-up effects.

My results may be a statistical anomaly and not representative of what happens commonly in natural ecosystems. As mentioned in section 6.5, there are numerous alternative explanations that could explain my results. However, if intermediate consumers commonly drive the abundance of both their predators and prey then their role in natural food webs deserves much greater attention.

4.8) Limitations of the Study

There are several reasons why I might not have detected trophic cascades in my data even though they were occurring in ecosystems (see section 4.3). In addition, uncertainty around assigning trophic levels to individual species may have led to mistakes in assigning “trophic levels apart” to species-pairs. To mitigate those concerns, I assigned ‘certainty’ levels to trophic level apart assignments. I found no difference in mean correlation among certainty levels except for freshwater species-pairs one trophic level apart. My conclusion for the freshwater data if I had used only the high certainty species-pairs would have been that, rather than a borderline statistically significant positive mean correlation, there would have been no evidence that the mean correlation was significantly different from zero. However, this would not have changed my key findings.

My study also assumes that all species-pairs are equally efficient at harvesting energy from their prey or the primary producers (Power, 1992). If that is not true, then it may be a much smaller subset of species-pairs that are driving top-down cascades than the entire set of 777 species-pairs that I used. The effects of this smaller subset of species-pairs are unlikely to be detected because they are included with a large group of species-pairs who have small or no effects on taxa beneath them in the food web. To mitigate the effects of including species-pairs experiencing weak or no interactions I analyzed subsets of the data that only included time series showing strong correlations. I was able to explore the idea that time series showing weak (and potentially random) correlations might obscure ‘true’ effects, but there was no evidence of such a bias.

4.9) Implications and Future Directions

Top-down trophic cascades have practical applications, notably as a strategy for managing eutrophic aquatic systems. Eutrophication is the promotion of plant and algal growth in oceans, lakes and rivers that can eventually lead to a decline of oxygen in the water, typically due to the runoff of nutrients such as phosphorus or due to reduced herbivore density (Khan & Ansari 2005). Gerke et al. (2021) reported success in mitigating the effects of eutrophication using herbivorous and omnivorous fish. Carpenter (1989) suggested that as manipulation of primary productivity in whole-lake experiments can influence piscivore biomass (and vice versa) will eventually lead to detectable ecosystem responses. In addition, Carpenter and Kitchell (1988) found that fish manipulation in whole-lake experiments produced responses in phytoplankton via indirect responses although the effects were very variable. By contrast, Östman et al. (2016) specified that overabundance of mesopredators were capable of doubling algae biomass, emphasizing that the complexity of top-down effects may limit practical applications. Thus, trophic cascades have been used to help with ecosystem recover from eutrophication typically by manipulating species.

Trophic cascades have been proposed to be a potential solution for the issue of mesopredator release. Mesopredator release, or the expansion in density or distribution of a middle-ranking predator due to the decline or removal of a top predator, has been a rising concern and been proposed as the explanation for decline in species such as reproductive failure in birds and loss of crops from baboon release (Brashares et al., 2010; Crooks & Soulé, 1999; Hill, 2000). Researchers have suggested the application of trophic theory to reverse or prevent mesopredator release (Prugh et al., 2009; Terborgh et

al., 1997). For example, Krofel et al. (2017) proposed the use of apex predators in reducing mesopredator abundance to maintain or restore an ecosystem. Therefore, the application of trophic cascade has been floated by researchers to manage impacted ecosystems.

However, my study fails to present evidence of trophic cascades. I found weak evidence of bottom-up effects between adjacent levels, but there is no evidence of cascading effects of any kind. The lack of trophic cascade in my study calls into question the efficacy of using top-down cascades to manage ecosystem productivity or bottom-up effects to manage taxa at higher trophic levels.

That being said, numerous weaknesses remain in my study that makes my findings tentative. For example, it is known that intraguild predators, or predators killing each other over a common resource, can destabilize food webs (Arim & Marquet, 2004). As mentioned previously, species diversity can dampen trophic cascades (Finke & Denno, 2004), so datasets with a complete census of all interactions occurring within natural systems or experiments with complex food webs are needed to determine the importance of diversity in obscuring or preventing trophic cascades. This is because tri-trophic interactions in a system with only three species may result in trophic cascades when tri-trophic interactions from complex food webs would not (Benincà et al., 2008; Hastings & Powell, 1991; Tanabe & Namba, 2005). However, Gauzens et al. (2013) have found aggregating species as a means of simplifying complicated food webs was able to preserve statistical effects. Despite the findings reported by Gauzens et al. (2008), the findings from my study remains tentative as other drivers of species abundance can obscure trophic cascades in natural systems.

Future research attempting to study trophic cascades in natural systems can take measures to avoid the weaknesses present in my study. Studies should either use species data where the position of taxa in the food web are very unambiguous or develop a method to resolve the issue of species capable of interacting across multiple trophic levels. The issue of omnivory should be given attention as research regarding omnivory in food webs remains mixed. Several studies have reported that omnivores can stabilize or destabilize food webs (McCann et al., 2005; Kratina et al., 2012; Tanabe & Namba, 2005). An additional factor that could be considered is the impact of abiotic factors on species abundance. For example, Savopoulou-Soultani et al. (2012) report that insect abundance is heavily dependent on temperature, rainfall, and humidity. In a freshwater system, Kratina et al. (2012) report that higher temperatures can strengthen trophic cascade and reduce the sensitivity of predators to nutrient enrichment. It is possible that after controlling for abiotic factors trophic cascades may be more easily detectable. An additional factor to consider is the impact of varying species diversity on trophic cascade, so one could control for the effects of diversity using species diversity as a covariate. By accounting for alternative factors, future research can understand the relevance of trophic interactions in natural systems.

If we can confirm that cascades are rare and / or weak in natural systems, the next step is to ascertain the reason for the lack of reverberation of trophic forces beyond one trophic level. In particular, whether factors such as dispersal ability, system diversity and predator-prey size ratios are dampening trophic cascades. However, we should also explore new ideas such as the hypothesis that intermediate species commonly regulate

both their predators and prey thus, preventing cascades from occurring as this concept has not been investigated.

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List of Appendices

Appendix A - Overview of the Data

Table A1: The sample size, mean correlation, and standard deviation of the distribution of correlations segregated by number of years in time-series.

Yearcount	n	Mean r	SD
3	57	-.108	.709
4	71	.118	.600
5	41	.341	.479
6	22	.202	.538
7	51	.0616	.471
8	27	.0443	.510
9	108	-.0447	.359
10	27	-.0889	.401
11	14	.346	.344
12	7	.153	.457
13	27	.116	.327
14	62	-.00277	.318
15	59	.00732	.309
16	75	.0614	.283
17	4	-.00399	.365
18	6	-.209	.146
19	18	.0532	.255
20	16	-.0216	.480
21	4	.457	.655
22	4	-.0554	.225
23	2	-.0856	.0346
24	8	-.174	.156
25	31	.00861	.346
26	3	.169	.211
27	1		
28	4	-.124	.473
30	1		
31	2	.461	.208
32	10	.148	.167
34	1		
36	1		
41	1		
42	15	.260	.216

Table A2: The countries or ocean from which the time-series were collected from sorted from the most to least.

Country	Time-Series Count
United States	642
Canada	44
Pacific Ocean	36
Australia	17
Finland	8
Ireland	5
Japan	4
Russia	4
Scotland	4
Sweden	4
Baltic Sea	3
Mexico	3
Netherlands	3

Appendix B – Certainty Data for all 1 TLA Time-Series

Figure B1: The distribution of high certainty correlations for time-series pairs that are one trophic level in distance ($n = 472$).

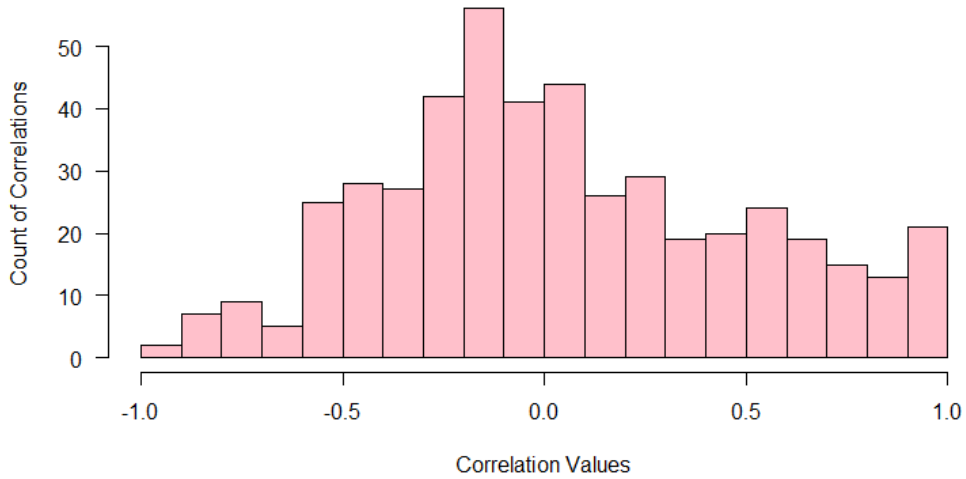


Figure B2: The distribution of the correlations of moderate certainty for time-series pairs that were 1 TLA ($n = 207$).

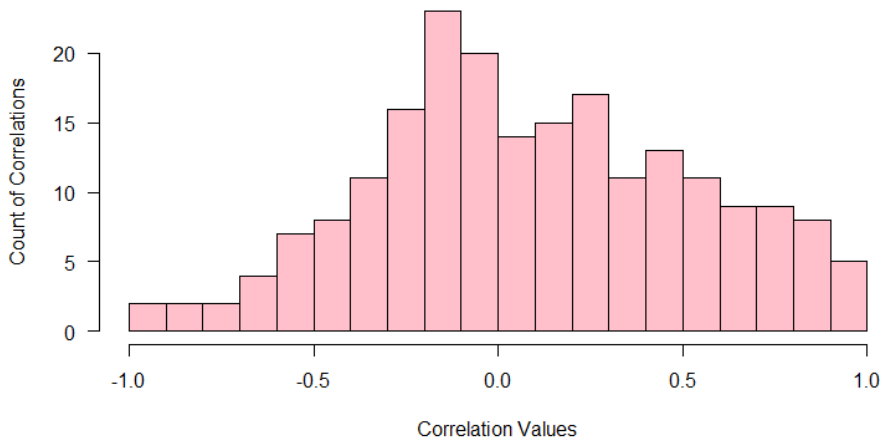


Figure B3: The distribution of low certainty correlations for time-series pairs that were 1 TLA ($n = 34$).

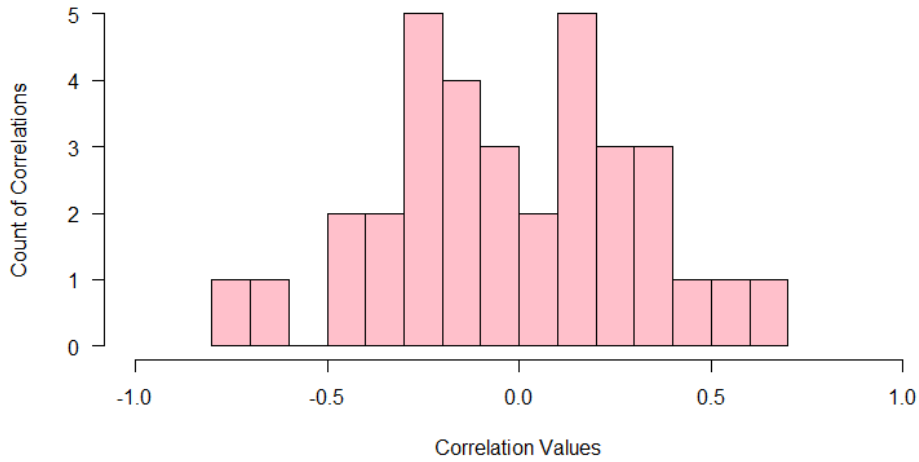


Figure B4: The mean (filled box) and standard deviation (vertical 'whiskers') of correlations for high, moderate, and low certainty for all time-series pairs that were 1 TLA.

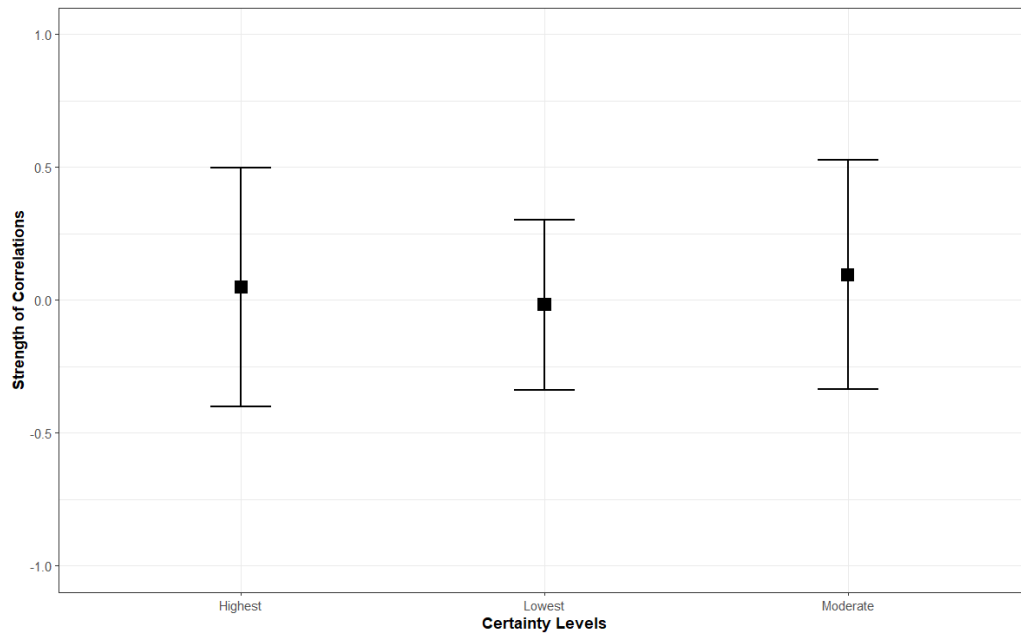
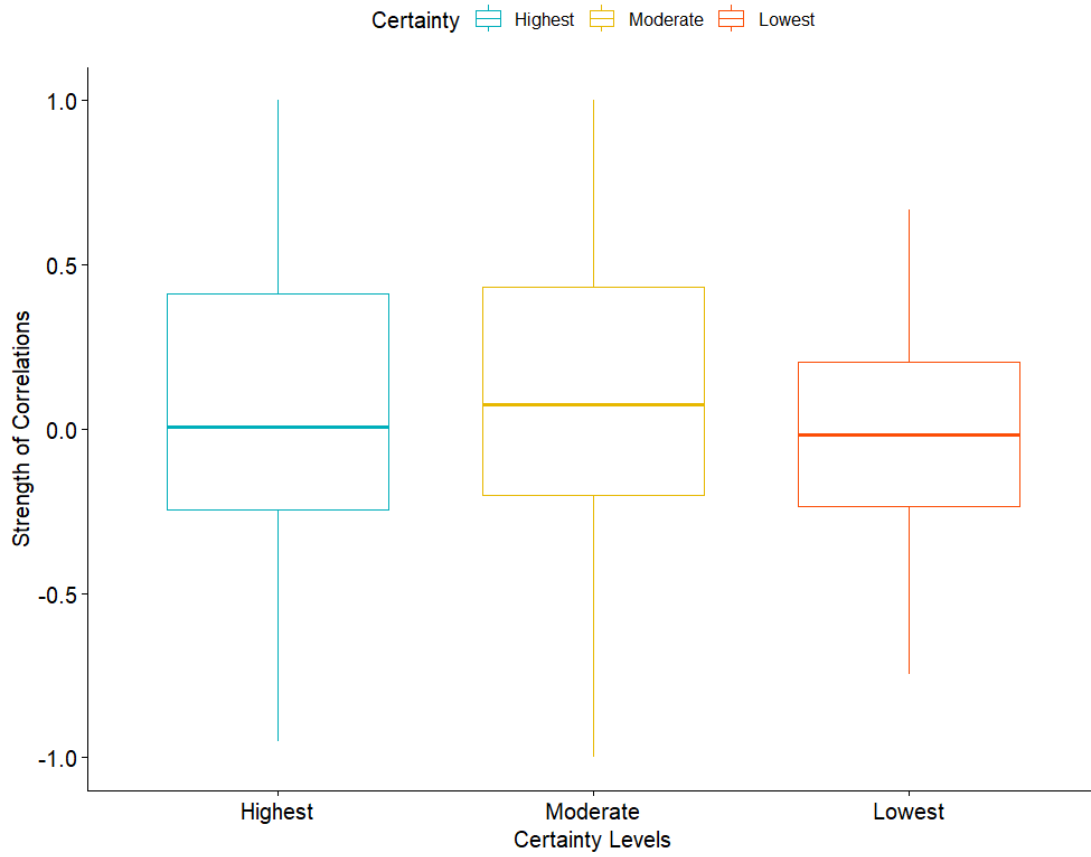


Figure B5: The boxplot for the distribution of correlations of high, moderate, and the low certainty for all time-series pairs that were 1 TLA.



Appendix C – Certainty Data for 2 TLA Time-Series

Figure C1: The distribution of correlations of high certainty for time-series pairs that were 2 TLA ($n = 15$).

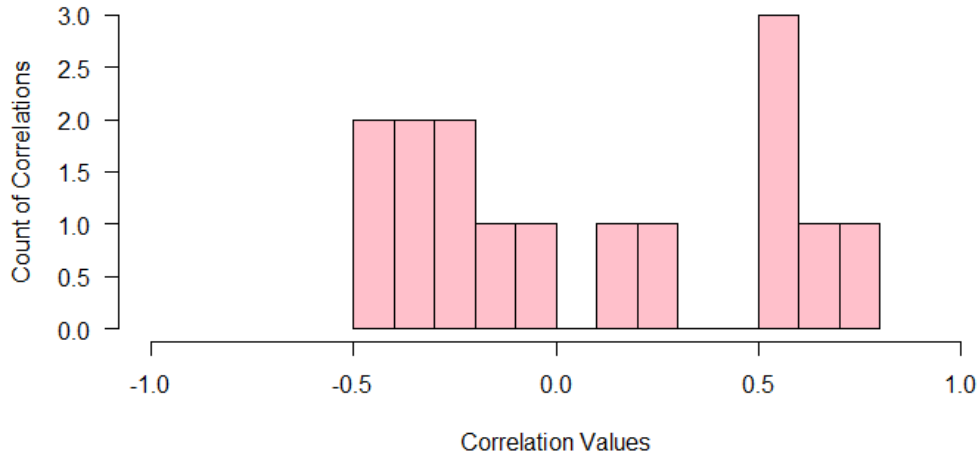


Figure C2: The distribution of correlations of moderate certainty for time-series pairs that were 2 TLA ($n = 43$).

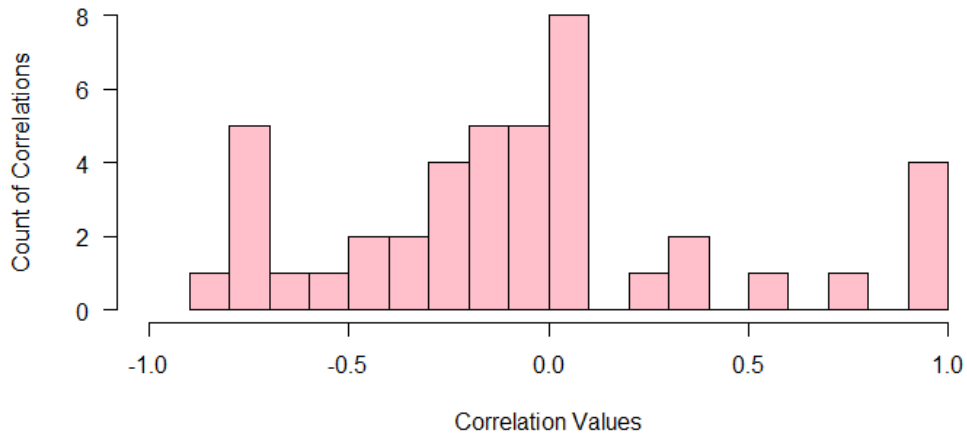


Figure C3: The distribution of correlations of low certainty for time-series pairs that were 2 TLA ($n = 7$).

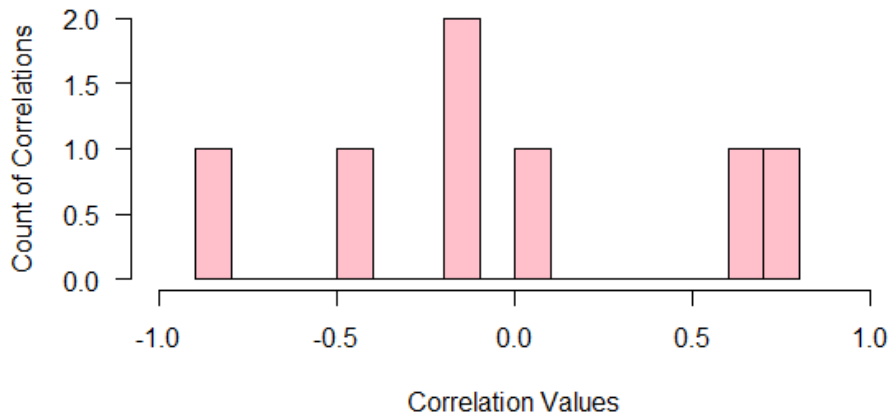


Figure C4: The mean (filled box) and standard deviation (vertical 'whiskers') of correlations for high and the combination of moderate and low certainty for all time-series pairs that were 2 TLA.

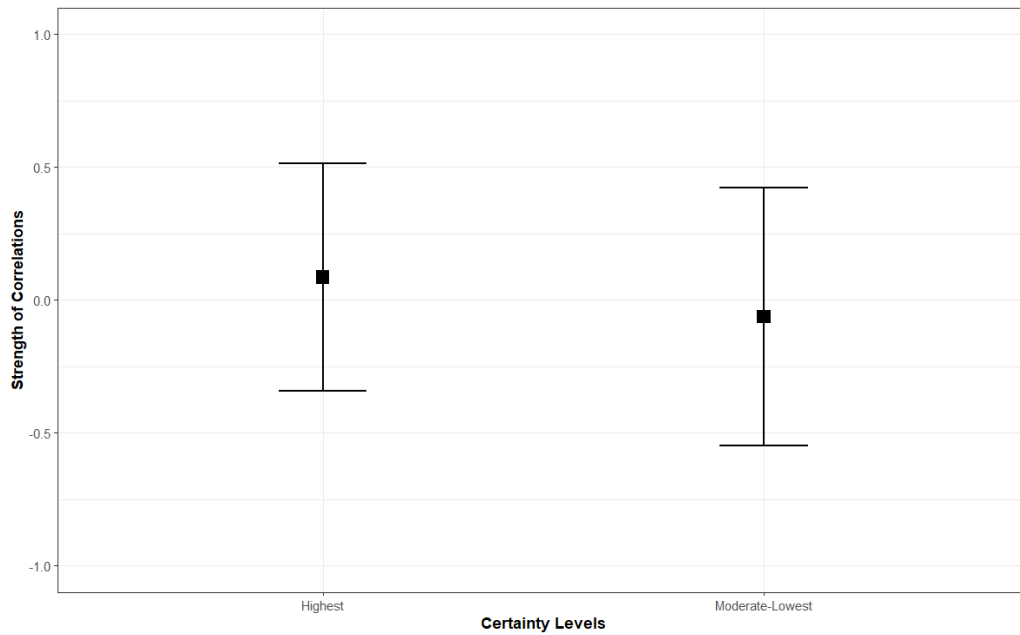
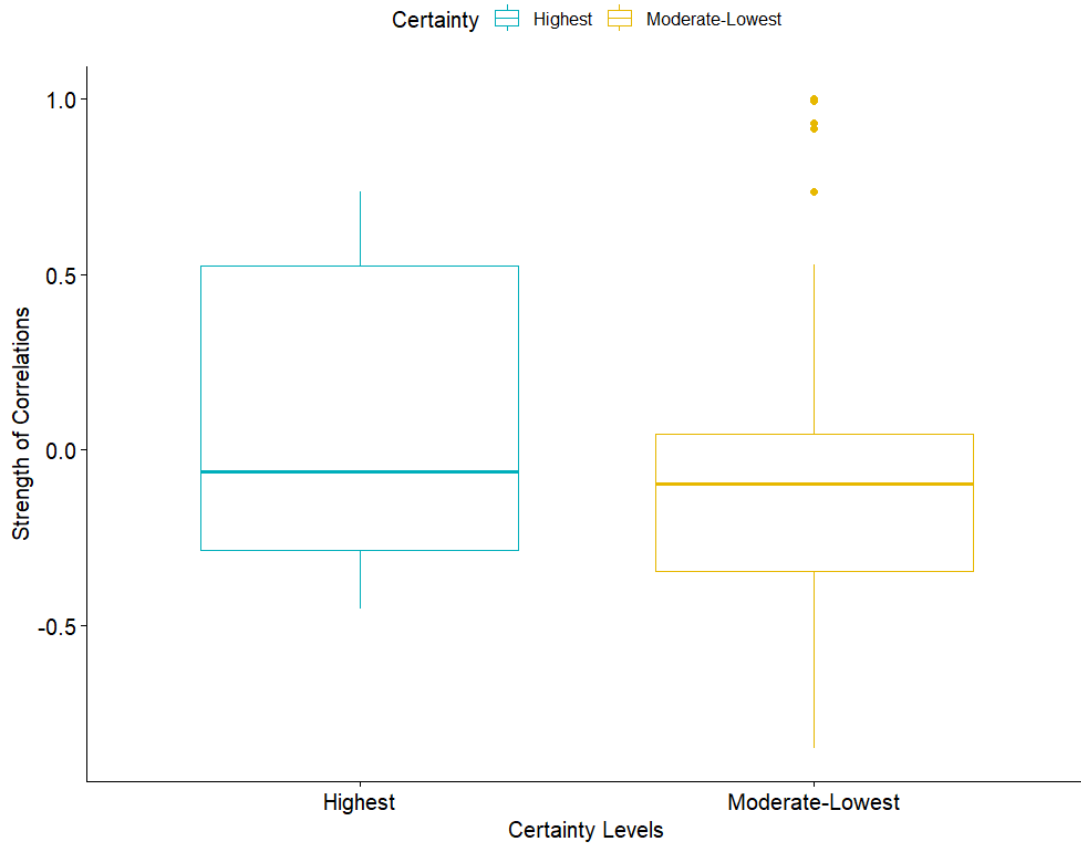


Figure C5: The boxplot of correlations of 2 TLA species-pairs for high and the combination of moderate and low certainty for all time-series pairs that were 2 TLA.



Appendix D – Freshwater Time-Series

Figure D1: The distribution of high certainty correlations for time-series pairs of freshwater taxa that were 1 TLA ($n = 357$).

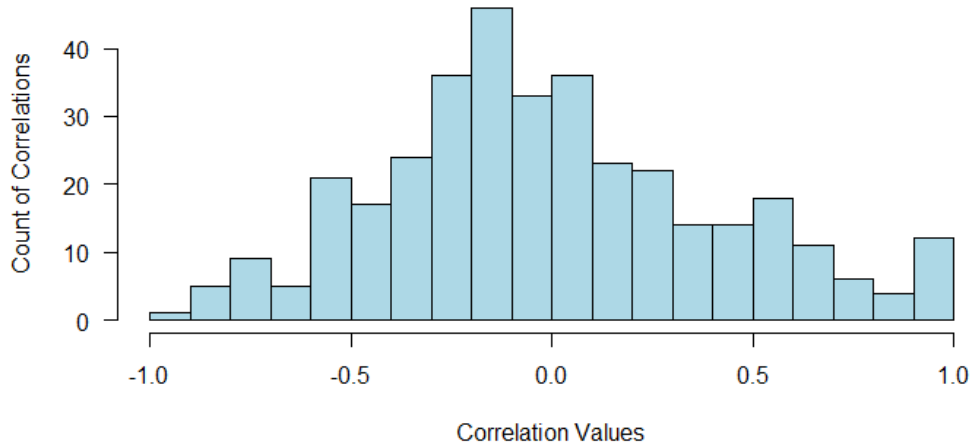


Figure D2: The distribution of moderate certainty correlations for time-series pairs of freshwater taxa that were 1 TLA ($n = 207$).

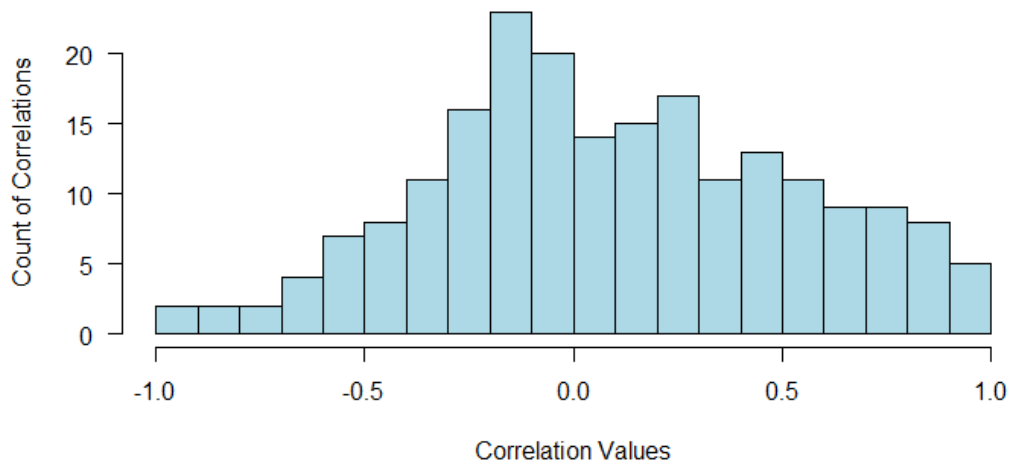


Figure D3: The distribution of low certainty correlations for time-series pairs of freshwater taxa that were 1 TLA ($n = 34$).

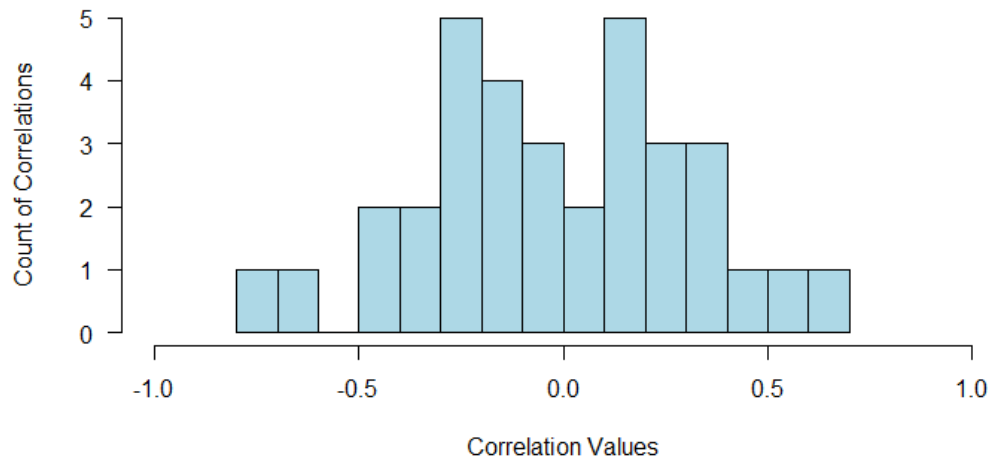


Figure D4: The mean (filled box) and standard deviation (vertical ‘whiskers’) of correlations for highest, moderate, and low certainty for freshwater time-series pairs that were 1 TLA. The letter “B” indicates a significant difference whereas “A” indicates a non-significant difference.

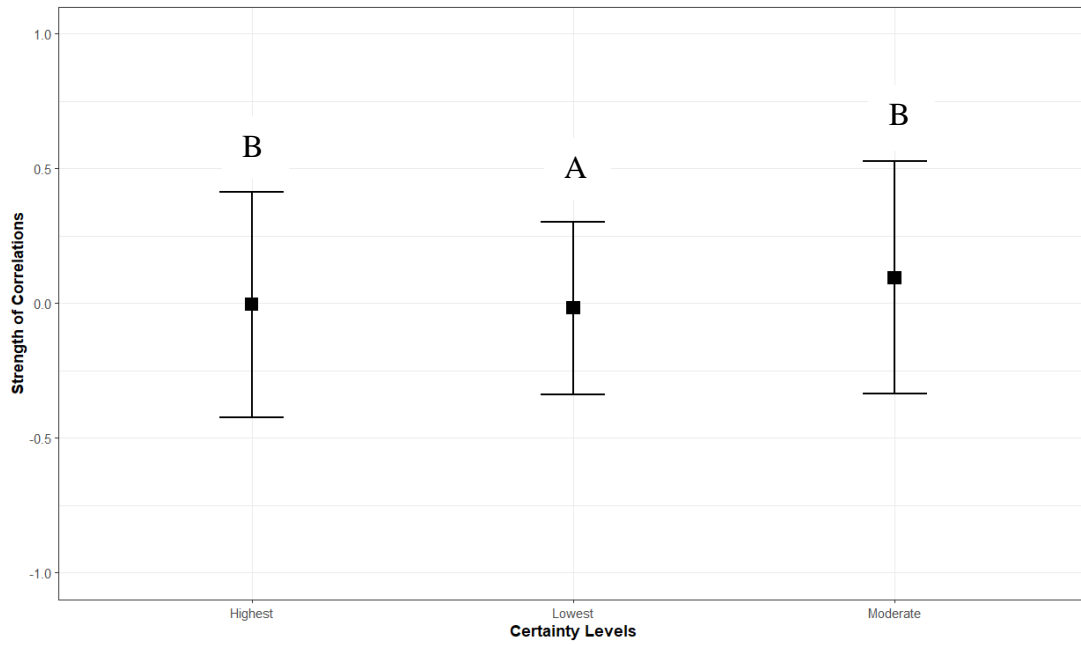
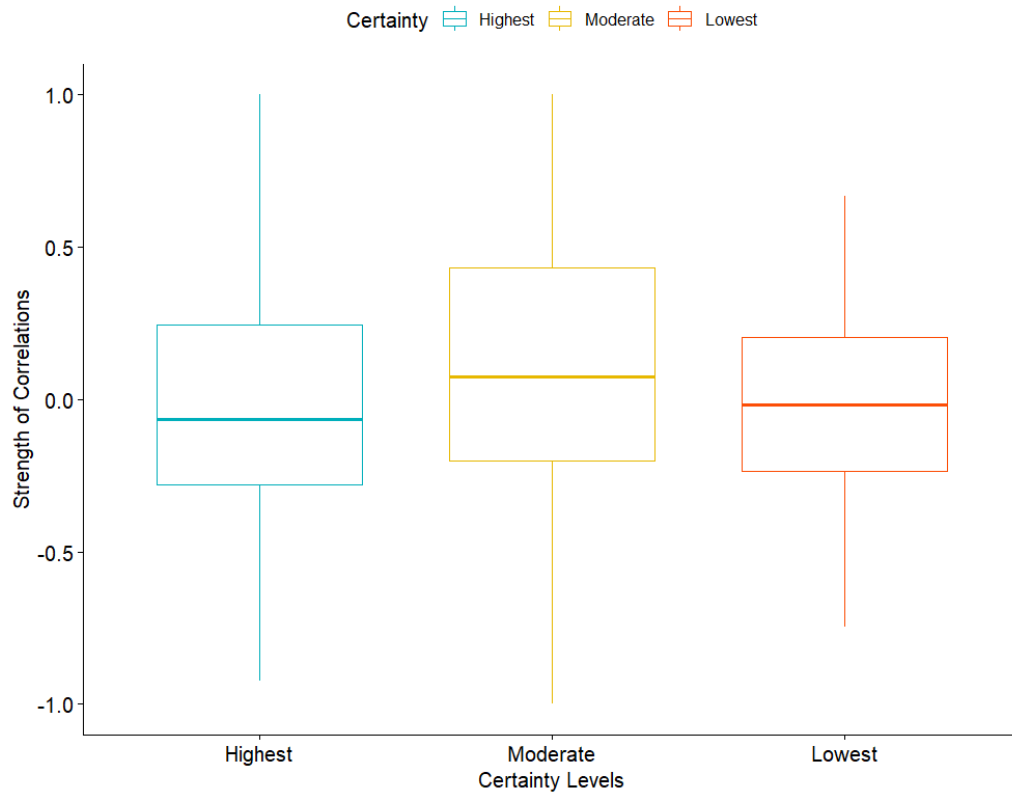
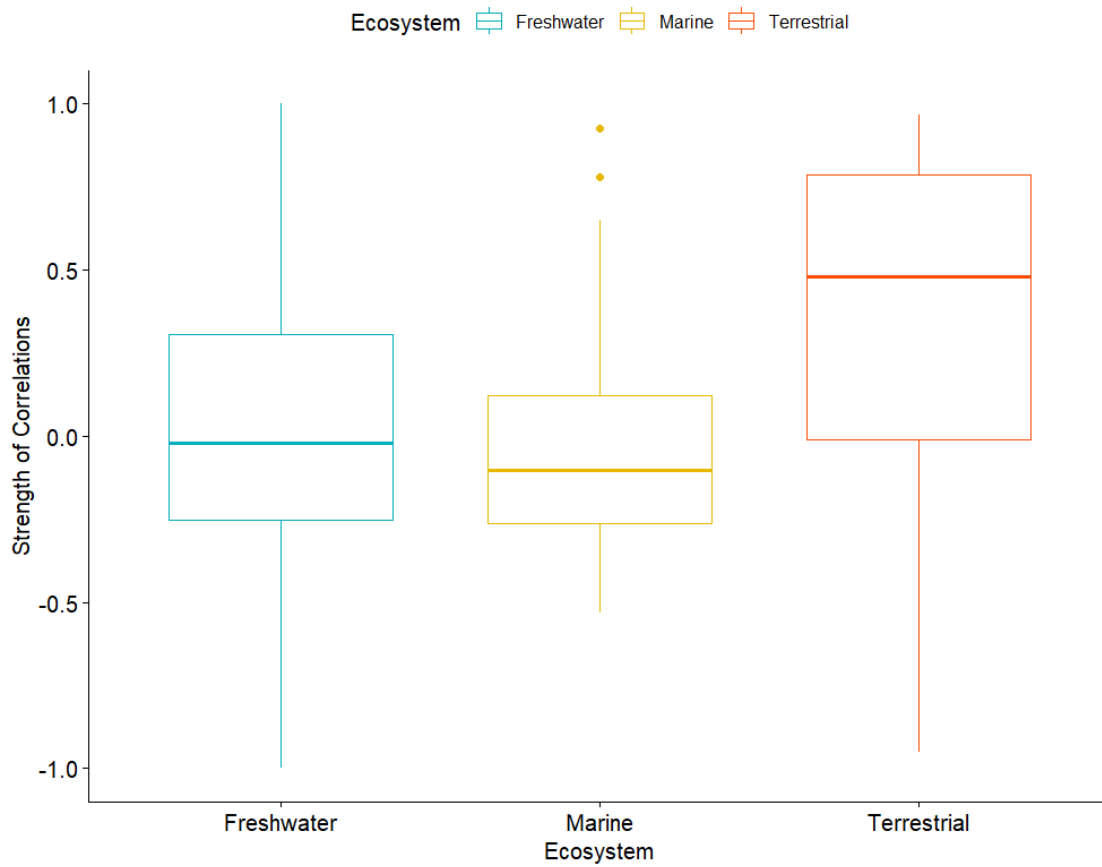


Figure D5: The boxplot for the distribution of freshwater correlations for species-pairs with high, moderate, and low certainty that were 1 TLA.



Appendix E – Comparison of Ecosystems of 1 TLA Species-Pairs

Figure E1: The boxplot for the distribution of correlations of freshwater, marine, and terrestrial species-pairs that were 1 TLA.



Appendix F – Unlinked 2 TLA Species-Pairs by Ecosystem

Figure F1: The distribution of correlations for time-series pairs for freshwater organisms that are two trophic levels in distance ($n = 52$).

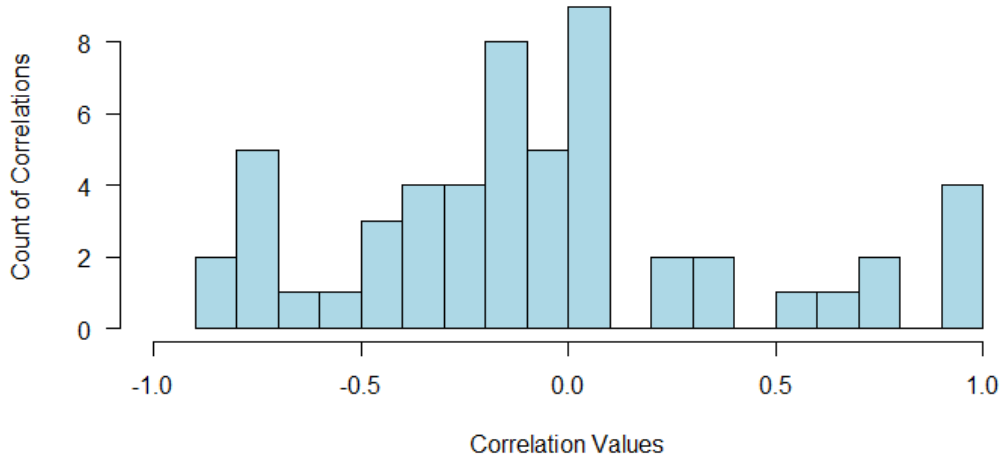


Figure F2: The distribution of correlations of high certainty for time-series pairs that were also the overall data for 2 TLA ($n = 10$).

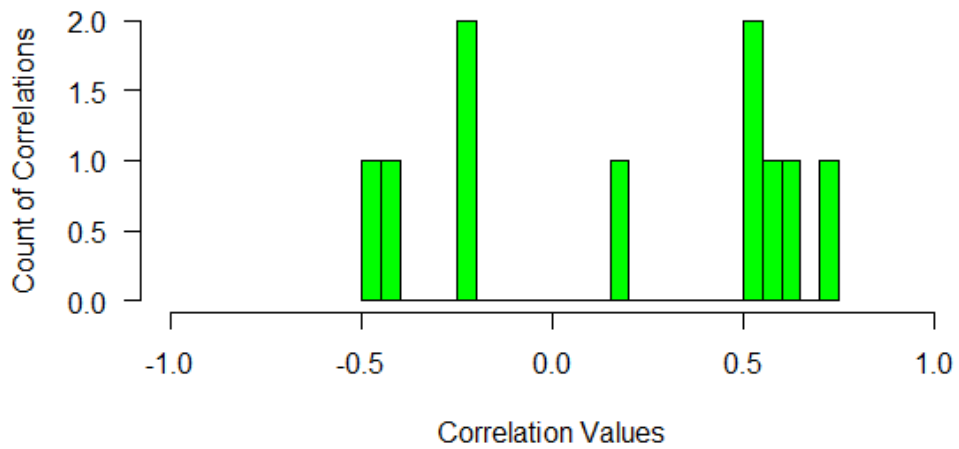
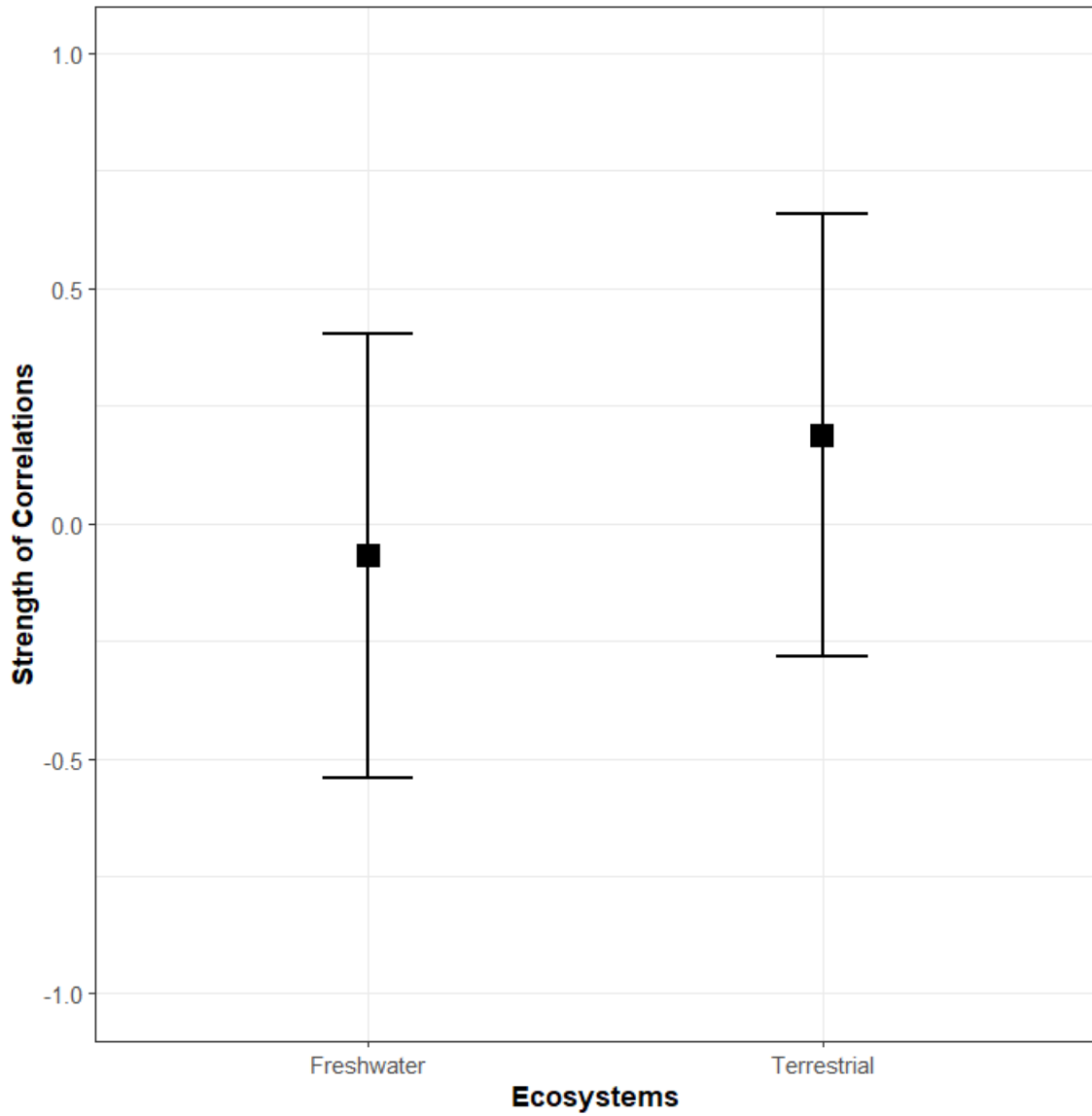


Figure F3: The mean (filled box) and standard deviation (vertical 'whiskers') of correlations for freshwater and terrestrial species-pairs that were 2 TLA.



Appendix G – Time-Series Pairs with Primary Producers

Figure G1: The distribution of correlations for time-series pairs interacting with a primary producer that were 1 TLA ($n = 78$).

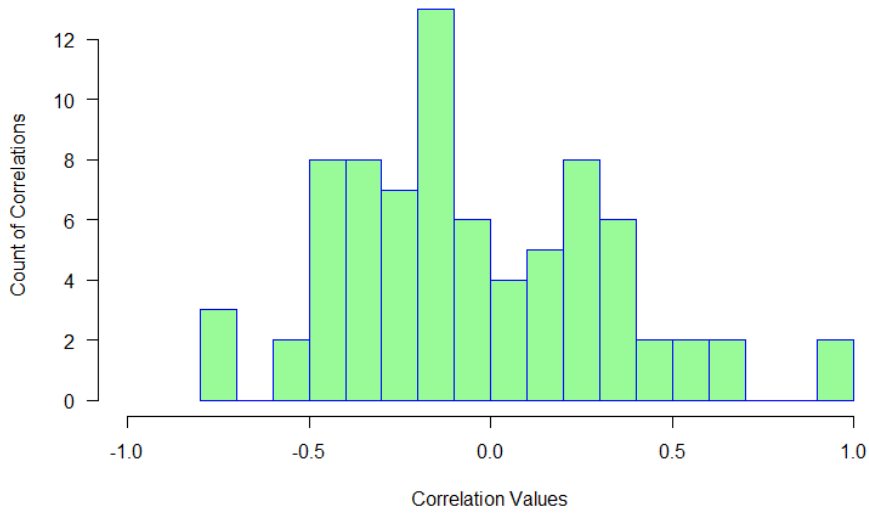


Figure G2: The distribution of correlations for time-series pairs without a primary producer that were 1 TLA ($n = 635$).

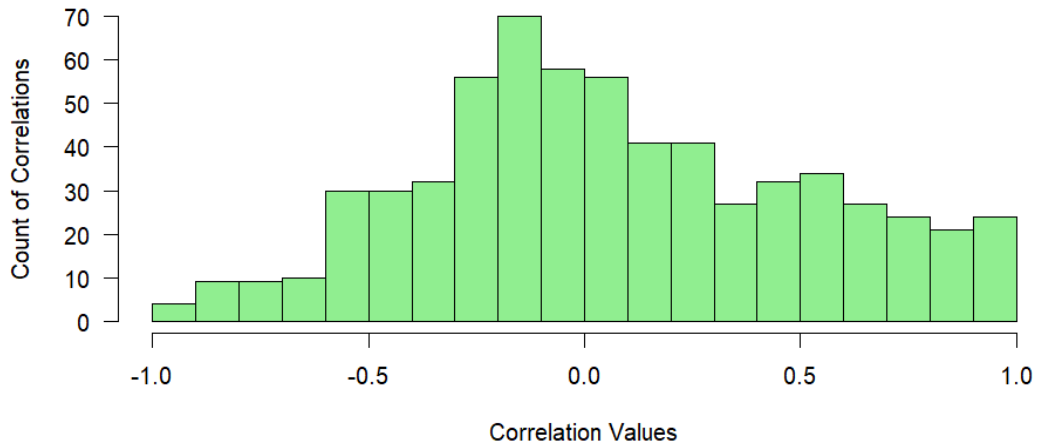


Figure G3: The boxplot for the distribution of correlations of 1 TLA species-pairs with a primary producer present or absent.

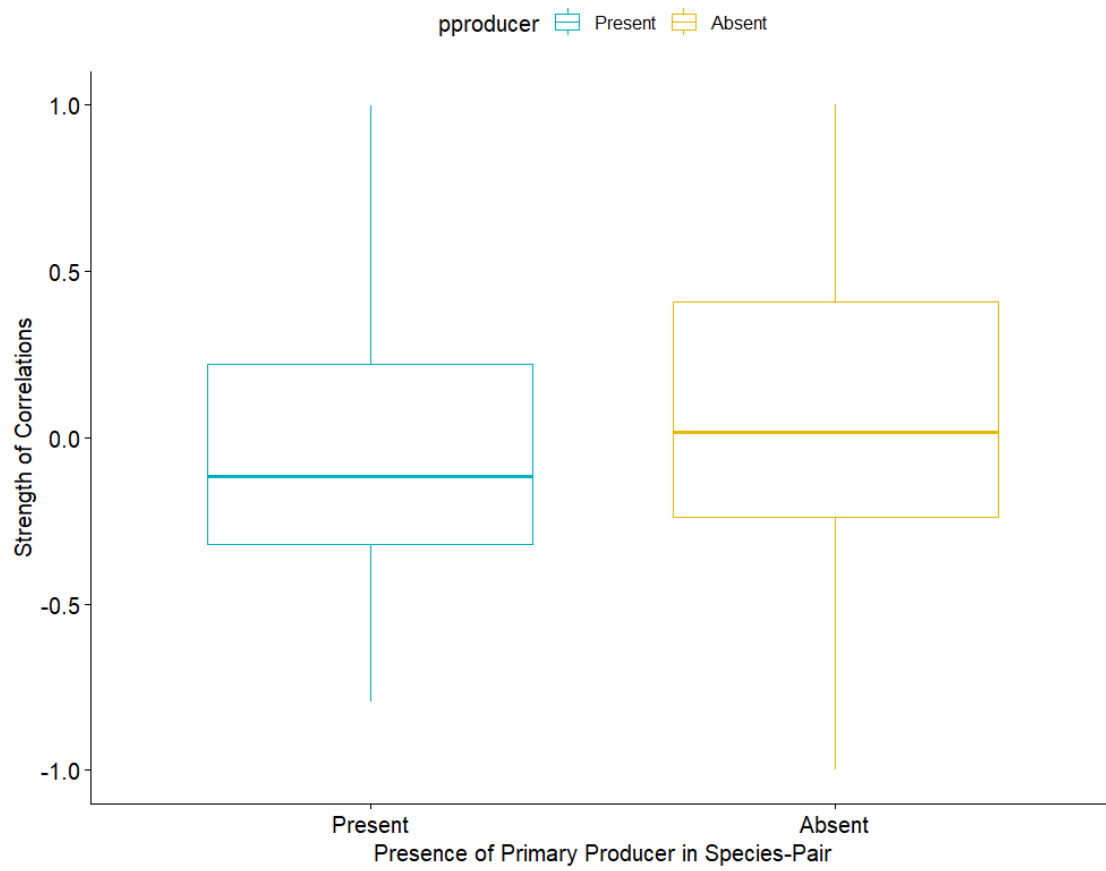


Figure G4: The distribution of correlations for time-series pairs interacting with a primary producer that were 2 TLA ($n = 45$).

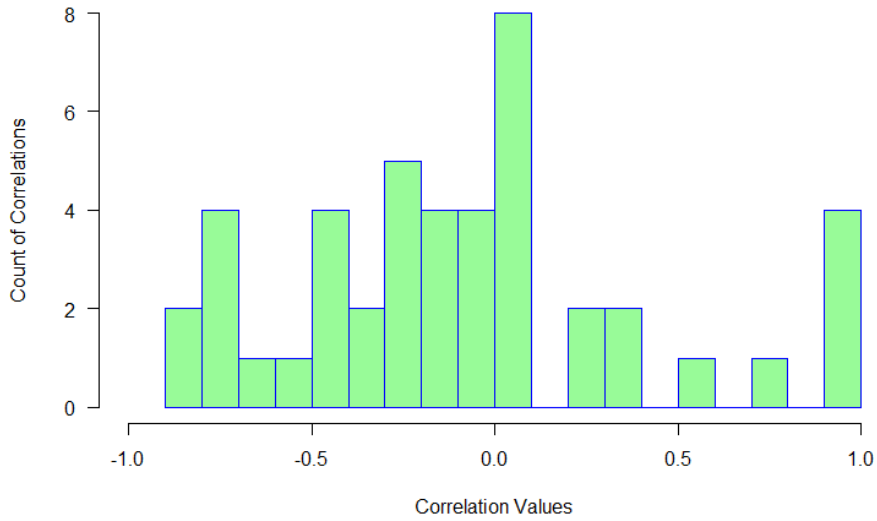


Figure G5: The distribution of correlations for time-series pairs interacting without a primary producer that were 2 TLA ($n = 18$).

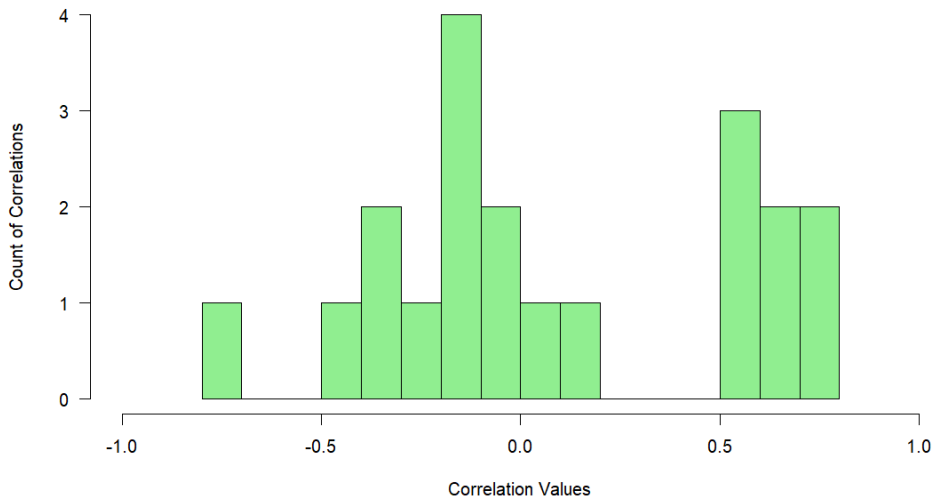
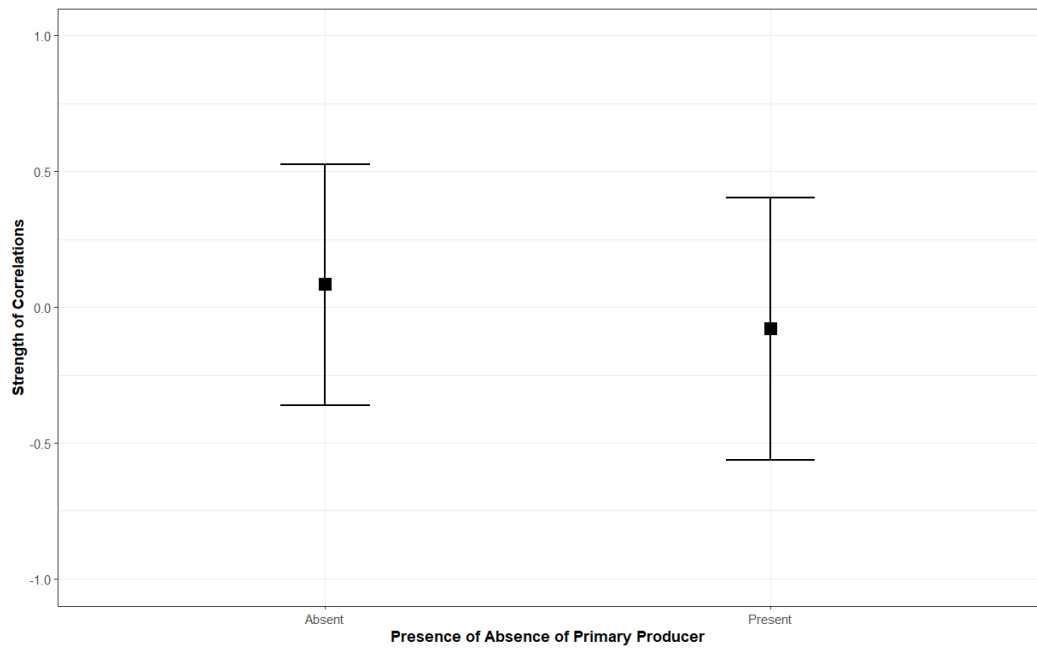


Figure G6: The mean (filled box) and standard deviation (vertical 'whiskers') of correlations for species-pairs with a primary producer present and absent that were 2

TLA.



Appendix H – Time-Lagged Correlations

Figure H1: The distribution of correlations of time-lagged pairs that were 1 TLA, or adjacent in trophic levels ($n = 698$).

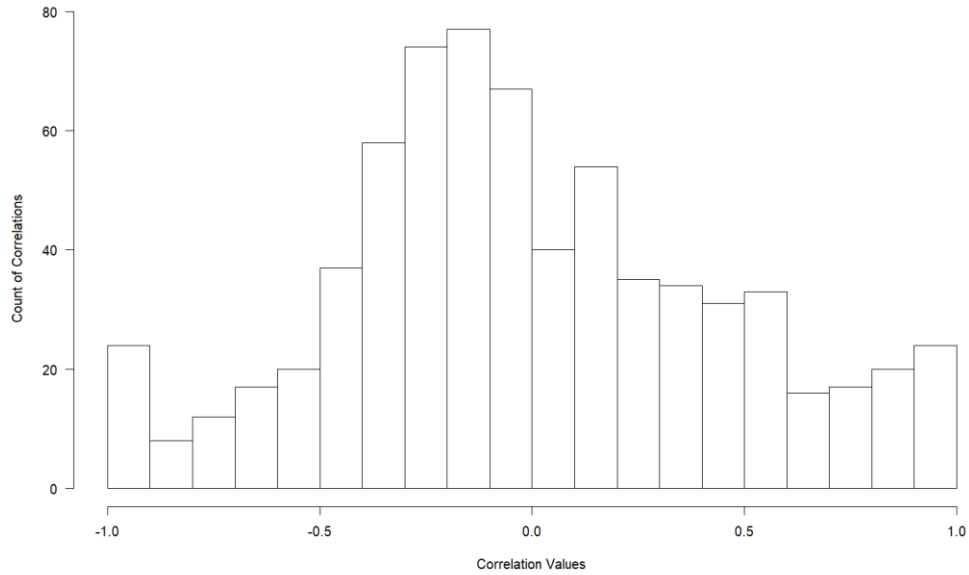
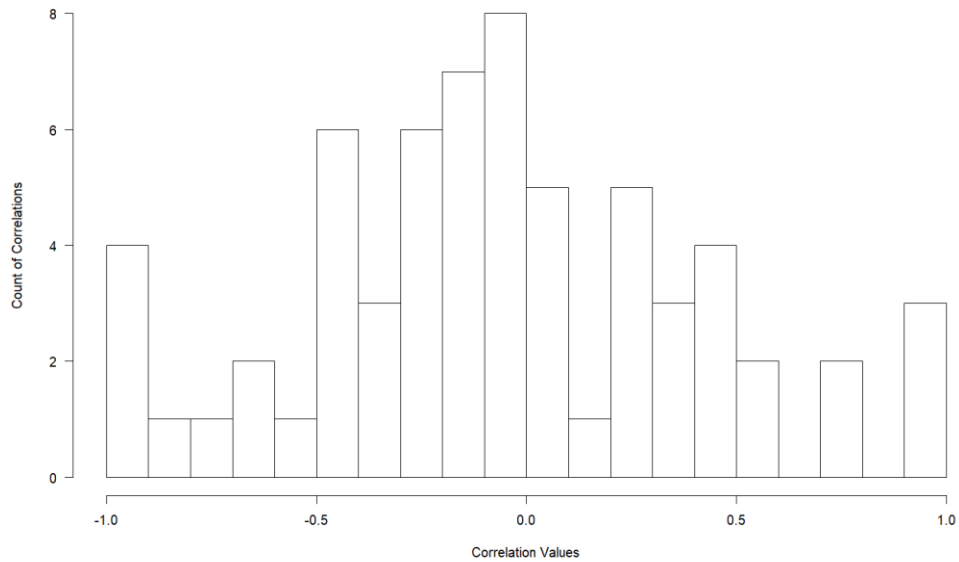
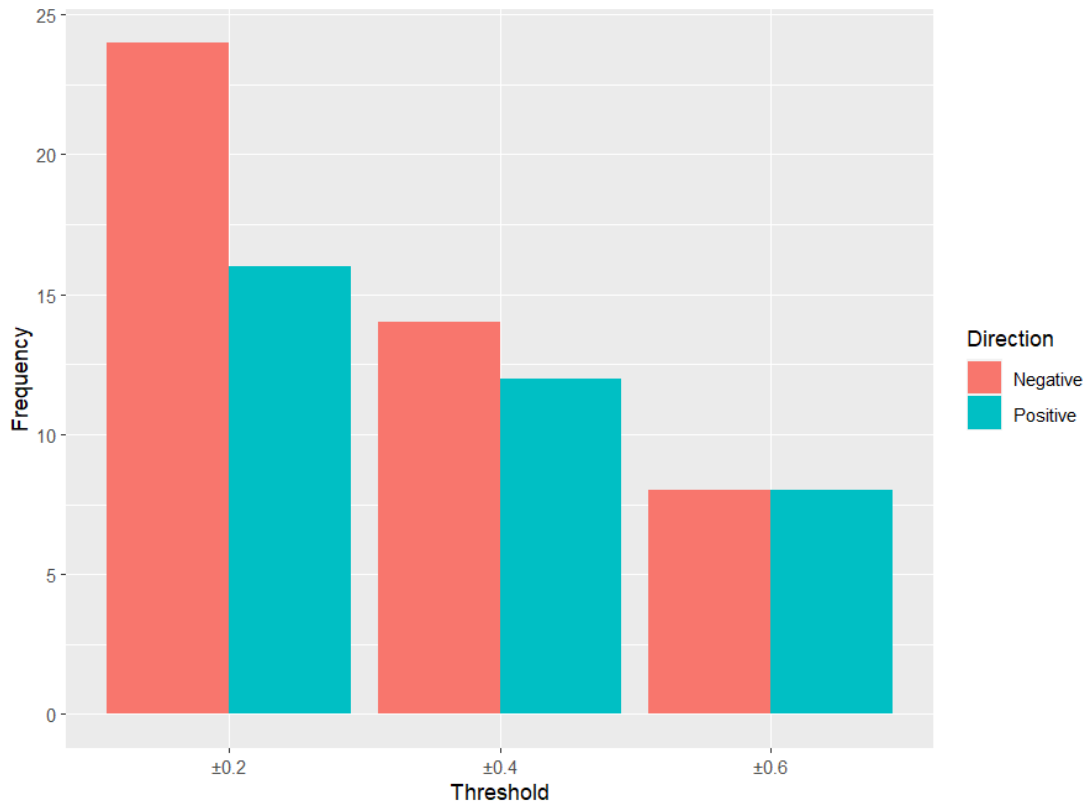


Figure H2: The distribution of correlations of time-lagged pairs that were 2 TLA ($n = 64$).



Appendix I – Comparison between Positive and Negative Correlations

Figure I1: The number of positive and negative correlations of species-pairs that were 2 TLA at thresholds of correlations $\geq \pm 0.2$, ± 0.4 , and ± 0.6 .



Curriculum Vitae

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