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# THE DIVERSITY - DISTURBANCE RELATIONSHIP REVISITED

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## ABSTRACT

The Intermediate Disturbance Hypothesis has been widely accepted in ecology ever since it was first proposed in the 1970s. The IDH states that diversity and disturbance are strongly linked and that the diversity of a system is maximized at an intermediate level of disturbance to form a unimodal peaked relationship. However, diversity-disturbance relationships of a far wider variety of shapes are recorded in the ecology literature. Mackey and Currie (2001) tested the IDH by analyzing the literature from 1985 to 1996 and cataloguing 197 diversity-disturbance relationships by shape. They found that unimodal peaked relationships made up only a small minority of documented relationships. Since Mackey and Currie (2001), the diversity-disturbance literature has expanded greatly. I analyzed the ecological literature from 2008 to 2018, using a protocol similar to that in Mackey and Currie (2001), and catalogued 581 relationships by shape to assess the relative frequency of different diversity-disturbance relationships recorded in more recent publications. As in the earlier work, I found a lack of consistent patterns in diversity-disturbance relationships. Unimodal peaked relationships still did not make up a majority of the relationships seen, comprising only 32.2% of relationships. When the observed relationships were categorized by disturbance and system characteristics, used species evenness as a diversity measure, measured disturbance on a ‘time since last disturbance’ gradient, or were derived from experimental studies, all displayed a significant decrease in the percentage of unimodal peaked relationships when compared to the overall distribution of relationships. Overall, diversity-disturbance relationships can still not be fully described by the Intermediate Disturbance Hypothesis.

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## Chapter 1 : Introduction

Determining the factors that affect species diversity has long been a goal for ecological researchers. While the exact factors influencing diversity are still being debated, disturbance has been widely accepted as an important driver of diversity patterns. The effect of disturbance on diversity has been studied since the 1940s (Eggeling, 1947; Watt, 1947; Tansley, 1949) and has resulted in a wide range of hypotheses to explain the relationship. One of the most popular of these has been the Intermediate Disturbance Hypothesis (Grimes, 1973; Horn, 1975; Connell, 1978).

The concept behind the Intermediate Disturbance Hypothesis (IDH) was first introduced in Grime's 1973 paper 'Competitive exclusion in herbaceous vegetation' and Horn's 1975 paper 'Markovian properties of forest succession', but the IDH in its current form was first popularized by Connell's 1978 paper 'Diversity in tropical rain forests and coral reefs.' The Intermediate Disturbance Hypothesis states that diversity is maximized at an intermediate level of disturbance, with the relationship characterized by a 'hump-backed' or 'peaked' shape. According to the IDH, if disturbance levels are low then competitive species will outcompete others and reduce overall diversity, while if disturbance levels are high only the most disturbance-tolerant species will survive and diversity will be similarly lowered. An intermediate level of disturbance is postulated to create balance between competitive species and disturbance-tolerant species, thus causing a high level of species diversity. This effect was theorized to act on a spatial and temporal scale, so that an intermediate level in intensity of the disturbance, frequency of the disturbance, or time since a single disturbance would all result in maximum diversity (Connell, 1978).

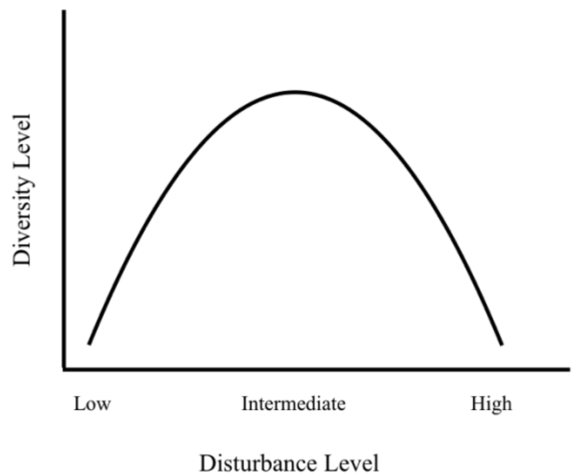


**Figure 1: A 'hump-backed' or 'peaked' relationship seen under the intermediate disturbance hypothesis.**

The IDH was originally proposed to explain disturbance-diversity relationships seen in coral and terrestrial plant systems, but it has since been applied to a wider disturbance regimes, ranging from logging on reptiles (Hu et al., 2013), to pollution on ants (Belskaya et al., 2017), to predation on shrimp (Feyrer and Duffus, 2011). Ever since Connell's 1978 paper, the IDH has been a popular rationale to explain quadratic relationships seen when comparing disturbance and diversity and has become a staple in ecological textbooks (e.g. Rickels, 1990; Colinvaux, 1993; Brewer, 1994; Krebs, 1994). The IDH has been embraced even to the point where some studies will use the level of diversity in a system as a tool to estimate the level of disturbance.

Although the IDH has gained wide acceptance, it has also been the subject of criticism. From the beginning, empirical evidence has shown inconsistent relationships between disturbance and diversity (Fox, 2013). Small changes in the studied system, or in the metrics used to measure diversity and disturbance, can result in radically different relationships. For example: a community may have a peaked relationship when comparing diversity to the intensity of flooding, but a negative relationship when comparing diversity to the frequency of flooding (Tanentzap et al., 2013).

These discrepancies have prompted some researchers to propose alternative theories to explain the patterns seen. Wootton (1998) suggests that the IDH may only be applicable for sessile communities, while others propose that regular disturbance may not be major component behind diversity at all. It has been hypothesized for communities with low competition that productivity (Huston, 1979) or rare catastrophic disturbances (Reice et al., 1990) may be larger driving forces.

In an attempt to reconcile these opposing hypotheses, Mackey and Currie (2001) conducted a meta-analysis of the existing disturbance-diversity literature. In 'The Diversity-Disturbance Relationship: Is it Generally Strong and Peaked?", Mackey and Currie surveyed the literature over a 12 year period, 1985 -1996, and cataloged how many empirical studies actually saw a 'peaked' relationship. In addition, Mackey and Currie also catalogued the system characteristics pertaining to each relationship and the diversity and disturbance measurements used in each study to address the possibility of the IDH only being applicable to certain types of systems or certain measures.

Mackey and Currie (2001) considered three different metrics of diversity: species richness (the number of species), species evenness (the relative abundance of individuals among the different species present), and factors combining species richness and species evenness (e.g. Shannon or Simpson's Index) that will be referred to as 'species diversity' in all reported results. The term 'diversity' will refer to any of these three metrics.

Mackey and Currie (2001) reported that only 16% of species richness, 19% of species diversity, and 11% of species evenness relationships were peaked and that the most commonly seen relationship shape was, in fact, non-significant. When taking into account system characteristics, peaked relationships were more likely to be seen when the sample area and number of disturbance levels recorded was small, when evapotranspiration was low, and when the disturbances were natural in origin.

These findings set off a new wave of criticism of the IDH and support for alternative hypotheses. Mackey and Currie (2001) has been cited 327 times as of March 2019 and has been widely used in papers to justify why disturbance-diversity relationships may not show a peaked form and why different diversity affecting factors may be more applicable. Fox (2013) even suggested that the IDH should be completely abandoned due to inconsistency in the empirical support and issues with the core logic behind the theory (Fox, 2013). Fox (2013) argued that while disturbance can affect species density and therefore competition, it also decreases the threshold needed for competitive exclusion. He also argued that while disturbance may decrease competitor fitness it should also lower the fitness of the whole community. A competitor may therefore still have a higher relative fitness and retain dominance (Fox, 2013). Criticisms like these have fostered doubt in the validity of the IDH, but it remains a popular hypothesis in species diversity literature, and a useful heuristic for teaching.

In the years since the publication of Mackey and Currie (2001), the diversity-disturbance relationship literature has expanded a great deal. Furthermore, improvements in physical and online database technology has resulted in access to a significantly larger volume of literature than was available at the time of Mackey and Currie's original study.

In this paper, I update the work started by Mackey and Currie (2001). By following Mackey and Currie's original protocol whenever possible, and updating the protocol to fit the database technology of today, I analyzed 11 years of disturbance-diversity literature, 2008 to 2018, to address how the empirical relationships reported in the peer-reviewed scientific literature have changed since the time of Mackey and Currie's study and to address the validity of the Intermediate Disturbance Hypothesis (IDH) according to the most current research available.

## Chapter 2 : Methods

Mackey and Currie's original search was conducted by searching the CD and hard-copy versions of Biological Abstracts using the following keywords: CD -- intermediate disturbance, disturbance, disturbance gradients, species richness, species diversity, species evenness, patterns in species richness (or diversity or evenness), community dynamics, and community structure; HARD COPY -- species composition, species diversity, species evenness, species richness, and succession. Mackey and Currie (2001) then supplemented their search with additional papers discovered through the bibliographies of previously collected papers.

My literature update attempted to replicate these search conditions by using a combination of all CD and Hard-Copy search terms, with overlapping search terms appearing only once, to search the Biological Abstracts Collection of the Web of Science database. The search terms were formatted as a single search string using 'OR' to separate them.

This search resulted in 516,298 results, yet nevertheless did not contain all of the papers found in Mackey and Currie's original study. Six of the original papers were not picked up in the results and it was later discovered that four of the original papers were not available in the Web of Science Biological Abstracts database. The other two papers were found indirectly, but were not picked up via the search terms used.

These results, summarized in Table 1, were extremely different from Mackey and Currie's (2001) original search in both result content and volume. In 2001, the time of Mackey and Currie's literature review, the exact same search terms picked up only 1962 studies. This disparity in search results made a complete replication of Mackey and Currie's (2001) original search outside of the scope of this study due to time and data processing constraints.

**Table 1: Search terms and results used by Mackey and Currie (2001) and this study**

| Study | Mackey and Currie (2001) | | This Study |
|---|---|---|---|
| Database: | Biological Abstracts CD Database (1996-1990) | Biological Abstracts Hard Copy Database (1990-1985) | Web of Science Database, Biological Abstracts Collection (2018-1900) |
| Search Terms: | intermediate disturbance, disturbance, disturbance gradients, species richness, species diversity, species evenness, patterns in species richness (or diversity or evenness), community dynamics, and community structure | species composition, species diversity, species evenness, species richness, and succession | 'intermediate disturbance' OR 'disturbance' OR 'disturbance gradients' OR 'species richness' OR 'species evenness' OR ' species diversity' OR 'patterns in species richness' OR 'patterns in species diversity' OR ' patterns in species evenness' OR 'community dynamics' OR 'community' OR 'species composition' OR 'succession' |
| Number of Results: | 1962 | | 516,298 |

To address these issues, I altered the search terms to simultaneously more fully utilize the Web of Science database and nonetheless create a more targeted search. This updated literature search was conducted using a subset of Mackey and Currie's search terms in the Web of Science's Core Collection Database. The Core Collection was used because it contained a broader collection of studies, while still containing the results of the Biological Abstracts database.

The search string used was: ‘intermediate’ AND ‘disturb*’ AND (‘species richness’ OR ‘species evenness’ OR ‘species diversity’); the asterisk represents any group of characters. This collected all papers containing those terms as keywords or as part of the abstract. This search string was chosen to find papers that compared some aspect of diversity across a disturbance gradient, papers that framed their results in the context of the Intermediate Disturbance Hypothesis, and papers that explicitly tested the Intermediate Disturbance Hypothesis.

Mackey and Currie’s original protocol for retaining papers was followed as strictly as possible. Papers were included in this study if they fulfilled the following criteria, laid out in Mackey and Currie 2001: 1) Data were recorded for three or more disturbance levels. At least three disturbance levels are required, because two disturbance levels are not enough to determine a non-linear relationship. 2) Disturbance was calculated directly from intensity, frequency, or time since the disturbance occurred. If biological responses of the organism (for example, biomass, percent cover) were used to infer a disturbance, the paper was not included. 3) All disturbances were represented as being of a single type. Though this may be impossible to know definitively for many systems, author interpretation was trusted. If a mixed disturbance type was used an effort must have been taken to create a weighted analytical gradient. 4) The study used species evenness, species richness, or species diversity measures.

Mackey and Currie (2001) also required papers to provide statistical information to be retained. For my review, this requirement was replaced with an author interpretation of the results. Mackey and Currie (2001) used statistical information to characterize the shape and strength of the relationships. The amount of data analysis required to mimic this aspect of Mackey and Currie’s (2001) review was outside of the scope of the current study.

A total of 1495 abstracts were screened and 662 papers were marked for relevance. At this point, the search years of this study were confined to 2008 - 2018 to address time constraints. This resulted in 378 papers relevant for further processing. These papers were collected through the Penn State University Library's access to online journals, as well as via their inter-library loan services. A second round of analysis of the 378 full papers resulted in 245 retained papers and 581 recorded relationships.

The higher number of relationships than retained papers arises because multiple relationships were sometimes observed in a single paper. Recorded relationships for different taxa, disturbance types, and diversity measures within a single paper were treated as distinct relationships to determine how often and under what conditions the Intermediate Disturbance Hypothesis is valid. Relationships seen in different habitats and conditions were recorded as separate relationships as long as there was little overlap between the conditions. When multiple non-independent categories were analyzed (for example, exotic vs. native plants and river vs. field habitats (Bourgeois et al., 2017)) categories separating different taxa and habitats were prioritized over categories within a single habitat or taxa (for example, relationships involving changes in salinity, canopy cover, or winter/summer measurements).

The shape of the relationship was determined through author interpretation of the results and was sorted into one of the following categories: Peaked, No Relationship, Positive, Negative, or U Shaped.

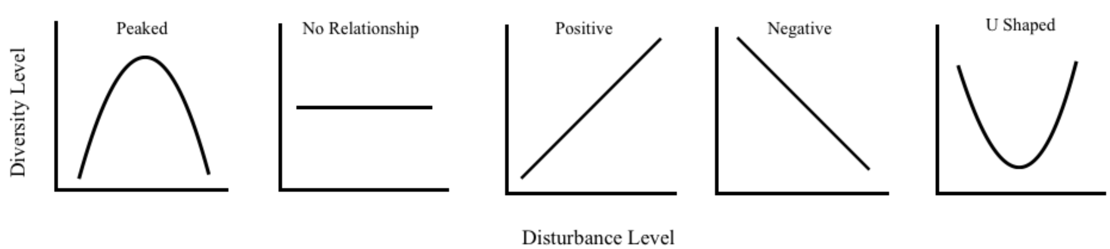


**Figure 2: Relationship shapes used to categorize diversity-disturbance relationships.**

The type of disturbance and type of diversity (Species Richness, Species Diversity, Species Evenness) being measured were recorded for each relationship, along with the type of organism experiencing the disturbance. The attributes of the system were also recorded for each relationship. These attributes were selected to mirror Mackey and Currie (2001) and to determine how differing conditions influence the Intermediate Disturbance Hypothesis. The study systems were categorized as Animal vs. Plant, Terrestrial vs. Aquatic, and Sessile vs. Motile. Disturbances were categorized as Abiotic vs. Biotic, Anthropogenic vs. Natural, Observational vs. Experimental, and Gradient Measured (Time, Frequency, or Intensity).

**Table 2: A list of the variables used to analyze disturbance-diversity relationships.**

| Predictor Variables |
| --- |
| System Attributes |
| Diversity Metric: Species Richness vs. Species Diversity vs. Species Evenness |
| Animal vs. Plant |
| Terrestrial vs. Aquatic |
| Sessile vs. Motile |
| Disturbance Attributes |
| Abiotic vs. Biotic |
| Anthropogenic vs. Natural |
| Observational vs. Experimental |
| Gradient of Time since last disturbance vs. Frequency vs. Intensity |

Following Mackey and Currie (2001), the overall distribution of relationships was tallied using vote counting. While vote counting has been criticized as a meta-analysis tool (Gurevitch et al., 1992), Mackey and Currie (2001) chose this method due to the difficulty of measuring effect size across the wide variety of papers in the literature. Furthermore, it is appropriate for the simple classification questions addressed in the present work.

To evaluate the possibility of the IDH only being relevant under specific conditions, I performed $\chi^2$ tests to assess whether different system attributes or disturbance attributes affect the disturbance-diversity pattern observed across studies. This was done by testing for a statistical difference between the distribution of relationships of a specific attribute and the overall distribution of relationships. I also used $\chi^2$ tests to compare this study's results and those of Mackey and Currie 2001.

Standard $\chi^2$ tests (Crawley, 1993) were performed using the following formula, where O is the observed results and E is the expected results given by the null:

$$\chi^2 = \Sigma \ \frac{(O-E)^2}{E}$$

For the analyzes used in this paper, the null came from the overall distribution of relationships when comparing system attributes, and from Mackey and Currie's results when comparing across literature reviews.

Details of the 581 relationships examined in this study are provided in the online Appendix.

# Chapter 3 : Results

## 3.1 Distribution of Relationship Shapes across Studies

Of the 581 recorded relationships, 32.2% of the relationships were 'Peaked', 25.6% of the relationships were 'No Relationship', 15.3% of the relationships were 'Positive', 22.0% of the relationships were 'Negative', and 4.3% of the relationships were 'U Shaped' (Figure 3).

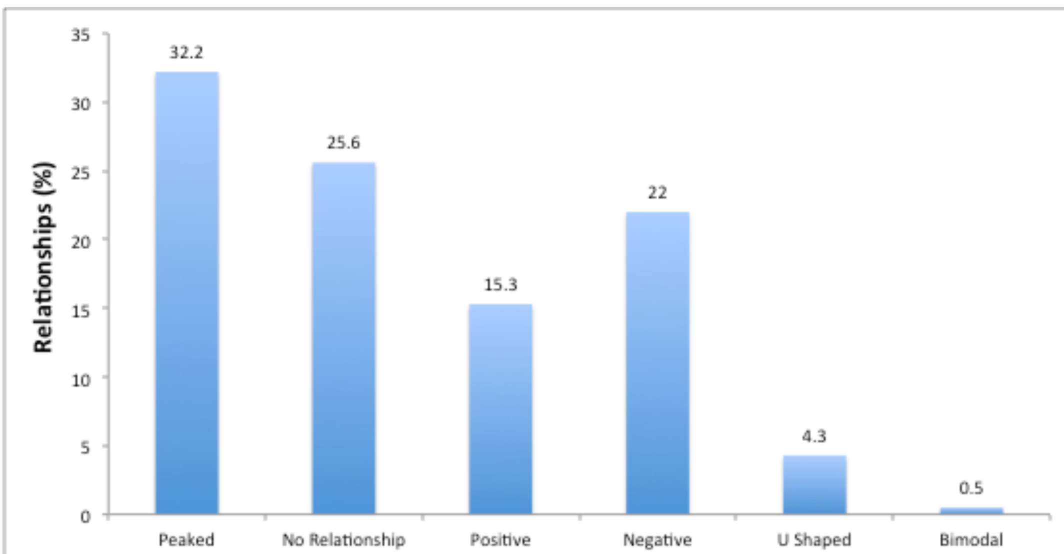


**Figure 3: The percentage of disturbance-diversity relationships exhibiting each classified shape: Peaked, No Relationship, Positive, Negative, U Shaped, and Bimodal. The percentage is indicated above each bar.**

A possible sixth shape that could not be sorted into any of the pre-determined categories was also seen, making up 0.5% of relationships. This sixth shape was 'Bimodal'. The 'Bimodal' relationships will not be addressed in any data analyses and instead will be discussed as unique cases.

### 3.2 Different Diversity Measurements Impact the Relationship Distribution

The majority of relationships, 61%, recorded used species richness as their diversity measure, followed by diversity at 27%, and then species evenness as the least used diversity measure at 12% (See Appendix).

Both species richness and species diversity measurements exhibited a similar distribution of relationships to the overall data set and neither measurement was significantly different from the distribution described above (Species Richness $\chi^2 = 4.5$, Species Diversity $\chi^2 = 3.9$, $p < 0.05$, df = 4).

Species evenness measurements were significantly different however ($\chi^2 = 17.9$, $p < 0.005$, df = 4). Of the species evenness relationships recorded 17.4% of the relationships were ‘Peaked’, 39.1% of the relationships were ‘No Relationship’, 18.8% of the relationships were ‘Positive’, 14.5% of the relationships were ‘Negative’, and 10.1% of the relationships were ‘U Shaped’ (Figure 4).

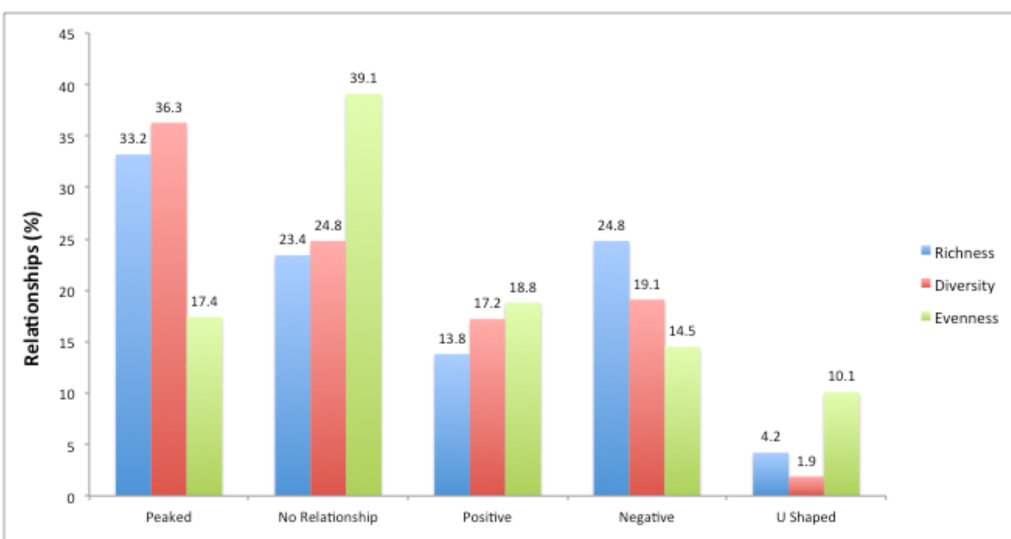


**Figure 4: The percentage of species richness, species diversity, and species evenness relationships exhibiting each of the classified shape: Peaked, No Relationship, Positive, Negative, and U Shaped. The percentage is indicated above each bar.**

### 3.3 Different Disturbance Measurements Impact the Relationship Distribution

Overall, 61% of the relationships used an intensity disturbance gradient. A frequency disturbance gradient was used for 15% of relationships and a time since last disturbance gradient was used for 19% of relationships. The other 5% of relationships used mixed gradients and could not be separated into a single category (See appendix).

The distribution of relationships using a time gradient was more even across relationship types and was significantly different from the overall distribution ($\chi^2$ = 13.4, p<0.01, df = 4). Of the time since last disturbance gradient relationships recorded 25.0% were 'Peaked', 25.0% were 'No Relationship', 26.8% were 'Positive', 21.4% were 'Negative', and 1.8% U Shaped (Figure 5).

The distribution of relationships for intensity and frequency relationships were not significantly different from the overall distribution (Intensity $\chi^2$ = 4.1, Frequency $\chi^2$ = 0.56, p<0.05, df = 4).

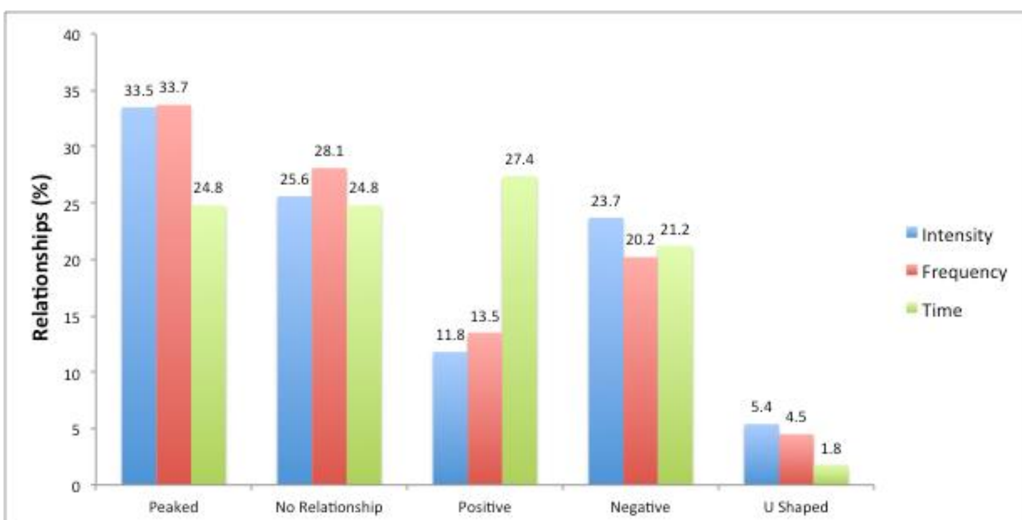


**Figure 5: The percentage of relationships measuring disturbance on an intensity, frequency, and time since last disturbance gradient exhibiting each classified shape: Peaked, No Relationship, Positive, Negative, and U Shaped. The percentage is indicated above each bar.**

### 3.4 Attributes of the Studied System Impact on Relationship Distribution

Experimental Studies, when separated from Observational Studies, was the only system attribute category that was significantly different from the overall distribution ($\chi^2 = 10.76$, $p < 0.05$, df = 4).

Of the recorded experimental studies 21.5% of the relationships were 'Peaked', 25.6% of the relationships were 'No Relationship', 24.0% of the relationships were 'Positive', 24.0% of the relationships were 'Negative', and 5% of the relationships were 'U Shaped' (Figure 6).

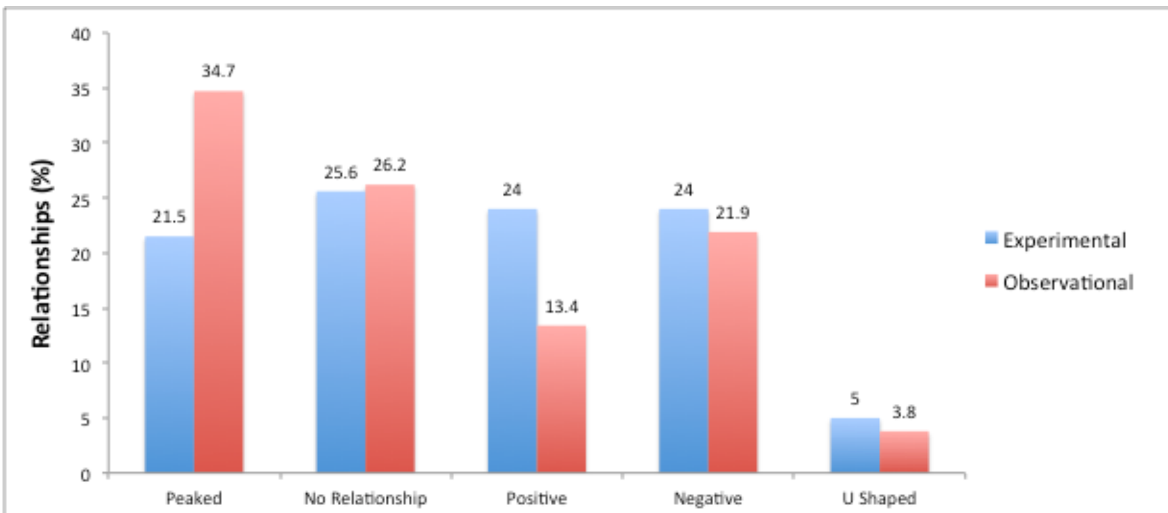


**Figure 6: The percentage of relationships, separate by experimental and observational disturbance, exhibiting each classified shape: Peaked, No Relationship, Positive, Negative, and U Shaped. The percentage is indicated above each bar.**

Categorizing the relationships by all other system attributes had no significant effect on relationship distribution (See appendix).

### 3.5 Differences between this study and Mackey and Currie 2001

Qualitatively, this review of recent studies addressing the IDH agreed with Mackey and Currie's earlier findings. Neither study found that peaked relationships made up the majority of relationships examined. Instead, the four major relationship shapes varied between 10 to 35% of the overall data set, and U Shaped relationships were the least common relationship shape.

The overall proportion of published relationships that used each diversity measurement also remained consistent across studies. Mackey and Currie documented that 59% of relationships measured species richness, 14% of relationships measured species evenness, and 27% of relationships measured species diversity (Mackey and Currie, 2001). The present study documents that 61% of relationships measured species richness, 12% of relationships measured species evenness, and 27% of relationships measured species diversity.

Some similarities also existed with the distribution of relationships for each diversity measure. Both studies saw an elevated number of 'No Relationship' outcomes when looking at species evenness studies, as compared to studies that used species richness and species diversity measurements.

Quantitatively, however, the two studies had significantly different results for both the overall distribution of relationships and the distribution of relationships for each diversity measure (Overall $\chi^2 = 120.1$, Species Richness $\chi^2 = 103.6$, Species Evenness $\chi^2$ = Undefined, Denominator Zero, Species Diversity $\chi^2 = 107.3$, $p < 0.05$, df = 4). The major differences between studies is that this study found a higher percentage of peaked relationships and a lower percentage of non-significant relationships than Mackey and Currie for all diversity measure types.

The impact of different disturbance measurements and system attributes on the distribution of relationships could not be compared to Mackey and Currie's original study. Mackey and Currie (2001) used the proportion of variation explained by each factor to examine the impact of these factors on the overall averaged relationship shape, which is outside of the planned scope of the current study and therefore could not be directly compared.

# Chapter 4 : Discussion

## 4.1 Validity of the Intermediate Disturbance Hypothesis

There is widespread belief that a strong relationship exists between diversity and disturbance and that the shape of that relationship should be a peak around intermediate disturbance. However, just as Mackey and Currie found in their 2001 meta-analysis, my review found that the actual data are more ambiguous than theory suggests. Peaked relationships were not seen in the majority of studies and made up only 32% of the overall data. Instead of a majority of peaked relationships, relationships of all shapes were seen with no single shape making up a majority.

None of the system conditions considered here had a majority of peaked relationships. The highest percentage of peaked relationships, 40%, was seen for natural disturbances (when separated from anthropogenic disturbances), but this result was not statistically different from the overall distribution of relationships. This would suggest that the discrepancies in the data surrounding the IDH might not be the result of the IDH only applying to certain systems, but might come from some deeper conceptual flaw with the IDH. In fact, the only significant deviations from the overall distribution of relationships were decreases in the proportion of peaked relationships, seen in experimental disturbances and when using a ‘time since last disturbance’ gradient.

### 4.2 Explanations for the Distribution of Diversity-Disturbance Relationships

This more even distribution of relationships contradicts much of the literature supporting the IDH, but makes sense in the context of overall disturbance literature. The lack of consistent patterns in diversity-disturbance relationships could be explained by both theoretical ideas that suggest the IDH may not actually apply in some systems and also study limitations where the IDH may apply for a given system, but the studies investigating that system fail to detect it.

One explanation for the wide variety of relationships seen comes from the hypothesis that the intensity and frequency of a disturbance cannot be separated from each other and that it is the interaction between intensity and frequency that shapes the overall relationship. Miller et al. (2011) demonstrated how this interaction might affect diversity-disturbance patterns by modeling competition across an intensity and frequency gradient (Figure 7). The grey region in Figure 7 represents the region of coexistence or higher diversity and the white regions represent areas without coexistence or lower diversity. Different ranges sampled in this system would result in different observed relationships. For example, if you sampled across a frequency gradient, represented by line A on Figure 7, you would see a peaked relationship, but if you sampled across the same frequency gradient, but at a higher intensity, represented by line B, you would see a U shaped relationship. A similar shift can be seen when measuring across intensity gradients at different frequencies: a peaked relationship would be seen if measuring the range of line C, and a positive relationship would be seen if measuring the range of line D (Miller et al., 2011)

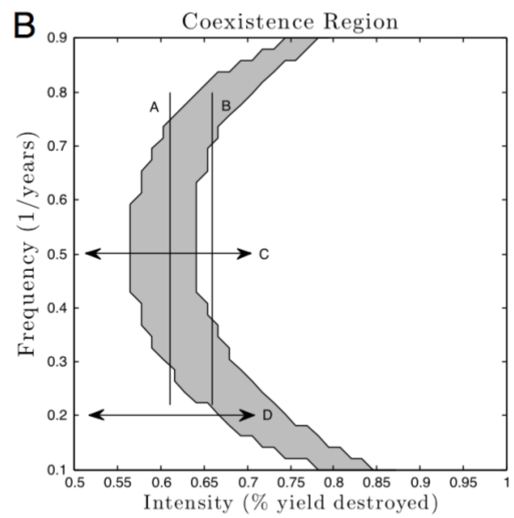


**Figure 7: Graph from Miller et al. 2011 (reproduced with permission), depicting the effect of frequency-intensity interactions on the disturbance-diversity relationship. The areas of coexistence, which will lead to higher diversity in the system, are shaded grey. Vertical lines illustrate the effect of intensity on a changing frequency gradient. Horizontal lines illustrate the effect of frequency on a changing intensity gradient.**

It is thus clear that the relationship observed is dependent on both the range of intensity and frequency sampled. This interaction between frequency and intensity has also been observed experimentally by Hall et al. (2012) in bacterial systems and observationally by Pastro et al. (2011) in Australian wildfires.

Interactions of frequency and intensity can create systems with complex relationships, but even simple relationships can be subject to sampling error. Another explanation for why few peaked relationships are seen comes from the possibility that even in systems with a peaked relationship, it may not be detected, because studies are sampling too narrow a range. Figure 8 demonstrates how this could occur. If only a small section of the overall relationship is sampled, a study could observe a positive relationship, a negative relationship, and a non-significant relationship instead of the true overall peaked relationship of the system.

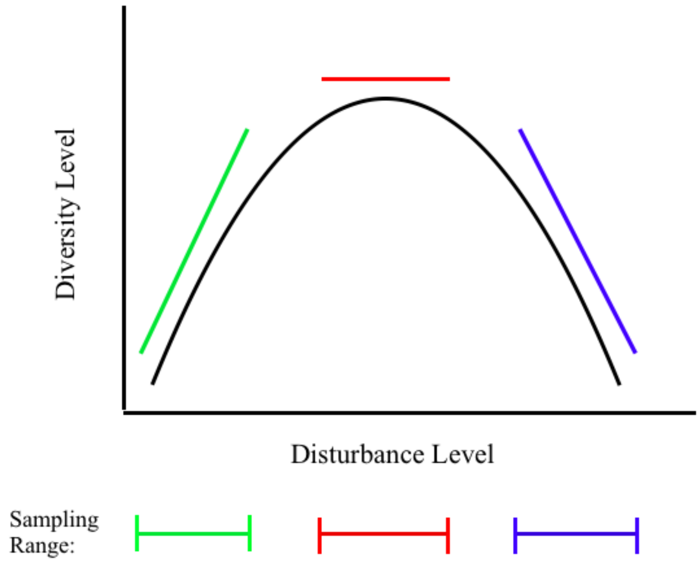


**Figure 8: An illustration of how a narrow sampling range may result in a positive (green), non-significant (red), or negative (blue) observed relationship despite an overall peaked relationship in the system.**

Another rationale for why peaked relationships are not seen in the majority of cases is that many systems do not meet the conditions of the IDH. For a system's diversity to be linked to disturbance, the system needs to be driven by a competition hierarchy. If there is no superior competitor in the system, to drive low diversity under low disturbance, then disturbances would not be expected to alter diversity in the way predicted by the IDH. In systems like these, processes other than disturbance could be the dominating force influencing diversity. In that case, hypotheses like the productivity-diversity hypothesis would be more applicable for explaining diversity in the system and system characteristics like nutrients or non-competition biotic interactions may be more important drivers in the system.

**4.3 Issues with Variation between Studies**

Besides theoretical explanations for the distribution of relationships observed, there are also explanations stemming from how the diversity-disturbance relationship studies examined in this review are designed and how this review treated this variation in design. Every author included in this review invoked the IDH, designed their methods, and interpreted their data in a slightly different way. This makes comparing studies difficult, as it's hard to standardize their interpretations and obtain a balanced analysis.

To properly compare results each study would have had to follow the same guidelines and examine the system on the same scale of detail. This is difficult to accomplish, as resources, the target question, and interpretation of the data will vary from study to study. To explore how variation in design and interpretation could impact the relationships seen, I will detail the most common discrepancies between studies:

1) What is a disturbance? Different people define disturbance in different ways. Disturbance is commonly defined as a destruction of biomass leading to the opening up of space and resources which can then be utilized by new individuals (Roxburgh et. al, 2004), but the idea of disturbance can be expanded to include any change in an environment. This leads to a grey area between disturbance and stress and creates difficult questions about what constitutes a disturbance: Are waves a disturbance? Is changing water salinity? Is a change in the nutrient level of the soil? If these disturbances conflict with the definition of disturbance used in theory then predictions may not pertain.

2) How should disturbance be measured? Ranking the level of a disturbance can be difficult if there is not a clear measurement available, especially when estimating the level of disturbance after the disturbance has already occurred. Some studies attempt to fill this gap of

knowledge by using biotic factors, such as intensity by percent cover or time since last disturbance through successional stage, but these biotic factors can add bias into the measurement. The diversity-disturbance relationship compares a level of disturbance to the biological state of the system; if the biological state of the system is used to measure the level of disturbance the argument becomes circular. Another issue with measuring disturbance comes with how to treat mixed disturbance gradients. Often multiple types of disturbance will occur in an area and make sites difficult to compare. Can a forest that experienced fire and flooding be compared to one that experienced grazing and flooding? Is it possible to compare farming to construction across a 'land use' gradient? Many studies measuring anthropogenic disturbances attempted to create a standardized gradient to weigh and compare different disturbance types, but it can still be difficult to properly rank the level of disturbance or create an analytical weighted gradient. For example, creating an agriculture intensity gradient with multiple crop types (Zheng et al., 2017) or a human land use intensity gradient with construction, livestock grazing, and mowing (Kati et al., 2011). These gradients can be weighted in multiple ways and thus be difficult to compare systematically.

3) What scale should be used to measure a disturbance gradient? As discussed in previous theoretical points, the scale that disturbance is measured on impacts the relationship seen. When using too narrow of a gradient, a peaked relationship can be observed as positive, negative, or non-significant depending on the range over which the gradient is sampled. Deciding how wide a gradient should be used however, can be difficult. Some studies looking at a forest consider 60 years as a long time since disturbance (Lu et al., 2016), while other studies consider 200 years a long time since disturbance (Yeboah et al., 2016). Each gradient needs to be calibrated to the individual characteristics of the system, but it can be difficult to confidently capture the full

gradient. This can also be an issue when determining how many levels to record. Three levels of disturbance are required to even theoretically see a peaked relationship, but sometimes three data points are not enough. If those three data points are part of a larger trend, a false relationship could be concluded. This can also be an issue when determining what constitutes an 'intermediate' level of disturbance. Some studies noted and then excluded from this review only measured two data points, saw a positive relationship, and then concluded a peaked relationship using the justification that the study did not capture the full gradient and only measured up to an 'intermediate' level of disturbance.

4) What diversity measure should be used? The results of this review demonstrate that different diversity measures can create different relationships. Relationships using species evenness as a diversity measure were significantly different (Figure 4) from the overall distribution and showed the highest percentage of non-significant relationships across any category, 39%. Although the species richness and species diversity distributions of relationships were very similar, species richness and species diversity relationships within single studies were often different. There can also be variation within each diversity measurement. For example, Shannon's index and Simpson's index may give different results although both are a species diversity measurement, as will alpha and beta diversity (Pastro et al., 2011). It can be difficult to decide which diversity measure to use, as each comes with their own assumptions and limitations. Diversity measurements are also limited by a lack of community information. This review only addresses the overall diversity of a community. If the overall diversity remained constant after a disturbance it was labeled as a non-significant relationship between diversity and disturbance, whether community composition shifted or not. These small changes could have large impacts on the function of the ecosystem and should be considered.

5) How should a ‘peak’ be determined? This review trusted study author interpretation to determine the shape of the diversity-disturbance relationship seen, but there was variation in the method used to determine this shape. Some studies used various statistical measures to see if a higher or lower level of diversity was seen between treatments, while other studies used fitted lines to see the proportion of variation explained. This lack of standardization could create issues when comparing results across studies.

6) How should analyses that included multiple diversity-disturbance relationships be reported? Most papers reported multiple relationships. Many of these relationships were different diversity measures or different organisms, for example bird vs. squirrel reaction to fire, but there was still subjectivity in how the relationships were categorized and how many relationships each study published. One of the largest discrepancies occurred when determining a new relationship for each ‘new’ habitat. Data from multiple sites are often combined to create a gradient of a single disturbance type. These multiple sites could be sites in different areas of a single forest, sites in different forests across the state, or sites in different forests across the world. Depending on how the data is broken into categories different relationships will be observed. Some studies summarize their data in one relationship, while others treat each new site as a new relationship. This could potentially skew the overall proportion of relationships seen in the literature, especially in cases where breaking the habitat into multiple sectors creates relationships of differing shapes. Discrepancies also existed when diversity was sampled on different spatial scales, in different seasons, and at different levels of community organization. While general guidelines for what relationships to record were used during data collection for this study, not all discrepancies could be accounted for. Ultimately, each study’s decision about what factors to

represent as separate relationships influence the overall distribution of relationships and weight the results of this review.

### 4.4 Issues with Publication and Reporting Bias

There could also be bias affecting the results coming from publication bias and the 'file drawer effect'. Since the IDH is a prominent theory, a study might be more likely to be published if it reports a peaked relationship than a non-significant relationship.

Selective reporting may introduce bias as well. If a study stumbles upon a peaked relationship they might report the result and make it the focus of their paper, but they may be less likely to invoke the diversity-disturbance relationship if it is not significant or not what they expected. This could create an artificially high level of peaked relationships in all categories.

This trend could explain why experimental studies and time since last disturbance studies reported fewer peaked relationships. Experimental studies may be more likely to report their results even if they are non-significant, because there is a clearer established research question than in a community survey. Time since last disturbance studies may have fewer reported peaked relationships because there are other prominent explanations for how diversity changes via succession, so there may be less expectation for a peaked relationship.

### 4.5 Recommendations

There are many issues with how disturbance-diversity relationships are recorded and published. These issues cannot be easily addressed, but if we desire a clearer picture of the disturbance-diversity relationship they should be discussed and recognized as affecting the relationships observed.

While there will always be some areas of subjectivity in recording relationships, there are still some basic guidelines that if used would create a more standardized data set: 1) Report the nature of the disturbance and the details of the system they are investigating and justify why they expect the IDH to apply in their system. 2) Record data at three levels or more, across as large a disturbance gradient as possible. 3) Record the level of disturbance via a direct non-biotic measure. 4) Record the intensity AND frequency of a disturbance to account for interaction between the two gradients. 5) Select sampling area carefully and recognize other environmental factors that may influence the relationship. 6) Outline the research question before conducting the study to avoid issues of separating out multiple relationships or cherry-picking data.

**4.6 Future Directions**

This review focuses on testing the IDH by cataloguing the distribution of relationships seen in diversity-disturbance literature, but other potentially interesting research questions have arisen during the process of data collection.

This study agreed with Mackey and Currie (2001) in terms of its general conclusions, but the exact distribution of relationships seen conflicted with the results of Mackey and Currie (2001). This distribution shift across time could be the result of multiple different factors. It could be a side effect of more studies focusing on diversity-disturbance relationships or it could have a more sociological source. If publication or reporting bias is influencing the proportion of relationships published in the literature, the distribution shift could be linked to a rise in popularity of the IDH. On the other hand, studies published after 2001 may be influenced by Mackey and Currie's conclusions and the knowledge that peaked relationships are not always expected. If a systematic review was conducted spanning pre-1978 to the present, the distribution of relationships could be compared across time to see how this shift might be occurring.

Alterations to the relationship categories used is another potential area of research. Most studies fit into the five categories (Positive, Negative, Peaked, No Relationship, U Shaped) used in this review, but two studies recorded a bimodal shaped relationship. Gingold et al. (2010) saw a bi-modal relationship between the diversity of marine nematodes and across a tidal exposure gradient and Bartels and Chen (2015) saw a bi-modal relationship between the diversity of macro-lichen and a time since last fire gradient. This bimodal relationship can be explained through the findings of Miller et al. (2011). Miller et al. (2011) proposed that the diversity-disturbance relationship seen in a study is highly dependent on the aspect of disturbance studied and that at certain intensities bi-modal relationships between frequency of disturbance and diversity might be observed. If you extend line B in Figure 7, then you would see a bimodal distribution of diversity. This suggests a possible sixth shape, illustrated in Figure 9, to consider while categorizing disturbance-diversity relationships. It is also important to consider that if researchers were not expecting a bi-modal relationship or if they used a quadratic modeling formula to determine the relationship shape, the bi-modal relationship would likely be recorded as no relationship.

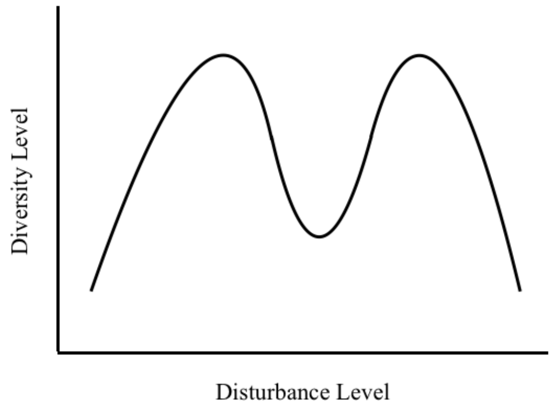


**Figure 9: An example of a bimodal relationship.**

Finally, there could be system conditions not addressed in this study that might influence the proportion of peaked relationships seen. This study looked at multiple characteristics of the disturbance and the community, but did not analyze cross sections between these characteristics. It is possible that the IDH is only valid under very specific conditions. In that case, separating out single attributes (for example, aquatic vs. terrestrial systems) may not influence the distribution of relationships, but targeting combinations of attributes (for example, aquatic sessile systems with natural disturbances) might influence the results greatly.

As technology improves, these questions might be able to be answered more easily. This review was conducted using the Web of Science database, improving on the CD and hardcopy papers used in Mackey and Currie's study, but the papers of this review were still collected through manually reading and sorting abstracts. Automated content analysis may be the next step for improving the efficiency and feasible scope of literature reviews. Automated content analysis uses groups of algorithms to identify concepts within papers and sort them by relevance, greatly decreasing the work necessary when dealing with the exponentially growing scientific literature (Nunez-Mir et al., 2016). With the use of automated content analysis, the research questions proposed in this paper may be easily answered in future literature reviews.

## Chapter 5 : Conclusions

The results of this study cover 11 years of diversity – disturbance literature, 245 studies, and 581 documented relationships. Combined with the 85 studies and 197 relationships from the 12-year time period studied by Mackey and Currie, generates an incredible amount of information. This study both reinforces and updates the conclusions of Mackey and Currie. It shows that peaked relationships are not the majority of relationships seen and that the diversity-disturbance relationship cannot be fully described by the IDH.

Overall, when looking at the data and the theoretical concerns there does not yet seem to be a single unifying diversity-disturbance theory that applies to all systems. The IDH is a useful tool for thinking about how these systems work, and is relevant when thinking about competition driven systems, but it cannot be expected to apply uniformly and explain all empirically observed results.

Systematic reviews are important as they can determine patterns that would otherwise not be easily seen. No one has time to read every paper that is published and the ones that are highly read are rarely the papers that have presented no results. This can create a skewed perception of support for any theory. Individual experiments can be used to draw conclusions about specific systems, but to make conclusions about unifying theories a wider data set is necessary. With current technology and databases, that data set is available; it just needs to be synthesized. Only through synthesizing data and systematic reviews can we get a full accurate picture of what is happening.

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## APPENDIX

The details of the 245 studies and 581 diversity-disturbance relationships used in this thesis can be found alongside this thesis in the collection of Penn State Electronic Theses for Schreyer Honors College.

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