RESPONSE DIVERSITY AND ECOSYSTEM STABILITY IN THE WESTERN GHATS

by

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Certificate

This is to certify that this dissertation entitled **Response Diversity and Ecosystem Stability in the Western Ghats** towards the partial fulfilment of the BS-MS dual degree programme at the Indian Institute of Science Education and Research, Pune represents study/work carried out by **Aayush Manchalwar** at the National Center for Biological Sciences, Bengaluru under the supervision of **Dr. Meghna Krishnadas**, Community and Funcitonal Ecology Lab, NCBS during the academic year 2025-26

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Dedication

To my parents, Mohini and Praful Manchalwar, and my sister Laasya, for supporting me in all my endeavors and enabling me to be the best person I can be. I am more thankful than you all will ever know.

And to my beautiful partner, Sahana Kannan, for being the kindest, most loving, and most supportive person I have ever met :).

Declaration

I hereby declare that the matter embodied in the report entitled "Response Diversity and Ecosystem Stability in the Western Ghats" are the results of the work carried out by me at the Community and Functional Ecology Lab, NCBS, under the supervision of Dr. Meghna Krishnadas, and the same has not been submitted elsewhere for any other degree. Wherever others contribute, every effort is made to indicate this clearly, with due reference to the literature and acknowledgement of collaborative research and discussions.

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Abstract

My thesis deals with the recently developed concept of response diversity, applying it to the Western Ghats of India. Simply put, this is a measure of the variation in organismal responses to the environment, and is thought to be a driver of ecosystem stability. I quantify this for the Western Ghats and also assess its relationship with stability directly. In doing so, my research becomes the first of its kind to apply this concept to the Western Ghats and joins a very small list of studies that empirically test the response diversity-stability relationship.

My research found that response diversity does not track with traditional biodiversity measures in the Western Ghats. This is contrary to *a priori* expectations and warrants further examination. Furthermore, ecosystem stability also followed unexpected patterns, showing no relationship with two different diversity metrics. Combined, my results indicate lacunae in our understanding of both the diversity-stability relationship and the patterns of stability in the Western Ghats. By setting up the foundations, they open up multiple avenues for future analysis of stability and its drivers in the region.

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I would like to begin by thanking Dr. Meghna Krishnadas for her trust in allowing me to develop my own ideas and for her guidance when these ideas needed it. This thesis would not be possible without her supervision and insight, and I am highly grateful for the same.

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Contributions

Contributor name	**Contributor role**
Aayush Manchalwar, Meghna Krishnadas, Sam Ross	Conceptualization Ideas
Aayush Manchalwar, Meghna Krishnadas	Methodology
RStudio, R v4.5.1	Software
-	Validation
Aayush Manchwalar	Formal analysis
Aayush Manchalwar	Investigation
Meghna Krishnadas	Resources
Aayush Manchalwar	Data Curation
Aayush Manchalwar	Writing - original draft preparation
Aayush Manchalwar	Writing - review and editing
Aayush Manchalwar	Visualization
Meghna Krishnadas	Supervision
Meghna Krishnadas	Project administration
-	Funding acquisition
Claude Sonnet 4.6	AI attribution

Claude Sonnet 4.6 was used to refactor and debug code in sections 2.2, 2.3, 2.5. It was then verified and appropriately edited before usage

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Chapter 1

Introduction

1.1 Ecosystems, processes, and services

An ecosystem is defined as a biotic community or assemblage and its associated physical environment in a specific place. The main components of this concept are the abiotic and biotic factors and interactions between them (Pickett and Cadenasso, 2002). Specifically, interactions between organisms are termed ecological processes, and they frequently regulate the dynamics of ecosystems and the structure and dynamics of biological communities. Ecological processes in combination with environmental interactions in turn give rise to ecosystem processes, which are essentially defined as changes in the amounts and fluxes of material in an ecosystem (Mace et al., 2012).

These ecosystem processes confer ecosystems with functions or features that are desirable to humans for a large variety of reasons, ranging from basic needs such as food and shelter to moral or aesthetic criteria. All these benefits are largely grouped together as so called "ecosystem services". Services may be useful in and of themselves, or may be transformed into goods via additional capital input (Mace et al., 2012). Hence, ecosystem services are valuable to people, and it is in our best interests to ensure optimal provision of the same.

An example tying together the concepts outlined above: consider a forest ecosystem. A crucial process within this ecosystem is biomass production. This in turn leads to large tree populations (i.e., an ecosystem service), which can be beneficial as is, or be further utilised for timber - a commercial good.

It is clear to see that spatio-temporally consistent provision of ecosystem services is highly desirable. In addition, one would also want ecosystems to resist disturbances (environmental or anthropogenic as they may be), and when affected, to recover rapidly and restore prior levels of service (Donohue et al., 2013, Pimm, 1984). These ideas are bought together under the umbrella of "ecosystem stability", a multifaceted and complex concept which has been a core focus of ecology since the 1950s (K. S. McCann, 2000).

1.2 Ecosystem stability

Ecosystem stability encompasses multiple metrics, all capturing different ideas. Expanding on the brief description in the previous section below (White et al., 2020):

- Variability - this represents the temporal stability in the ecosystem output of a given place. It aims to capture information about how ecosystem productivity fluctuates away from its typical behaviour, and can be estimated as the coefficient of variation or variance in the relevant ecosystem function.
- Resilience - quantifies the post-disturbance recovery of an ecosystem function/property back to its stable state. It is often characterised as a rate (Pimm, 1984).
- Resistance - the capacity of an ecosystem to absorb disturbances is called resistance, and it is usually calculated as the change or drop in ecosystem function immediately after a environmental disturbance (Pimm, 1984).

The three metrics above can have a variety of relationships within themselves, depending on type of disturbance (Donohue et al., 2013). This makes it important to consider and study each one separately when it comes to questions of ecosystem management and/or conservation. Understanding the dynamics of these may be crucial to our understanding of ecosystem stability.

1.3 Determinants of ecosystem stability

Classical understanding of ecosystem stability posits biodiversity as the primary driver of stable function provision. Early research suggested that in addition to increasing the productivity of ecosystems, biodiversity also conferred stability, with more diverse systems being more resistant in their ability to resist invasions or in the magnitude of their fluctuations (MacArthur, 1955; Miller and Odum, 1954; Richardson and Pyšek, 2007).

This was thought to occur via a range of mechanisms. For example, high complexity of a food web (i.e. high diversity) would mean that the energy input into the lowest trophic levels via the sun has a large number of paths to transfer upwards through the producer-consumer(s) chain. This in turn implies that an overabundance of any one species would have a reduced impact on the whole food web, since there would be a large number of pathways through which the excess energy could be distributed. Conversely, an abundance of species would also imply a larger buffet of prey for predators, minimising the effect of the reduction or disappearance of any specific species (MacArthur, 1955).

However, using randomly structured model communities, it was shown that diversity per se did not increase stability (in the sense of dampening population fluctuations), but rather decreased it (May, 1973, Pimm and Lawton, 1978, Yodzis, 1981). Subsequent research indicated that richness tends to stabilise ecosystem functions and/or processes when complexity is high (Ives et al., 1999).

Yachi and Loreau then formalised the general idea of biodiversity stabilising ecosystems in 1999, bringing forth the insurance hypothesis - in a variable environment, aggregate ecosystem properties (e.g. total biomass or production) will vary less in more diverse communities because declines in the performance or abundance of some species or phenotypes will be offset, at least partly, by smoother declines or increases in others (Yachi and Loreau, 1999).

The insurance hypothesis forms the basis of much diversity-stability research, with a large variety of results. Summarily, it has been established that biodiversity is merely the face of stability - that is to say, stability acts via many different specific mechanisms, which themselves may or may not result in high diversity communities (K. S. McCann, 2000; Shade, 2017).

Broadly speaking, it is asynchronous or compensatory dynamics that determine the diversity-stability relationship of ecosystems (Craven et al., 2018; Sasaki et al., 2019). The specific mechanisms vary from system to system and a few stabilising ones are outlined below:

- Variable interaction strengths - the presence of a range of interaction strengths in a food web/ecosystem adds stability to it. This is because weak/intermediate interactions maintain population densities away from zero by dampening consumer-resource oscillations, and this distance makes extinction of any species statistically unlikely (K. McCann et al., 1998).

- Trophic flexibility and food web rewiring - The adaptive food choices of consumers allows for rewiring of food webs in complex systems facing environmental change - in static food webs without these adaptive foragers, complexity in ecosystems is destabilising and negatively affects long-term community persistence (Kondoh, 2003).
- Dominant species - Empirical research provides strong evidence for the mass ratio hypothesis, which posits that most ecosystem functions, including stability, are characterised by the traits of the dominant or abundant species (Sasaki and Lauenroth, 2011). Their removal may increase species diversity, but this is not necessarily reflected in stability (Lepš, 2004; Wayne Polley et al., 2007).

Adding to the above, a new driver of stability called response diversity has also emerged (Ross et al., 2023). This concept forms the crux of this thesis, and in order to understand it we must first go through the history of the biodiversity-stability relationship.

1.4 A brief history of biodiversity and stability

The relationship between biodiversity and ecosystem function has been a focus of ecology for a long time. In particular, it has been posited that biodiversity positively contributes to ecosystem stability and functionality (Tilman et al., 2006). This was formalised in 1999 by Yachi and Loreau, who formed the insurance hypothesis - which suggests that in more diverse communities, variation around ecosystem function will be relatively reduced since a decline in the performance of some species or phenotypes will be compensated for at least partially by increases in the performance of others (Yachi and Loreau, 1999). More broadly, biodiversity is said to have two kinds of effects on ecosystems: one is a 'performance-enhancing' effect, wherein the temporal mean of function is increased, and a 'buffering' effect, wherein the temporal variability is reduced (Yachi and Loreau, 1999).

Literature shows that most studies use basic diversity metrics such as species richness (Balvanera et al., 2006; Cardinale et al., 2007). In general, these studies show that on average a polymixture of species performs better than any of its constituent species individually. However, they tend to focus on mechanisms rather than on providing empirical evidence of stable, optimal ecosystem function, and often have little relevance for real-world systems (Srivastava and Vellend, 2005). Further, the evidence that does exist comes from environments where both the number and identity of species is under experimental control, and this may not accurately reflect scenarios in actual communities. In addition, as previously mentioned, richness itself need not elevate function and/or stability (May, 1973).

Alternatives to richness as a diversity metric come from the field of functional ecology, with an emphasis on traits of species. Traits are roughly categorised into two groups: effect and response traits. Response traits are those that mediate the interactions between environment and species, determining how a particular phenotype/species responds to environmental variables such as soil moisture content, temperature, etc. An example of these is seed mass. On the other hand, effect traits are those traits that capture information regarding the contribution of a species to its ecosystem's function, and an example of the same is nitrogen fixation capacity.

Functional diversity is thus measured as the ranges and values of functional effect traits of species in a community (Díaz and Cabido, 2001; Hooper et al., 2005). This is more useful than taxonomic measures like species richness since it presupposes a mechanistic link between diversity and ecological processes (Cadotte et al., 2011; Díaz and Cabido, 2001).

Therefore, a loss of any functional types would lead to loss of some ecosystem functions. Important to note here that the aforementioned loss is of a *functional type*, not a species. That is to say, while species loss is important from a conservation/moral standpoint, it may not necessarily have a functional impact if there are other species filling the same functional role that the extinct species did. This is called functional redundancy. However, functional redundancy alone is insufficient to confer stability to ecosystems in fluctuating environments, and studies show that communities with high functional redundancy are not necessarily highly stable in generation and provision of ecosystem functions (Elmqvist et al., 2003; Laliberté and Legendre, 2010). The missing link here is response diversity.

1.5 The concept of response diversity

Response diversity is defined as a metric capturing the variation in species responses to environmental factors. It contains information about the range of different responses to some environmental factor, and response diversity is *a priori* expected to enhance aggregate ecosystem stability (Elmqvist et al., 2003; Mori et al., 2013). For example, Ives and Carpenter, 2007 found that in models of randomly structured competitive communities, response diversity acted as a stabilising force opposed to the destabilising nature of inter-specific interactions. They concluded that species-environment interactions, rather than species-species interactions, were more important for community stability.

Response diversity, or RD, acts as a mechanism underlying the insurance effect outlined by Yachi and Loreau in 1999 - namely that biodiversity stabilises ecosystem function because within a biodiverse community, declines in performances of a few species are likely to be offset by smoother declines or increases in performances of other species. RD has been under investigation for the last two decades, with reviews providing strong theoretical models for its conceptualised link with stability (Mori et al., 2013). Figure 1.1 illustrates the differences between response diversity and functional redundancy.

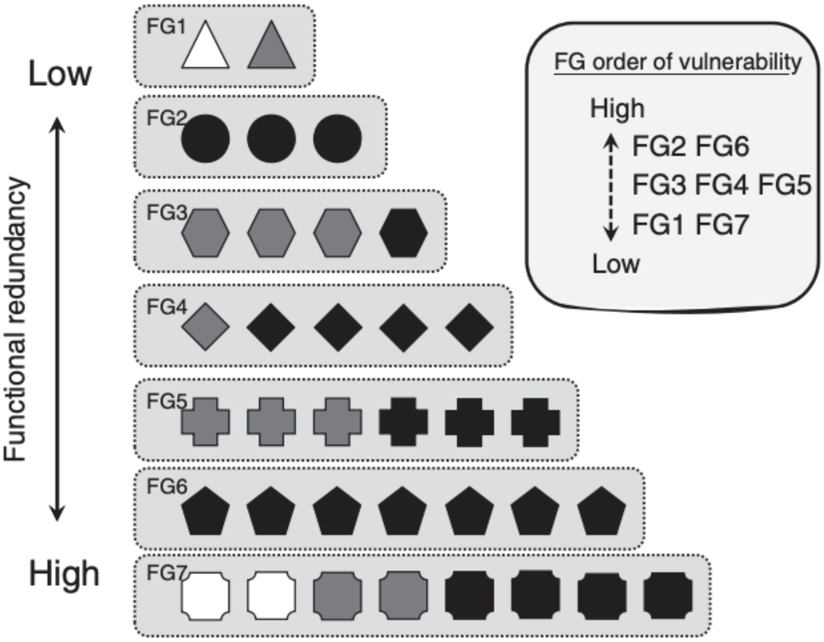

Figure 1.1: Each instance of a symbol represents a different species, with its shape representing its functional effect traits and its colour representing its functional response traits. See text for explanation. Taken from Mori et al., 2013

The figure above represents a scenario wherein there are different groups or communities. Each community has a different number of species with similar effect trait collections (number of shapes), and therefore each community has differing levels of functional redundancy - FG1 being the lowest, FG7 the highest. Across the groups, there is variation in the range of within-group response traits (shades) - and this represents different levels of response diversity. FG6, despite being more functionally redundant, has less response diversity than FG5. In the traditional understanding, FG6 would be more stable since it is more functionally redundant. However, consider a scenario where these communities exist in a fluctuating environment. In this case, any environmental driver that is negatively correlated with the species in FG6 would wipe out all of them, since there is low response diversity in it. Ecosystem function would drastically drop. The same environmental driver in FG5, however, would cause extinction in 3 out of 6 species, and ecosystem function would persist. Thus this toy example illustrates that utilising traditional measures of biodiversity (such as richness or functional effect diversity) as proxies for the biodiversity-stability relationship may be unwise, and that RD may be a better indicator of ecosystem stability and resilience. This combined with studies showing that these traditional measures might be uncoupled with response diversity, indicates that conclusions and recommendations from earlier studies that used the traditional measures may be suspect (Mori et al., 2013).

1.6 Measuring response diversity

There is a large variation in the methodologies used to estimate response diversity. Some borrow from previous functional ecology literature by using the FDis concept that measures dispersion in response trait space (Hordley et al., 2021; Schnabel et al., 2021. Others take a binary approach that asks if some species-specific interaction term in a multi-species model of, say, abundance versus environment crosses a significance threshold - if it does, it is assumed that species differ in abundance and thus RD exists (Winfree and Kremen, 2009). A third approach considers some performance measure of a species as a function of an environmental variable, and then estimates RD as the range of slopes of this performance-environment relationship (Leary and Petchey, 2009). This thesis will utilise an approach similar to the one adopted by Leary and Petchey in their 2009 paper - expanded upon in Ross et al., 2023. The reasons for this are given below.

A systematic review of the literature turned up 46 studies that empirically measure response diversity (Ross et al., 2023). Of these, a common theme (28 out of 46 studies) is the usage of 'low-level' traits for RD estimation (Sasaki et al., 2019; Suding et al., 2008). Low-level traits here refer to those that are often assumed, instead of demonstrated, to have relationships with the environment. Examples include specific leaf area, nitrogen content, clutch size, etc. On the other end of the spectrum, high-level traits are those that more directly reflect performance, and these are generally likelier to relate to environmental conditions than low-level traits (Violle et al., 2007). Examples of these include per capita growth rate and carrying capacity (Ross et al., 2023).

The utilisation of low-level traits to measure response diversity has a few conceptual and practical problems. Chief among these is the lack of consensus on which traits are 'functional' (Violle et al., 2007), and this is further complicated by a lack of clarity in delineating whether a particular low-level trait falls into the effect or response camp for a given ecosystem function. For example, specific leaf area or photosynthetic pathway can be considered as either effect or response traits depending on the environmental context (Sasaki et al., 2019; Suding et al., 2008). This problem is considerably reduced when high-level traits are used as performance indicators, since their (by definition) proximity to a species' performance automatically makes them response "traits". Consider the cases of macroinvertebrate abundance, chlorophyll production, and bee mass loss shown in Ross et al., 2023. Each of these are a function of the environment the respective organisms/species exist in, and hence the response-effect conundrum is dissolved.

Practical problems include the scale of sampling effort with regards to low-level traits, the mobile nature of focal organisms, and temporal considerations (when to measure a trait?

Considering the response trait diversity of some average community through time (eg., Craven et al., 2018) ignores temporal community turnover which can weaken the expected RD-stability relationship (De Bello et al., 2021)).

The general framework laid down by Ross et al., 2023 addresses the aforementioned issues by shifting the focus to high-level traits as performance indicators. By using these, the relationship with the environment is measured rather than assumed, as is the case with low-level traits (Ross et al., 2023). The framework proceeds as follows:

1. Fit performance-environment relationships individually for each species in a community/region. Ross et al., 2023 specifically recommend Generalised Additive Models, since they are free of the assumptions of linear regression (homoscedasticity of residuals and normality) and are capable of evaluating a larger range of functional forms (linear, non-linear, or a mixture).
2. Take first derivatives of these models so as to estimate model slopes along the environmental gradient.
3. The variation in this collection of slopes represents response diversity, and a variety of metrics can be used to quantify the same depending on the use case

Of the different ways of measuring RD (Polazzo et al., 2025; Ross et al., 2023), this work will utilise the Imbalance metric proposed in Polazzo et al., 2025 (Eqn. 2.4). It improves on the conceptual limitations of previous metrics such as divergence (Ross et al., 2023), which only took into account the maximum and minimum species responses within a community. On the other hand, imbalance accounts for all species responses and in doing so more directly represents stability.

The aforementioned formulation of imbalance gives large values when all species respond similarly. This is a situation with low response diversity and therefore low stability. On the other hand, low imbalance can either occur via differential species response (i.e. both positive and negative slopes, leading to asynchronous dynamics) as mentioned previously, or if species responses are weak (shallow slopes) in the first place. In both cases, communities are hypothesised to be stable - via compensation and environmental invariance respectively.

1.7 The Western Ghats

In many ways, the Western Ghats of peninsular India provide a suitable system to work with response diversity and ecosystem stability/productivity. Firstly, this is a biodiversity hotspot with a large range of tree species spanning highly variable terrain (Myers et al., 2000). Secondly, the region is being subject to climate change in various ways, most prominently changes in temperature and rainfall (Katzenberger et al., 2021; Rajendran et al., 2012). Climate change is bound to affect biodiversity and ecosystem function in many ways - take for example the paper by Gopalakrishnan et al., 2011 which predicts that the northern Western ghats are especially vulnerable. Thirdly, the precipitation patterns of the region result in the formation of a natural north-south gradient in terms of seasonal drought – such a gradient presents an ideal opportunity to obtain performance-environment curves for species across the Ghats. And importantly, the aforementioned gradient patterns community assemblages in the region. More specifically, research has been carried out suggesting that longer/more intense drought periods might curb geographical ranges of wet-associated species or benefit dry-associated ones (Krishnadas et al., 2021). This in turn results in dry-associated species persisting into less seasonal sites, but not vice-versa – wet-species blink out of more seasonal sites. The implied loss of taxonomic diversity has been verified - Davidar et al., 2005, 2007, show that seasonality heavily influences alpha- and beta-diversity across the Western Ghats, with diversity increasing significantly with decreasing seasonality.

This background leads to the questions addressed in this thesis. Firstly, is it the case that a majority dry-species community (i.e. more seasonal and less diverse) necessarily has less response diversity than a more species-diverse (i.e. less seasonal) community consisting of both wet- and dry-associated species? If this is the case, it may have implications for the stability of the regions which go from having a mixture of wet- and dry-associated species to being dominated by dry-associated species due to climate change and subsequently experience a drop in RD. On the other hand, if communities made up of predominantly dry-associated species show similar or even increased RD with respect to mixed-association communities, one would have to re-assess the suite of traits that have previously been linked with drought tolerance.

The second question arises when one looks at climate change and its predictions in the Western Ghats – projections say that while the dry season will become drier and longer, mean precipitation will increase in the northern and central regions and decrease in the southern region (Katzenberger et al., 2021; Rajendran et al., 2012). In the face of this, it would be highly desirable to understand and empirically establish links between ecosystem stability and response diversity - the expectation being that high-RD regions will have been more stable temporally and hence may be less affected by climatic changes in the future. Towards this end, one could utilise results from the RD estimation study above and combine it with remote-sensed assessments of ecosystem stability - as was done by White et al., 2020 at a country-level scale. Furthermore, it would be interesting to see if a.) the long-established relationship between richness and stability is also seen, and b.) if there is an additional effect of RD over and above that operating via the hypothesised relationship with richness.

To summarise, my thesis aims to answer two key questions about the Western Ghats and response diversity:

- Does the relatively novel concept of response diversity track with more traditional diversity measures in the Western Ghats system? In addition, what is the relationship of imbalance with the abiotic CWD gradient in the region? A priori I expect response diversity to follow a similar pattern to taxonomic diversity, i.e., an increase from North to South. Ergo, imbalance and richness are expected to be negatively related.
- What is the nature of diversity-stability relationships in the Western Ghats? Do they follow the expected patterns? A positive diversity-stability relationship is expected, with lower variability in ecosystem function in the Southern than the Northern Western Ghats - in line with the theorised mechanism of action of response diversity on ecosystem stability.

Chapter 2

Data and methods

2.1 Data

Presence-absence data for 183 species spanning 286 sites across the 1600 km range of the Western Ghats was obtained from Krishnadas et al., 2021. Plots ranged in size from 0.09 to 1 ha, with 61,287 trees sampled. Only species occurring in more than 15 sites across the Western Ghats were considered so as to allow robust estimation of effects.

Drought stress was quantified as the climatic water deficit or CWD (Chave et al., 2014), which is the difference in millimeters per year between rainfall and evapotranspiration during the dry months. It spans from -1006 to -273 in the Western Ghats, with more negative values indicating higher drought stress. CWD data was taken from Krishnadas et al., 2021. Many CWD values were recorded as being the same across multiple sites, and hence sites with the same CWD were grouped and treated as one. This resulted in 143 analytical “units”. All analyses were conducted post-grouping. Within-group spatial spread is reported to check if groups share environmental context and form a meaningful ecological unit. All variables were log-transformed when necessary to account for skew and ranges spanning orders of magnitude.

2.2 Response diversity estimation

Response diversity was calculated following the methodology laid out in Ross et al., 2023. Within this framework, performance-environment curves are required in order to estimate response diversity as a measure of variation in organismal responses (characterised by the slope) to the environment. In this case CWD was chosen as the environmental variable since seasonal drought is known to shape communities in the region (Krishnadas et al., 2021). The performance variable was represented by occurrence probability, with a higher probability for a species in a given environmental state representing better performance within it. This follows from the discussion in Ross et al., 2023, where they call for a focus on high-level traits in response diversity research. Here, high-level traits are defined as those that are proximal to the performance of a species in its environment, and the relationship of these traits with the environment should be measured rather than assumed. Occurrence probability, although not a trait in the traditional sense, fits these criteria: by modelling it using presence-absence data from the field, we subsume all physiological, ecological, and demographic processes and obtain an idea of how the species performs across the abiotic gradient. Moreover, occurrence probability bypasses the need for an idea of the mechanistic link between a trait and the species' performance that has been cited as a shortcoming of previous response diversity studies

Generalised Additive Models, or GAMs, are a semi-parametric extension of generalised linear models that characterise response variables as being dependent linearly on some unknown smooth functions of the predictor variables (Wood, 2017). The models operate by relating some response variable Y to some predictors x_i. A distribution family and link function g for Y are specified, relating the expected value of Y to its predictors as follows:

$$g(E[Y]) = \beta_0 + f_1(x_1) + f_2(x_2) + f_3(x_3) + ... + f_m(x_m) \tag{2.1}$$

In this case, the above simplifies to:

$$g(E[P]) = \beta_0 + f(CWD) \tag{2.2}$$

For the purposes of logistic regression, a binomial distribution family with the logit link function was chosen (Jones and Wrigley, 1995; Wood, 2017). A thin-plate regression spline basis (bs = 'tp') was used for all species, with smoothing parameters estimated by restricted maximum likelihood or REML. The number of knots k was fixed at 10 (default for thin plate splines). GAM diagnostic tests were run using the DHARMa package in R (Hartig, 2024), testing for deviations from the expected distribution and the distribution of residuals relative to the expected value. For every GAM, the deviance explained is reported as the goodness-of-fit statistic (Wood, 2011; Wood, 2017), with AUC as the performance metric (Fielding and Bell, 1997). Sensitivity analysis was done to see if the inclusion of species with non-significant smooth terms for CWD affected imbalance estimation.

Probability of occurrence vs CWD curves were thus obtained for all 183 species in the dataset, and derivatives for these were approximated by central finite differences on the probability scale:

$$dP/CWD = \frac{P(CWD + h) - P(CWD - h)}{2h} \tag{2.3}$$

h was chosen to be 0.5 (mm/year), which is an extremely small step relative to the CWD range (-1006 to -273 mm/year)

The response diversity metric Imbalance is then calculated as per Polazzo et al., 2025. It is defined as the absolute value of the mean species response in a given site as follows:

$$Imbalance = |\frac{1}{S}\sum_{i=1}^{S}\frac{\Delta r_i}{\Delta E}| \tag{2.4}$$

Here, S represents the number of species at a given area. $\frac{\Delta r_i}{\Delta E}$ represents the change in performance Δr of species i for a given change in environmental variable ΔE. In my case, this is equivalent to the absolute mean derivative of the performance-environment curves of the species in a region. We take the absolute value since it is assumed that changes in the response variable r are equally destabilising in both directions (increase/decrease). Overall, values of I close to zero can indicate two stable situations: a community wherein each change in the response variable value of a species has an equal and opposite change in some other species, or a community where all species have weak/shallow responses to the environment. Conversely, larger imbalance values imply larger variability in aggregate community properties.

2.3 Ecosystem stability estimation

Ecosystem stability was assessed using Enhanced Vegetation Index data. EVI reflects the amount of photosynthetic activity (or "greenness") of a region which can be utilised as a proxy for ecosystem functioning of an area via its relationship with above-ground biomass production (Shi et al., 2017; Sims et al., 2006). It is a composite index that takes into account the reflectance of three different wavelengths, corresponding to red, near-infrared, and blue light. The inclusion of the blue band makes EVI particularly useful for high-biomass density estimation since it does not saturate in these conditions, unlike other vegetation indices (Huete et al., 2002).

The data was obtained from the Moderate Resolution Imaging Spectrometer (MODISv6.1, https://www.earthdata.nasa.gov/data/catalog/lpcloud-myd13q1-061) for the period December 2004 to December 2024. 16-day composite images (MODIS product MYD13Q1) were used to obtain an EVI time series for each pixel/site (250mx250m). Variability per unit $v_i$was then calculated as follows:

$$v_i = \mathrm{var}\Big[\mathrm{EVI}(i,\, t) - \underset{u \in m}{\mathrm{mean}}\,[\mathrm{EVI}(i,\, u)]\Big] \tag{2.5}$$

where $\underset{u \in m}{\mathrm{mean}}\,[\mathrm{EVI}(i, u)]$ is the mean EVI for unit i over all observations u across the full study period (2004–2024) falling within calendar month m and var is the variance in the monthly deviation from the mean across all time points t (adopted from White et al., 2020).

2.4 Taxonomic diversity

Taxonomic diversity was measured as the pooled species richness of a site/sites, representing the number of unique species at each CWD level. This is the most commonly used diversity metric in biodiversity-ecosystem function studies (Balvanera et al., 2006; Cardinale et al., 2007; Mori et al., 2013), and hence it acted as a comparative measure to imbalance.

2.5 Statistical analysis

Exploratory analysis was done using Pearson correlations and gradient scatterplots. However, the spatially auto-correlated data (characterised by Moran's I, as calculated on OLS and GAM residuals) and theorised interplay between imbalance, richness, CWD, and ecosystem stability warranted a deeper examination. Towards this end, structural equation modelling was employed. This is a powerful multivariate statistical technique used to test and evaluate multivariate causal relationships. It combines path analysis and multiple regression and is used to analyse structural and causal relationships between variables (Fan et al., 2016). Two main advantages are offered over other statistical modelling approaches. Firstly, SEM paths represent hypothesised causal links. Using previous knowledge and theory, one can construct a notional causal structure and test it using SEMs. This was particularly advantageous in my case, since previous work has posited and/or established links between the variables in my study. For example, between CWD and species distribution/assembly (Krishnadas et al., 2021), as well as between diversity (both richness and response diversity) and ecosystem stability (Balvanera et al., 2006; Mori et al., 2013; Yachi and Loreau, 1999). A second advantage of SEMs is the ability to treat variables as both predictors and responses. This is helpful when the nature and direction of relationships are unknown: between imbalance and richness or CWD and variability, in my case (Lefcheck, 2016).

In this specific study piecewise-SEM was utilised as it allows for the incorporation of varied models with different error structures, allowing me to account for spatial autocorrelation (Lefcheck, 2016). This is done by using generalised least squares (GLS) regression within the SEM. GLS regression incorporates a spatial covariance structure into the error term, allowing residuals to be correlated based on location (F. Dormann et al., 2007). In my case this was the exponential covariance structure, which models correlation as exponentially decreasing with distance. In addition, a "nugget" term to account for spatial variability at scales smaller than the smallest distance between units was also included (Christ, 2009; F. Dormann et al., 2007). The piecewise-SEM includes component models denoting the following: direct effects of CWD on variability, the hypothesised CWD → Imbalance → Variability pathway, the previously established CWD → Richness → Variability pathway, and an unknown Imbalance ↔ Richness link (Fig 2.1).

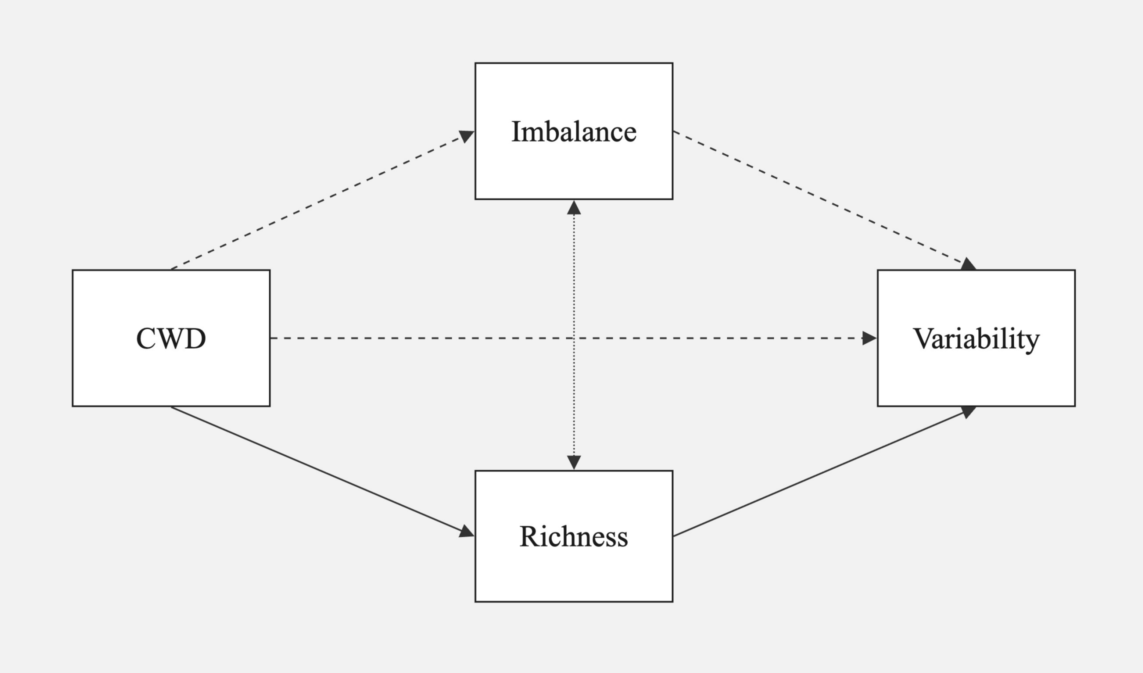

Figure 2.1: The hypothesised path diagram linking CWD, richness, imbalance, and variability. Solid, dashed, and dotted lines indicate known, hypothesised, and un- known relationships respectively

Standardised model coefficients in piecewise SEMs indicate the strength and nature of relationships. A coefficient of $+p$ in the $X \rightarrow Y$ pathway signifies that 1 unit of increase in the standard deviation of variable X corresponds to a p units increase in the same for variable Y. Piecewise-SEMs are evaluated using Shipley's test of directed separation. This tests for the significance of paths missing from the hypothesised pathway given by the component equations. These p-values in turn are combined to give Fisher's C statistic, which follows the chi-square distribution. P-values greater than 0.05 indicate a well-fit model with no significant missing paths (Lefcheck, 2016).

2.6 Software and data availability

All analyses were conducted in RStudio with R v4.5.1 (R Core Team, 2025). Plots were generated using the package ggplot2 (Wickham, 2016). Other packages used were piecewiseSEM (Lefcheck, 2016), mgcv (Wood, 2011; Wood, 2017), dplyr (Wickham et al., 2023), DHARMa (Hartig, 2024), and tidyverse (Wickham et al., 2019).

Data and code for reproducibility is available at https://github.com/aayushm2511/aayushm-masters-thesis.

Chapter 3

Results

3.1 CWD grouping

The spatial spread within CWD groups was calculated as the maximum on-ground distance between sites sharing identical CWD values, in order to assess whether aggregation may have grouped sites from different environmental contexts. Of the 143 groups, 71 had a single plot. The median spread was 0.6 km, with a maximum of 46.2 km occurring in a single group containing only two sites. This indicates that most aggregated groups are spatially compact, making it unlikely that sites from substantially different ecological contexts were grouped together.

3.2 Estimation of response diversity and richness

Generalised Additive Models for all 183 species converged fully. A large variety of CWD responses and their derivatives were observed (Fig. 3.1, Supp. Fig. 5.1), indicating the ability of GAMs as species distribution models. The distribution of EDFs (effective degrees of freedom) for the 183 GAMs (Supp. Fig 5.2) further demonstrates the power of GAMs: while a lot of species showcased near-linear (EDF $= 1$) responses to CWD, there are many that exhibit true non-linearity in responses (EDF ≥ 3).

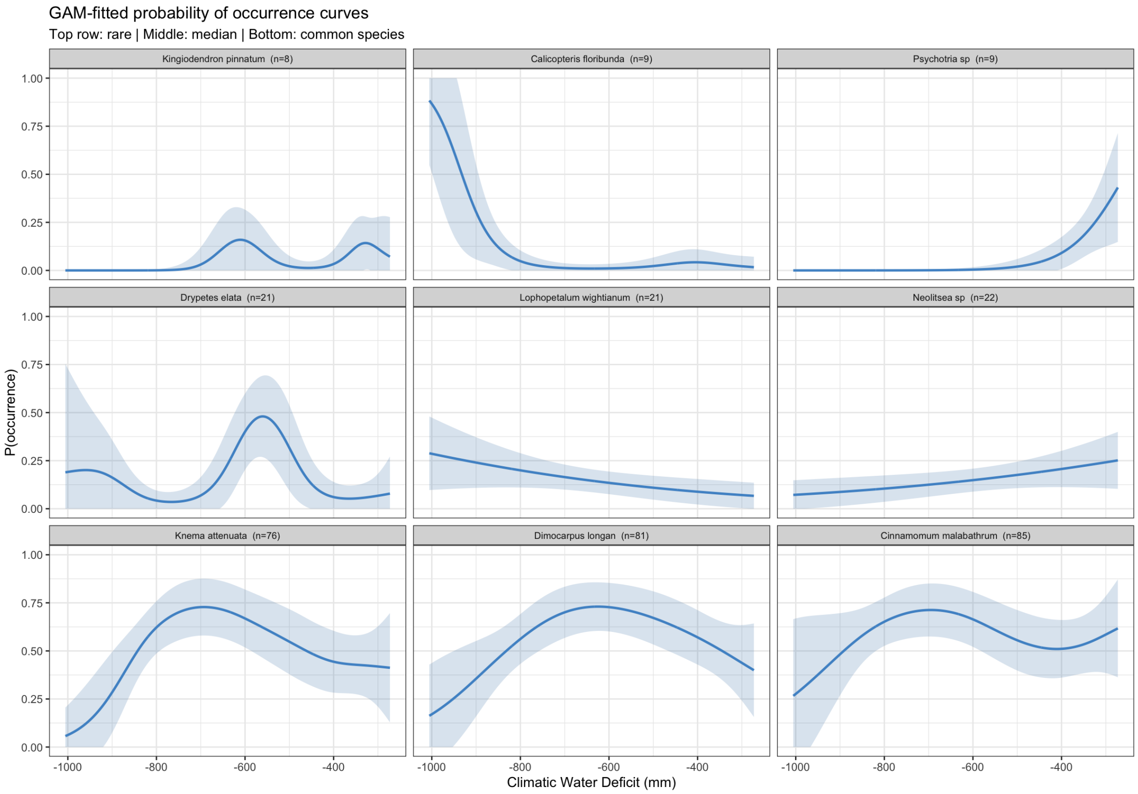

Figure 3.1: Representative probability-of-occurrence curves across a range of species prevalences

Using the probability curves, imbalance was calculated using Eqn. 2.4. It shows weak insignificant correlation with CWD (Pearson's r = -0.16, p = 0.062). Imbalance across the CWD gradient is shown in Fig. 3.2

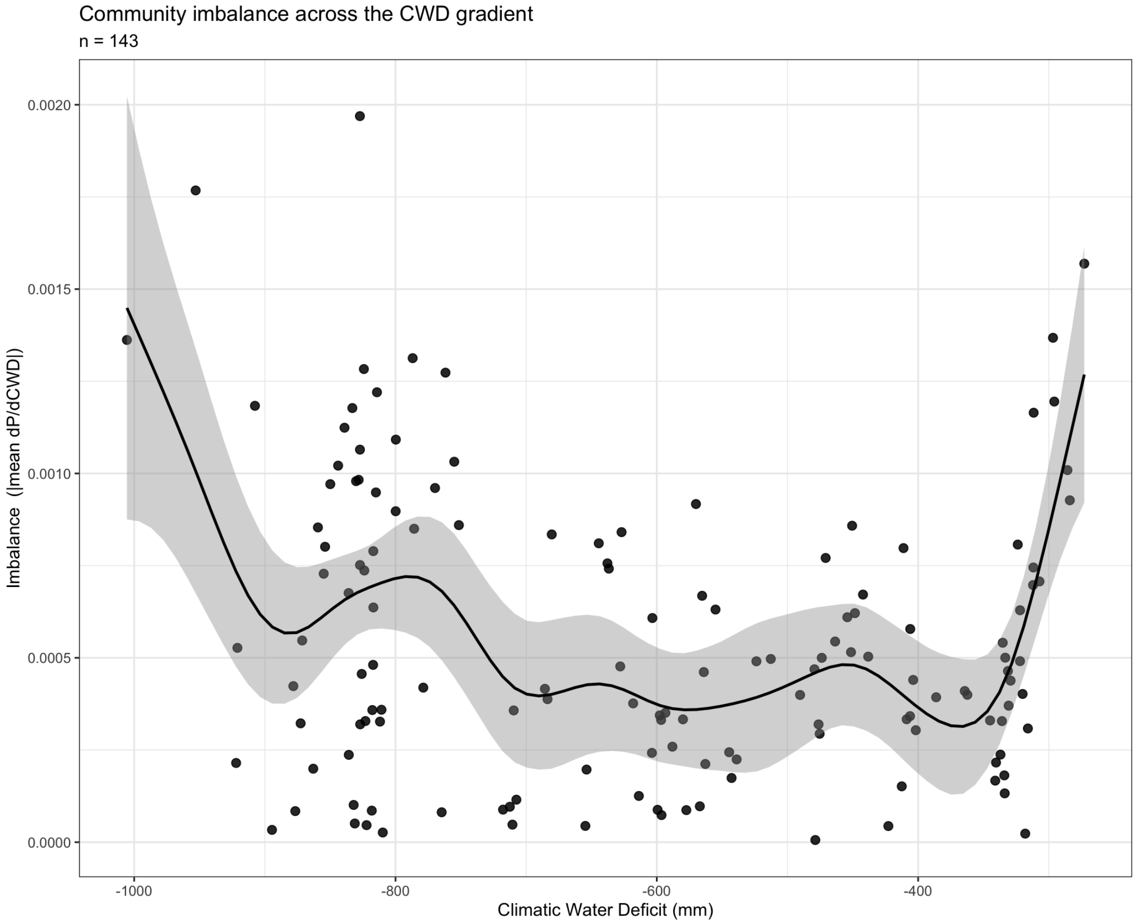

Figure 3.2: Imbalance across the CWD gradient. GAM smoother with k = 15

Of these 183 species, 88 (48%) reported a significant ($p \leq 0.05$) smooth CWD term in the GAM. Sensitivity analysis was conducted by estimating imbalance with the full set of species and then with only the aforementioned 88 species. These were significantly correlated (Pearson's $r = 0.787$, p-value $\ll 0.05$) with similar patterns across the gradient (Supp. Fig. 5.4), and hence it was concluded that inclusion of these species did not impact imbalance estimates significantly. Further analysis included all 183 models.

Two main model evaluation metrics were calculated (Supp. Fig. 5.3). Goodness-of-fit, measured as the deviance explained by a model, ranged from 0 to 64% with a median of 11.8% - to be expected in a models of complex ecological systems, with only one predictor. AUC ranged from 0.48 to 0.96, with a median 0.735 indicating a fair model performance (Çorbacıoğlu and Aksel, 2023).

Fig. 3.3 shows species richness across the CWD gradient. It was measured as the number of unique species per CWD level and ranges from 2 to 99 species with a mean of 35. Richness showed weak-to-no correlation with CWD (Pearson's r = -0.148, p = 0.079), similar to imbalance. A fitted GAM explained only 2.18% of deviance. This was contrary to the previously established richness patterns across the Western Ghats (Davidar et al., 2005, 2007), and warranted further examination. Interestingly, richness and imbalance were significantly negatively correlated (Pearson's r = -0.17, p = 0.048), signalling that sites with a higher number of unique species showed lower imbalance.

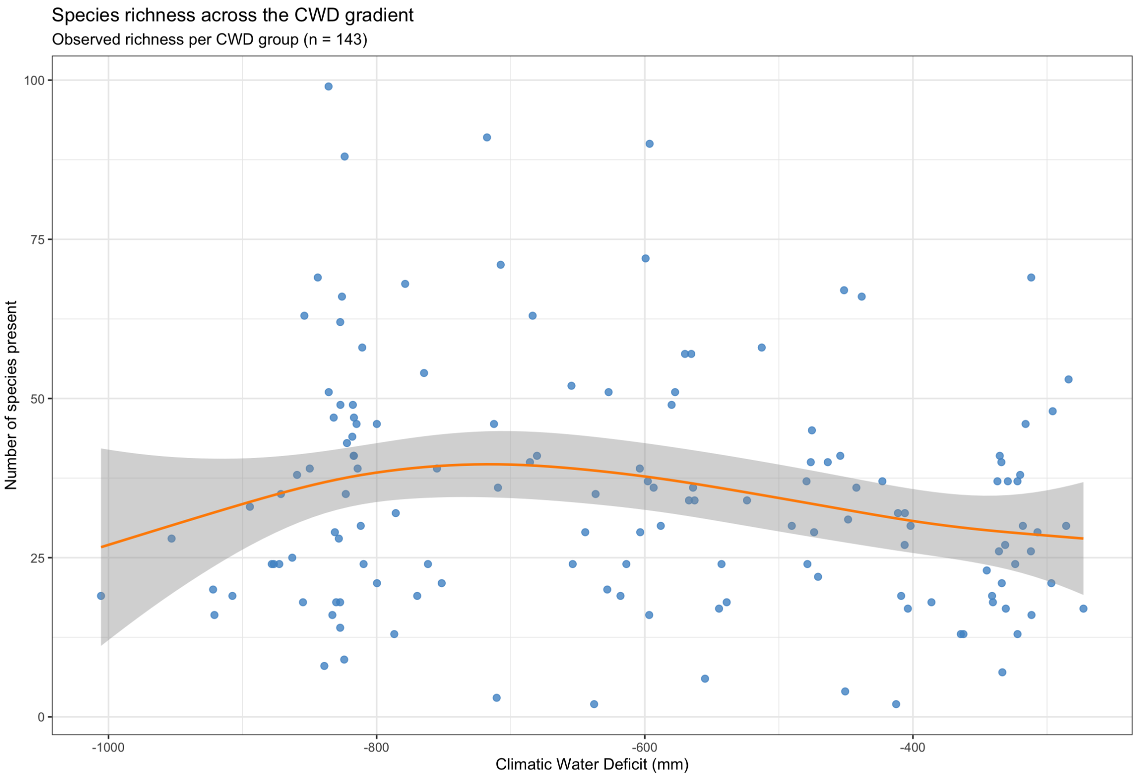

Figure 3.3: Species richness vs CWD. GAM smoother with k = 15.

3.3 Assessing EVI variability

Enhanced Vegetation Index data spanned 20 years, starting from December 2004 and extending to December 2024. Data was acquired using the Application for Extracting and Exploring Analysis Ready Samples (AppEEARS, https://appeears.earthdatacloud.nasa.gov/). This interface allows for the requisition of satellite products such as MYD13Q1 16-Day 250mx250m EVI data (https://www.earthdata.nasa.gov/data/catalog/lpcloud-myd13q1-061) for user-specified coordinates.

The data was grouped by month and filtered for index quality, cloud cover, and the presence of adjacent clouds (Didan, 2021). This revealed that the monsoon months of June (%), July (4%), August (5.3%), and September (17.2%) retained a very small fraction of observations. Compared to the other months (ranging from 45.3% to 98.1% retention), JJAS constituted data loss at a massive scale. June in particular retained data for only 90 out of 286 sites. The median number of valid observations per site for these months across the 20 year period was 7 (out of a possible 40). In addition, previous literature has also indicated deep convective cloud cover and rainfall during these months (Leena et al., 2023), and unreliability of data from these cloudy months in the region has been noted (Shang et al., 2018). Therefore, data from JJAS was excluded from further variability calculations. As a result, 65% of the total observations were retained.

Sites with negative EVI were clipped to zero to represent the absence of vegetation, following White et al., 2020. A baseline monthly mean was calculated for every unit by taking the mean EVI over all dates falling within the given month across the 2004-2024 time period. Variability index v_i was calculated as per Eqn. 2.5. To account for different levels of mean EVI around the year, coefficient of variation (defined as standard deviation divided by the mean) was also calculated. However, the strong correlation between CV and v_i (Pearson's $r = 0.84$, $p \ll 0.05$) indicated that downstream results were unlikely to differ and hence v_i was chosen for further analysis..

v_i ranged from 0.001 to 0.024, with a mean of 0.008 and SD of 0.004 (Supp. Fig. 5.5). It showed no correlation with imbalance (Pearson's $r = -0.06$, $p = 0.48$) or richness (Pearson's $r = -0.11$, $p = 0.19$). Perhaps surprisingly, EVI variability showed a strong positive correlation (Pearson's $r = 0.78$, $p \ll 0.05$) with CWD - implying that sites with higher drought stress were actually less variable in their ecosystem function as measured by EVI data (Fig. 3.4).

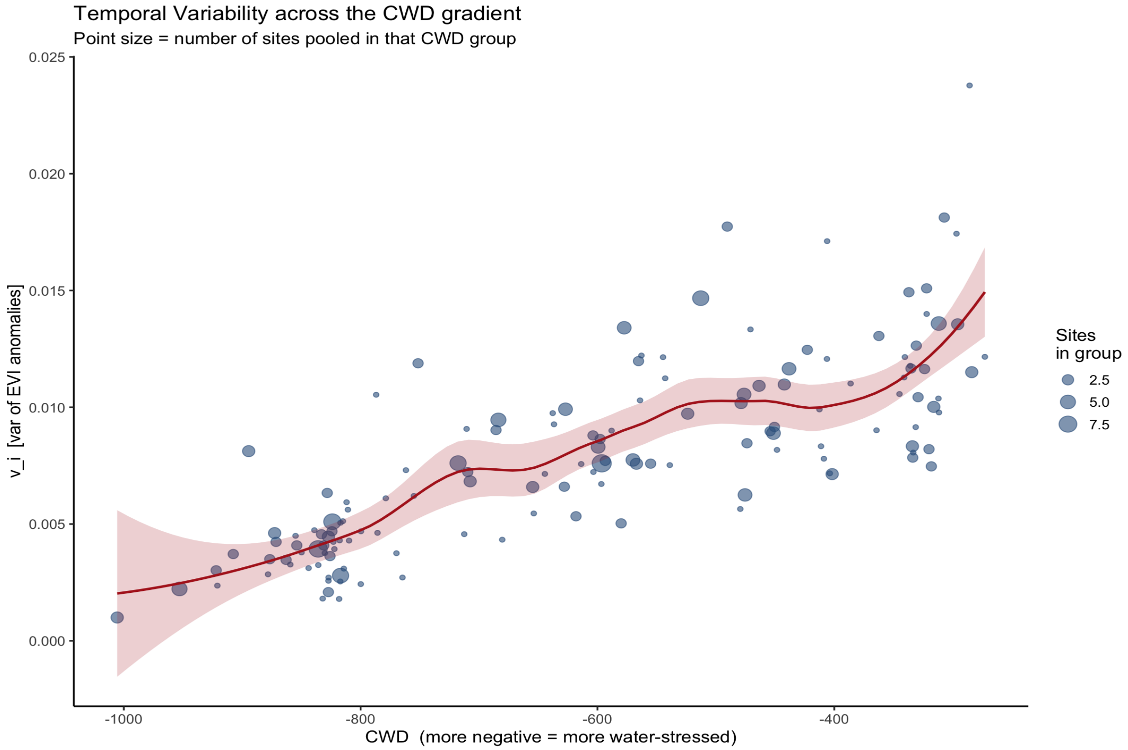

Figure 3.4: EVI variability vs CWD. GAM smoother with 95% CI shown.

A summary of the 4 variables involved - CWD, imbalance, richness, and variability - can be seen in Supp. Fig. 5.6.

3.4 Further results

Given that the study sites lie along a geographical gradient, spatial autocorrelation had to be tested and accounted for. EVI variability was tested using Moran's test with k = 8 nearest neighbours as spatial weights (F. Dormann et al., 2007). Moran's I = 0.69 with a p-value $\ll 0.001$ indicates the presence of spatial autocorrelation. In addition, OLS regression using variability as the response variable with CWD, imbalance, and richness as predictors also showed autocorrelation (Moran's I = 0.15, $p \ll 0.01$).

To account for the hitherto unexplored relationship structure between these variables and spatially correlated nature of data, structural equation modelling was utilised. GLS regression was used for the component models, since these allow for incorporation of different error structures. Particularly, an exponential spatial correlation structure was included with a nugget effect to account for small-scale spatial variability (Christ, 2009; F. Dormann et al., 2007). The full fitted model is given below.

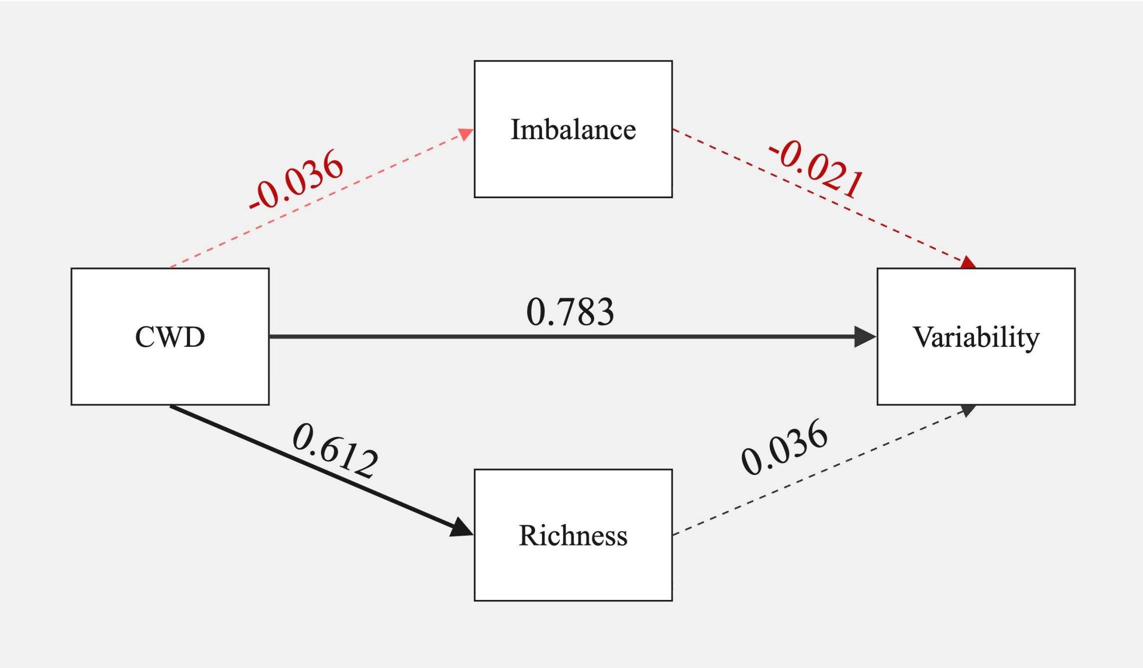

Figure 3.5: Fitted SEM with model coefficients. Solid lines indicate significant relationships. Black arrows represent positive relationships, and red arrows represent negative ones

A Fisher's C statistic of 2.055 with p = 0.358 was obtained. Running a chi-square test on this yields $\chi^2 = 0.861$ and $p = 0.353$, which indicates that the model is well-fit with no missing paths. Shipley's directional separation, or d-sep, test assesses if causally independent paths in the model (namely, the imbalance $\leftrightarrow$ richness path) are significant while controlling for variables on which these paths are conditional (CWD). A p-value of 0.357 indicates that the path between imbalance and richness is insignificant once CWD is accounted for. Model coefficients and p-values can be found in Table 5.1.

Chapter 4

Discussion

4.1 The imbalance-richness-CWD story

This thesis dealt with response diversity, species richness, EVI variability, and climatic water deficit in the Western Ghats. I aimed to quantify a novel diversity metric called Imbalance (Polazzo et al., 2025) acting in accordance with response diversity theory (Elmqvist et al., 2003; Ross et al., 2023). A negative relationship was hypothesised between imbalance and richness, since low imbalance and high richness are both linked with increased stability (Mori et al., 2013; Tilman et al., 2006). In line with this, a significant negative correlation was found (Pearson's r = -0.16, p = 0.048). Sites with a higher number of unique species did indeed have lower imbalance. In addition, though insignificant at the 95% level (p = 0.062), a negative correlation between CWD and imbalance was found (Pearson's r = -0.16). This could potentially indicate that drought stress regulates community assembly in the Western Ghats by acting on response diversity, with more arid sites also having less variation in organismal response.

Species richness showed no significant relationship with CWD. This is contrary to previous studies in the region (Davidar et al., 2005, 2007), but it must be noted that the dataset used for this study contained 183 species. The Western Ghats are known to contain upwards of 650 tree species (Krishnan and Ramesh, 2005). In addition, the biggest plots were 1ha in area, and this may have been insufficient to fully capture diversity trends in the Western Ghats. Despite the aforementioned limitations, the SEM showed a significant CWD → richness path coefficient - implying that an increase in CWD does cause an increase in richness. This result mechanistically links research showing that seasonal drought shapes species distribution (Krishnadas et al., 2021) and that species diversity decreases with seasonality (Davidar et al., 2005).

Further analysis using a structural equation model provided more clarity to the complicated relationships between imbalance, richness, and CWD. After accounting for the influence of CWD on both richness and imbalance (refer Section 3.4), it was found that they are conditionally independent (Lefcheck, 2016). This is in accordance with various quantitative studies indicating that traditional diversity measures such as richness may be decoupled with response diversity (Mori et al., 2013). Overall, the initial hypothesis of response diversity tracking with response diversity did not find support. Although the exact mechanisms linking these have not been elucidated, this may be because the factors that require a community to posses response diversity (for eg. a fluctuating environment, see Ross et al., 2023) for existence are unrelated to those that allow the co-existence of a large number of species (for eg. high/sustained resource levels). Alternatively, it is possible that response diversity and richness are both acted on by CWD/drought stress and therefore taking it into account removes any relationship between the two. Therefore, further research into the conditions necessitating response diversity as well as examination of the effects of drought on it would be highly illuminating.

4.2 Ecosystem stability

Perhaps the most interesting outcome of this thesis came upon the calculation of variability. It was expected that diversity (of the taxonomic and/or response kind) and variability relationship would be a negative one, but that was not found to be the case. Both types of diversity looked to be uncorrelated with EVI variability, and the SEM further confirmed this. The imbalance → variability and richness → variability pathways were found to be insignificant with path coefficients of -0.021 and 0.036 respectively. Since response diversity has been posited to confer stability majorly to systems in fluctuating environments (Ross et al., 2023), it may be possible that the environmental forces in the Western Ghats are relatively stable. In such a scenario, imbalance would not dampen EVI variability in tree communities. With regards to richness, it is possible that even at the lower end of the scale, there are sufficient species to make communities stable - and hence increasing richness does not significantly affect variability.

The major surprise came from the significant positive relationship between CWD and variability - one that has no priors in the literature. Indeed drought has been shown to *increase* variability of in ecosystems (Huang et al., 2016; Yan et al., 2025).

The finding that less drought-stressed sites experience more variability may be due to the fact that dry regions have inherently lower EVI and hence variation by itself does not indicate stability of ecosystem function. However, given that CV and variability were strongly correlated (Pearson's $r = 0.84$, $p \ll 0.05$), it is unlikely that the positive variability-CWD relationship is due to different baseline EVI values. Another possibility is that disturbances in the southern Western Ghats (Athamanakath et al., 2025; Bhat, 2011) have artificially increased variability in EVI by causing fluctuations in tree cover. This could potentially lead to the observed CWD-variability relationship, since CWD increases as one moves towards the south. Finally, it may be the case that aridity in the highly negative CWD regions constrains community composition to a few specialist species well adapted to the region. This may cause low fluctuations in EVI year-to-year and result in the observed pattern.

4.3 Conclusion

In conclusion, my work did not find support for either of the hypotheses constructed at the beginning. No significant relationship was found between the novel diversity metric of imbalance and the traditional metric of species richness. Further, no links were found between either of these and stability in the Western Ghats. However, these negative results have important implications and lay the ground for future work in many ways.

Firstly, given the lack of support for pathways between richness/imbalance and stability, it is of paramount importance to find better proxies of ecosystem stability so as to make management and conservation decisions reliably. As Mori et al., 2013 state, most work in this arena prioritizes species richness, and this may be especially misguided in systems like the Western Ghats. Future research focusing on the development of methods to assess stability in such areas would be fruitful. Work also needs to be done to probe the proposed stabilising effect of response diversity; as my thesis indicates, this is probably highly context-dependent and not yet fully understood.

Secondly, it may be highly useful to accelerate the direct usage of satellite data in the assessment of ecosystem properties. This is especially true in large-scale systems such as the Western Ghats, where logistical constraints are manifold and the need of the hour is rapid action against climate change and anthropogenic disturbances. Work at this scale has produced interesting results before (White et al., 2020), and it will definitely open up another avenue of investigation into natural ecosystems.

Another important finding from this thesis was that of CWD directly affecting variability in EVI. The positive relationship between the two is very contrary to expectations and previous work in the field, and thus research verifying and clarifying the same would be productive. It would add to our understanding of the true impact of climactic forces on trees and forests and aid in the global fight to restore our Earth to a sustainable state.

Chapter 5

Supplementary Figures and Tables

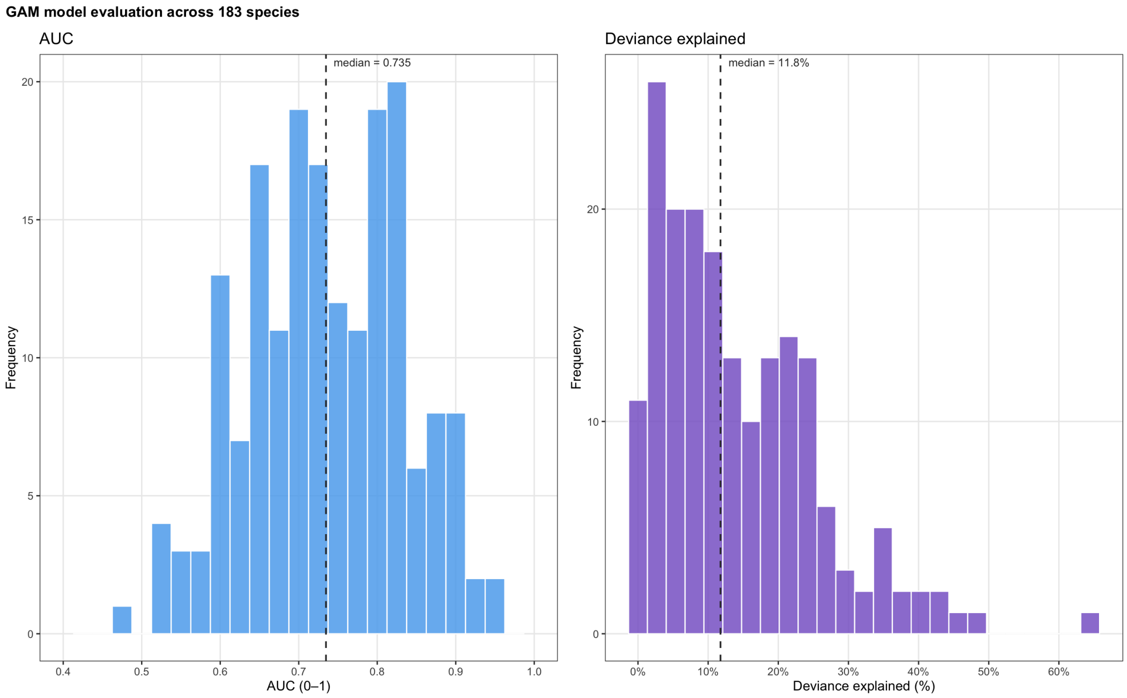

Figure 5.3: GAM evaluation metrics

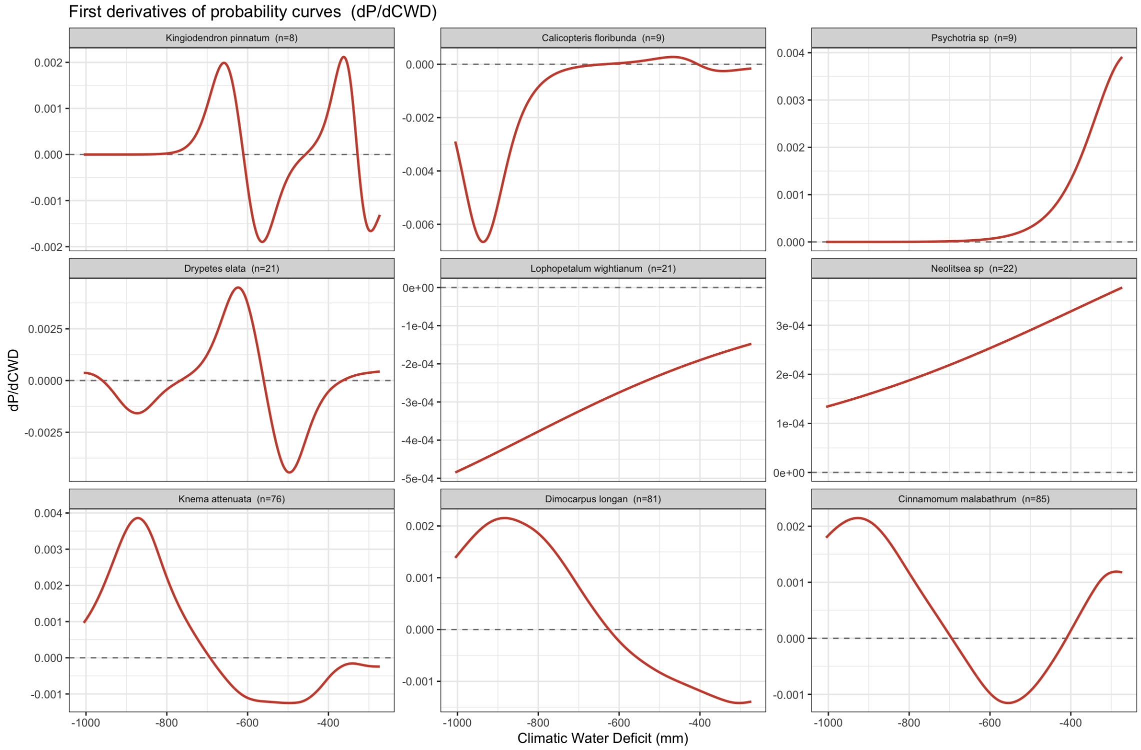

Figure 5.1: Derivatives of the occurrence probability curves across the CWD gradient

Path	Coefficient	p-value
Variability ← Imbalance	-0.0211	0.629
Variability ← Richness	0.0362	0.497
Variability ← CWD	0.7829	$\ll 0.001$
Imbalance ← CWD	-0.0356	0.683
Richness ← CWD	0.6127	0.001

Table 5.1: Model Coefficients from the piecewise SEM

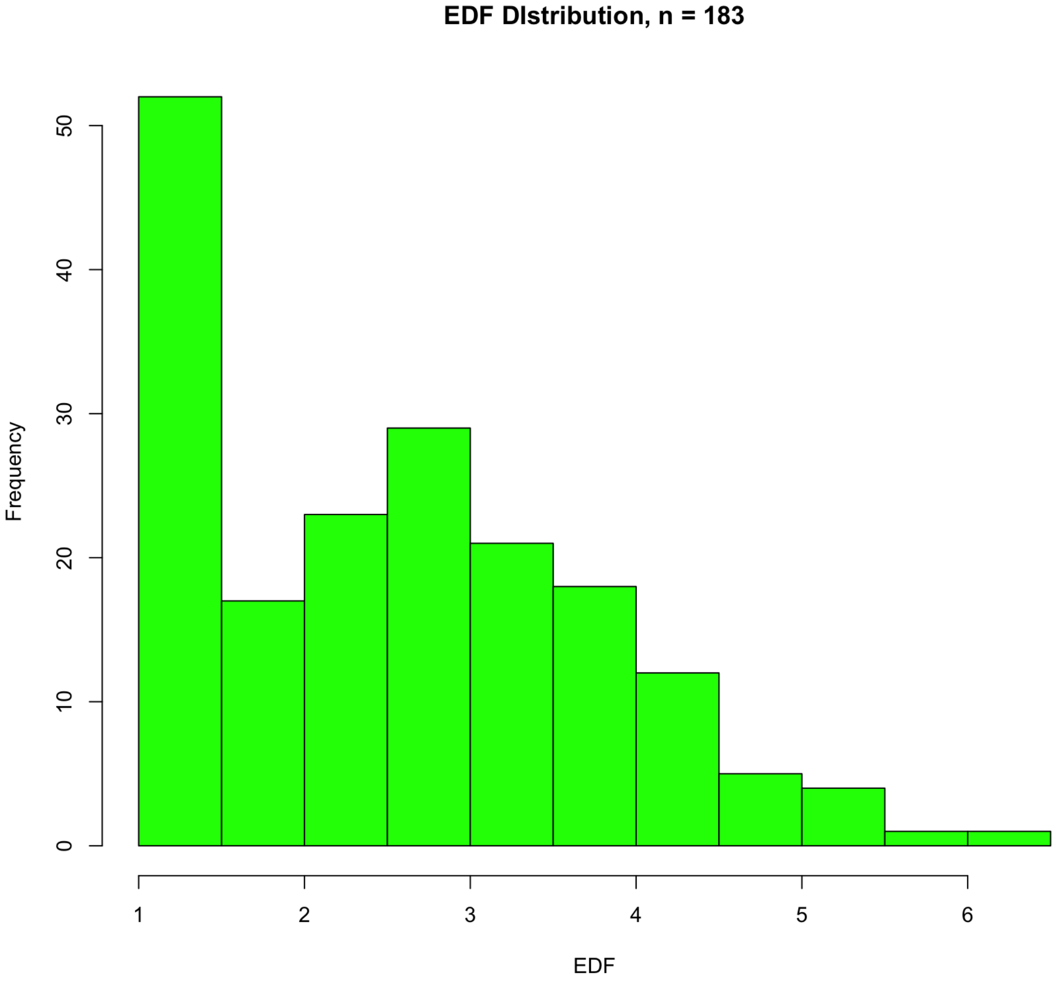

Figure 5.2: EDFs of the 183 GAMs, capturing the range of functional forms exhibited in the occurrence probability vs CWD curves.

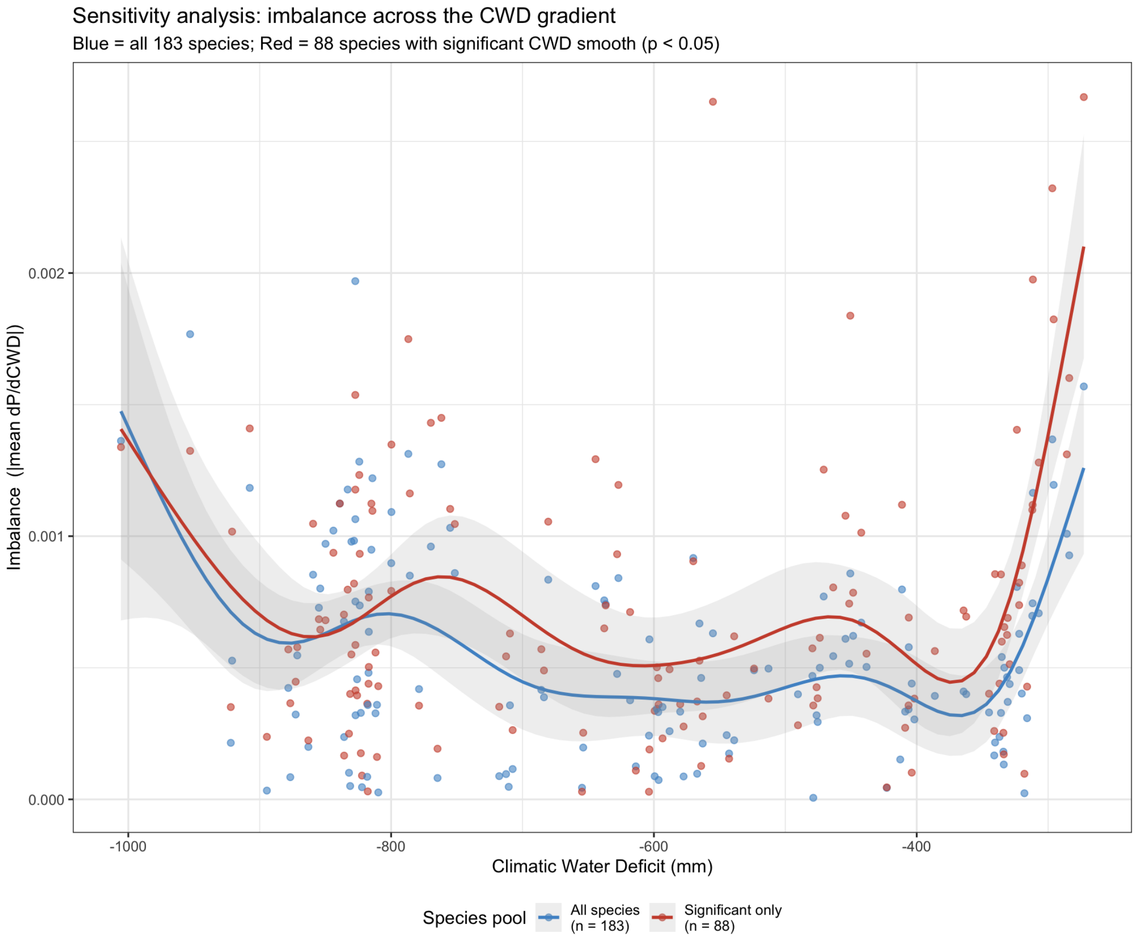

Figure 5.4: Imbalance estimated from the full set of species vs those with significant CWD smooth terms

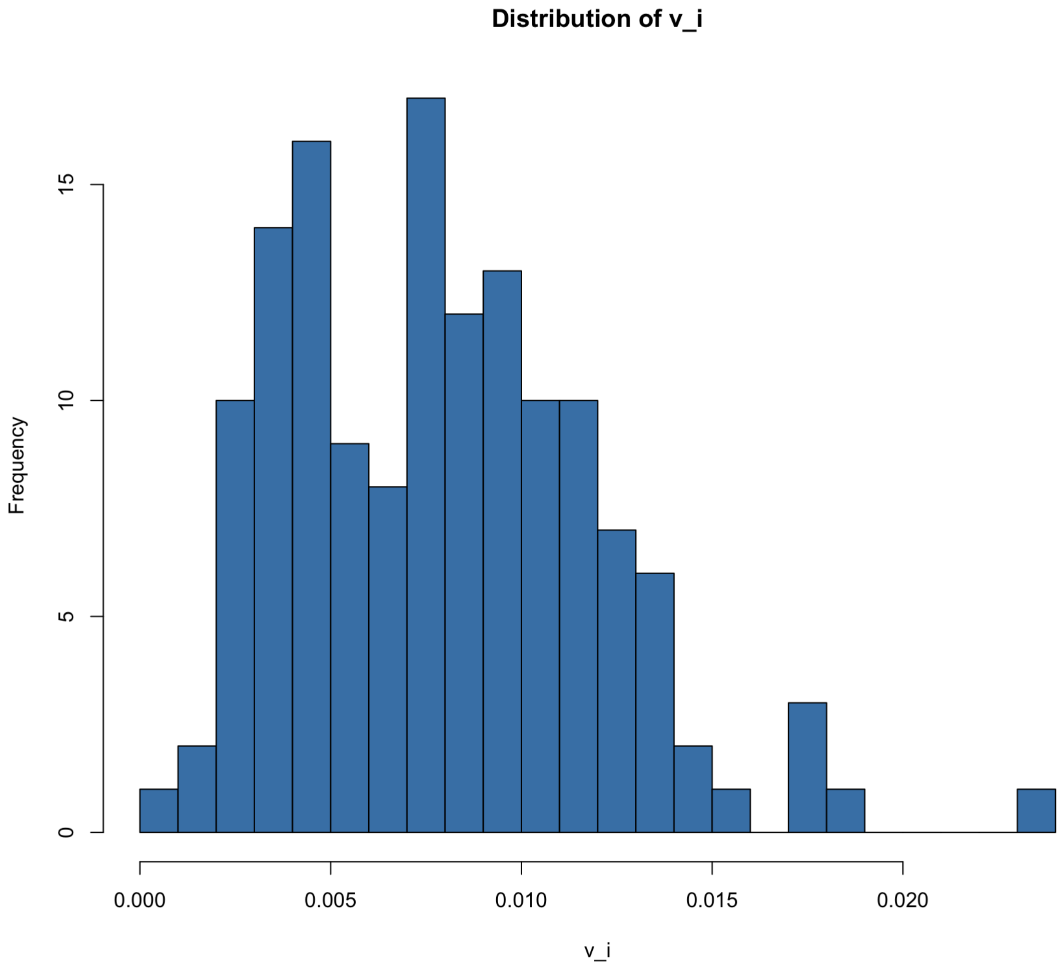

Figure 5.5: Distribution of estimated variability

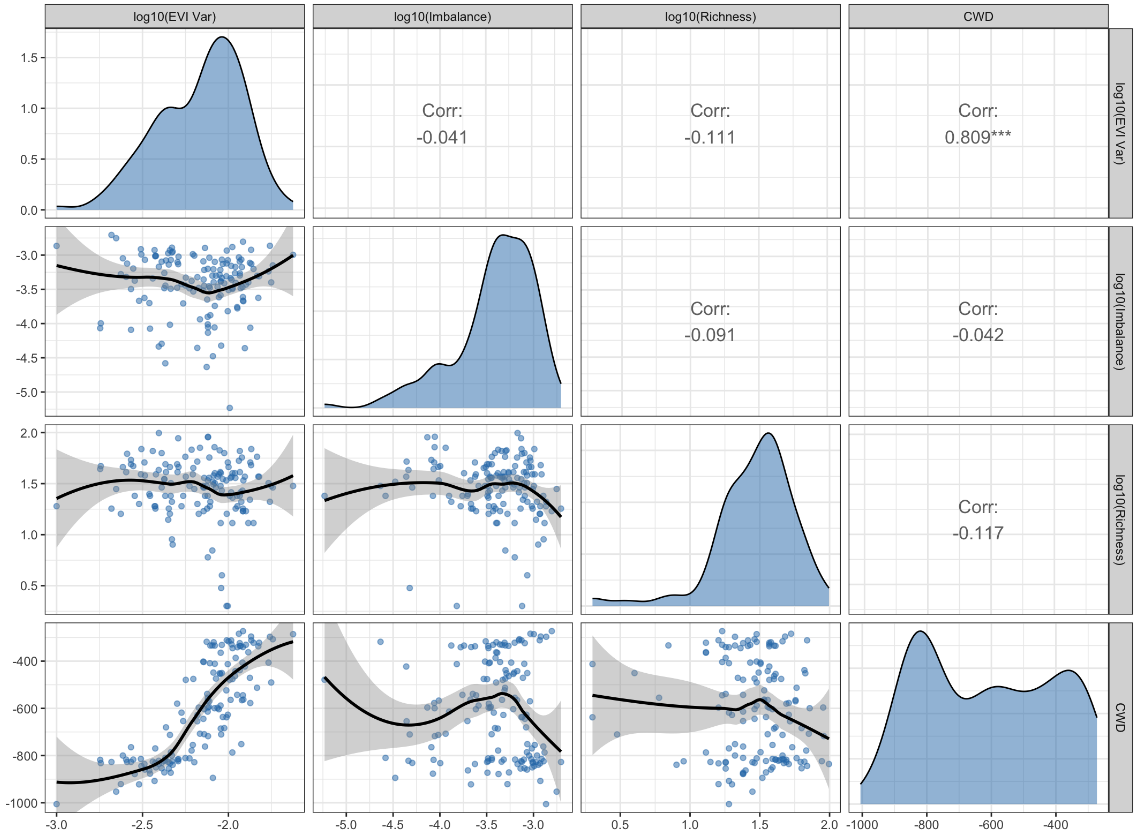

Figure 5.6: The four main variables of interest

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